

The first Neogene record of *Zygodont* (Mammalia, Proboscidea) in Thailand: implications for the mammutid evolution and dispersal in Southeast Asia

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Abstract.—Lower and upper third molars of a proboscidean from the Tha Chang sand pits, Nakhon Ratchasima, northeastern Thailand, show a zygodont pattern. The crescentoids are less well developed than those of the type specimen of *Zygodont gobiensis* but similar to those of late Miocene specimens from south China assigned to *Z. lufengensis* and *Z. chinjiensis*. On the other hand, the loph(id)s are less oblique and the zygodont crests are less well developed than in *Z. lufengensis* and *Z. chinjiensis*. However, it is difficult to erect a new species for these specimens because their anterior loph(id)s are so deeply worn that the morphology of the conelets on these loph(id)s is unclear. Thus, we identify the specimens as *Zygodont* sp. *Zygodont* is known from lower and middle Miocene sediments in Africa while they are usually dated to the early–late Miocene in Europe, South Asia such as Pakistan, and Central and North China. Based on its apparent grade of dental evolution, the new material of *Zygodont* from Thailand is probably late Miocene in age. In addition, this discovery is the first record of a zygodont proboscidean in Southeast Asia.

Introduction

Zygodont proboscideans (Tobien, 1975) have been referred to the family Mammutidae Hay, 1922. Shoshani and Tassy (2005) have reported this family containing two subfamilies, namely *Eozygodontinae* Mckenna and Bell, 1997 (including only *Eozygodon* Tassy and Pickford, 1983, from the lower Miocene bed of Africa) and *Mammutinae* Hay, 1922 (including *Zygodont* Vacek, 1877 from the middle-upper Miocene and its descendant *Mammut* Blumenbach, 1799 from the Plio-Pleistocene). However, the fossils of palaeomastodont-like proboscideans that first expressed mammutid characters (Sanders et al., 2004) were discovered from the late Oligocene at Chilga, Ethiopia as well as Rasmussen and Gutierrez (2009) also reported a new taxon of Mammutidae from the upper Oligocene bed at the Losodok (Lothidok), Kenya and named it *Losodokodon losodokius*. In this case, the Losodok mammutid is more primitive and older than *Eozygodon* so that the subdivision of *Eozygodontinae* and *Mammutinae* need to be revised or expanded. In addition, the late Oligocene palaeomastodont-like fossils from Chilga, which suggest the first expression of mammutid features, and possibly that *Palaeomastodontidae* is not monophyletic but instead is composed of ancestral gomphotheriids (Phiomia) and ancestral mammutids (*Palaeomastodon*) (Sanders et al., 2004). Hence,

the first mammutids occur in the late Oligocene of Africa and then they immigrated into Europe by the end of the early Miocene, and by the middle Miocene had spread throughout Eurasia and into the New World (Tassy, 1986; Mazo, 1996; Sanders, 1996; Tobien, 1996; Sanders et al., 2010).

Zygodont proboscidean fossils have flourished at middle to rather high northern latitudes, in the early Miocene to Pleistocene bed of North America, Europe, northern Africa, and Asia (China and Pakistan). However, there are some reported in low latitude regions such as in the late Oligocene to middle Miocene bed of Kenya, Uganda and Namibia (Pickford, 2007) that are important for the origin of mammutids. In particular, zygodonts have never been reported from Southeast Asia, although zygodont material referred to *Zygodont* is known from Lufeng and Kaiyuan in Yunnan Province, southern China (Chow et al., 1978; Zhang, 1982).

Although zygodonts have not been reported from Thailand, 10 proboscidean genera ranging in age from the middle Miocene to Holocene have been discovered in that country over the past several years. They include *Archaeobelodon* sp., *Prodeinotherium pentapotamiae*, *Gomphotherium* sp., cf. *Protanancus macinnesi*, *Tetralophodon* cf. *xiaolongtanensis*, *Tetralophodon* sp., *Stegolophodon nasaiensis*, *Sl.* cf. *latidens*, *Sl.* cf. *praelatidens*, *Sl.* cf. *stegodontoides*, *Stegodon elephantoides*, *S.* cf. *insignis*, *S.* cf. *insignis*, *S.* cf. *orientalis*, *Anancus* sp.,

Sinomastodon aff. *yangziensis*, and *Elephas* (von Koenigswald, 1959; Buffetaut et al., 1988; Tassy, 1990; Tassy et al., 1992; Saegusa et al., 1999; Nakaya et al., 2002, 2003; Chaimanee et al., 2004; Kunimatsu et al., 2004; Pickford et al., 2004; Suganuma et al., 2006; Thasod, 2007; Duangkrayom et al., 2010; Thasod et al., 2012).

In 2011, new materials representing a zygodont proboscidean were discovered by workers at the sand pit no.10 of Tha Chang sand pits (belonging to Takut Khon Village), Nakhon Ratchasima Province, northeastern part (Fig. 1). The Tha Chang sand pits were given the numbers 1 through 10 by the Thailand–Japan team, with the Takut Khon Village sand pit being number 10. A lower molar was collected by the Northeastern Research Institute of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, and an upper molar was collected by the Sukhothai Airport Natural History Museum. Although the two teeth did not come from the same individual skeleton, their morphology suggests that they

belong to the same zygodont proboscidean species. The specimens described in this paper are the first record of any zygodont proboscidean for Thailand, and indeed for Southeast Asia. They have important implications for understanding zygodont evolution and dispersal patterns.

Materials and methods

Materials for study include the right lower third molar (m3), NRRU-TKK-001 and the left upper third molar (M3), PRY–200 from Tha Chang sand pits (Figs. 2–4). The materials for comparison include AMNH19414, AMNH8137, AMNH26461, AMNH26476, DPC9009, DPC12598, DPC5920, F:AM23339, GIU, IVPP-V2485, IVPP-V5584, IVPP-V5585, IVPP-V4688.1, IVPP-RV77001, IVPP-unnumbered, KNM-LS18244, KNM-ME17, KNM-ME7545, KNM-ME7547, no. 2280/2, PIN2202-4, PIN2202-5, PIN2202-6, RAM908, THP-00079, THP-10022,

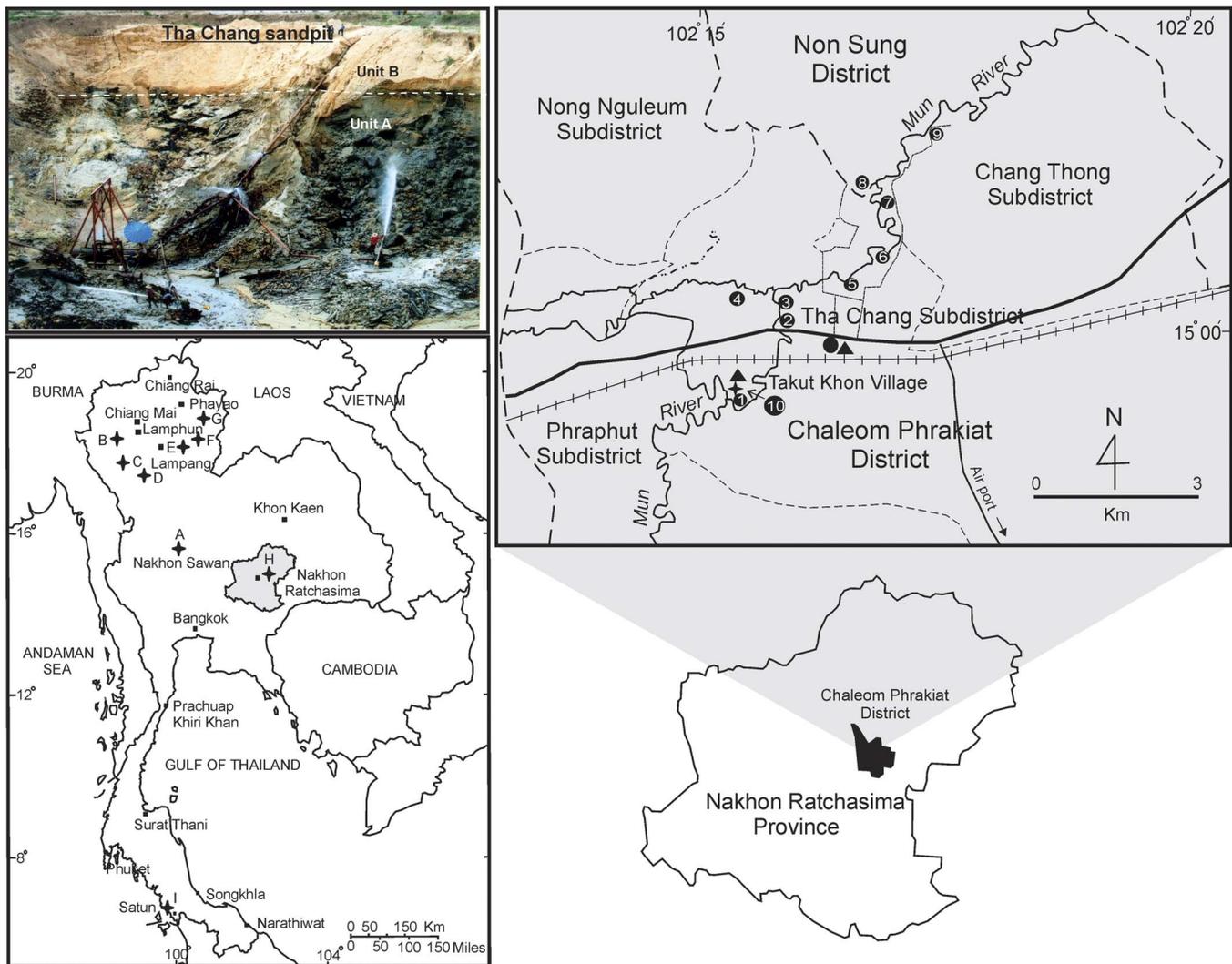


Figure 1. Map of Thailand showing fossil proboscidean localities. Lower left: **A**, Dechatiwongse Bridge, Nakonsawan Province; **B**, Mae Soi locality in Chom Thong District, Chiang Mai Province; **C**, Ban Na Sai coal mine, Lumpun Province; **D**, Mae Teep coal mine, Lumpun Province; **E**, Mae Moh coal mine, Lumpang Province; **F**, Sop Mae Tham locality, Lumpang Province; **G**, Chiang Muan coal mine, Proyao Province; **H**, Tha Chang sand pit, Nakhon Ratchasima Province (shaded); **I**, Wang Kuai cave, Thungwa District, Satun Province. Top left: Photo of the Tha Chang sand pit is marked to indicate the extent of the lower reduced unit (Unit A) and upper oxidized unit (Unit B). Top right: Map of Chaleom Phrakiat District shows the Tha Chang sand pits. The Takut Khon Village sand pit is in number 10.

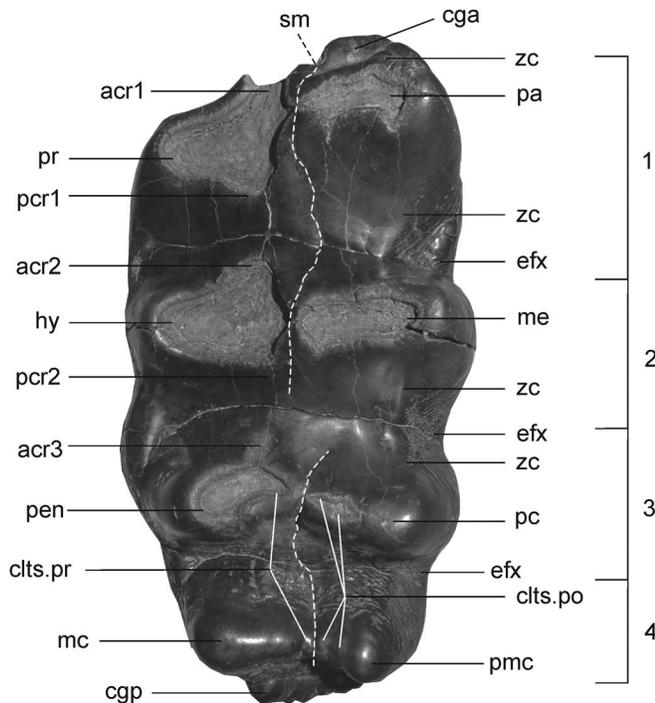


Figure 2. Dental nomenclature: (**acr1, 2, 3**), anterior pretrite crescentoids of the first, second and third loph(id)s; (**cga**), anterior cingulum; (**cgp**), posterior cingulum (talon(id)); (**clts.pr**), pretrite conelets; (**clts.po**), posttrite conelets; (**efx**), ectoflexus; (**hy**), hypocone (pretrite main cone of the second loph(id)); (**mc**), main cone (pretrite main cone of the fourth loph(id)); (**me**), metacone (posttrite main cone of the second loph(id)); (**pa**), paracone (posttrite main cone of the first loph(id)); (**pc**), third posttrite cusp (posttrite main cone of the third loph(id)); (**pcr1, 2**), posterior pretrite crescentoids of the first and second loph(id)s; (**pen**), postentoconule (pretrite main cone of the third loph(id)); (**pmc**), posttrite main cone of the fourth loph(id); (**pr**), protocone (pretrite main cone of the first loph(id)); (**sm**), median sulcus; (**zc**), zygodont crest.

THP-10031, THP-18908, THP-18903, YV031, and YV0132 (Table 1).

Repositories and institutional abbreviations.—AMNH, American Museum of Natural History, New York; DPC, Duke Primate Center, North Carolina; F:AM, Frick Collection, American Museum of Natural History, New York; IVPP-V, Institute of Vertebrate Paleontology and Paleoanthropology, vertebrate collection, Beijing; NRRU-TKK, Northeastern Research Institute of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, Takut Khon Village collection, Nakhon Ratchasima; PIN, Paleontological Institute, Moscow; PRY, Sukhothai Airport Natural History Museum, Sukhothai, Mr. Piriya Vachajitpan collection; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California; THP, Natural History Museum, Tianjin (Museum of Huangho and Paiho).

Systematic paleontology

Dental nomenclature follows Tassy (1996). Description of occlusal features of zygodont cheek tooth M3 follows Tobien (1975) (Fig. 2) and measurements are in millimeters.

Order Proboscidea Illiger, 1811
Family Mammutidae Hay, 1922
Genus *Zygodolophodon* Vacek, 1877

Type species.—*Mastodon turicensis* Schinz, 1824 (for more details including the non-validity of “*Mastodon tapiroides* Desmarests, 1822”, sometimes used by earlier authors, see Tassy, 1985).

Diagnosis.—A mammutid with intermediate and third molars in which the pretrite and posttrite elements are of bunodont character and arranged in clearly yoke-like transverse crests. D4 and all molars are zygodont, having a transverse or slightly oblique loph. In lateral view, the main cusps are wide at the base but taper to an apical point. Transverse valleys have few and small accessory cusps. Worn loph(id)s become sharpened at their summits and show a more zygodont character; zygodont crests show a sharp angle between the lingual and posterior surfaces of the principal lingual cusps in the lower molars, and between the corresponding surfaces of the buccal cusps in the upper molars; the accessory conules are not developed but rather have crescentoids descending into the transverse valley between loph(id)s on the pretrite side at both upper and lower molars; lophs of upper molars are normal to the long axis of the crown; lophids of lower molars are more or less oblique (i.e., postero-external to antero-internal); upper third molar bears three lophs plus a strong talon or four lophs plus a weak cingulum; and lower third molar bears four lophids plus a more or less strong cingulid (Tobien in Shoshani and Tassy, 1996; Mazo and van de Made, 2012).

Zygodolophodon sp.
Figures 3 and 4

Occurrence.—Both specimens were found in sand pit no.10 of Tha Chang sand pits (14°59'50.27"N, 102°14'47.50"E) belonging to Takut Khon Village, Tha Chang Subdistrict, Chaloeam Prakiat District, Nakhon Ratchasima Province (Fig. 1). Howard et al. (2003) and Haines et al. (2004) subdivided the sediments in the sand pits along the Mun River into a lower reduced unit (Unit A) and an upper oxidized unit (Unit B) (Fig. 1). The lower reduced unit is composed of reduced gray sediment in the form of cross-bedded, stratified to massive sand and gravel, with mud lenses. Abundant Neogene faunal and floral fossils were discovered in this unit (Suteethorn et al., 1997; Sato, 2002; Nakaya et al., 2002; Howard et al., 2003). The materials described in this study were found in the lower reducing unit. However, they were discovered by sand pit workers, and their detailed lithological context is unclear because the water jets used during the sand excavation process caused extensive damage to the strata and fossils collapsed.

Description.—**m3**, NRRU-TKK001 (Fig. 3). This right lower third molar is missing the first lophid. There are (×1)3× lophids plus a weak talonid (posterior cingulid). A crescentoid is present and the two half lophids are arranged as yoke-like transverse crests. The second lophid is oblique to the long axis of the crown, and the third lophid is slightly oblique. The lophids become more anteroposteriorly constricted at their apices. The first lophid is broken out. The second lophid is severely worn. The third lophid is also worn, bearing a narrow, transversely elongated wear facet.

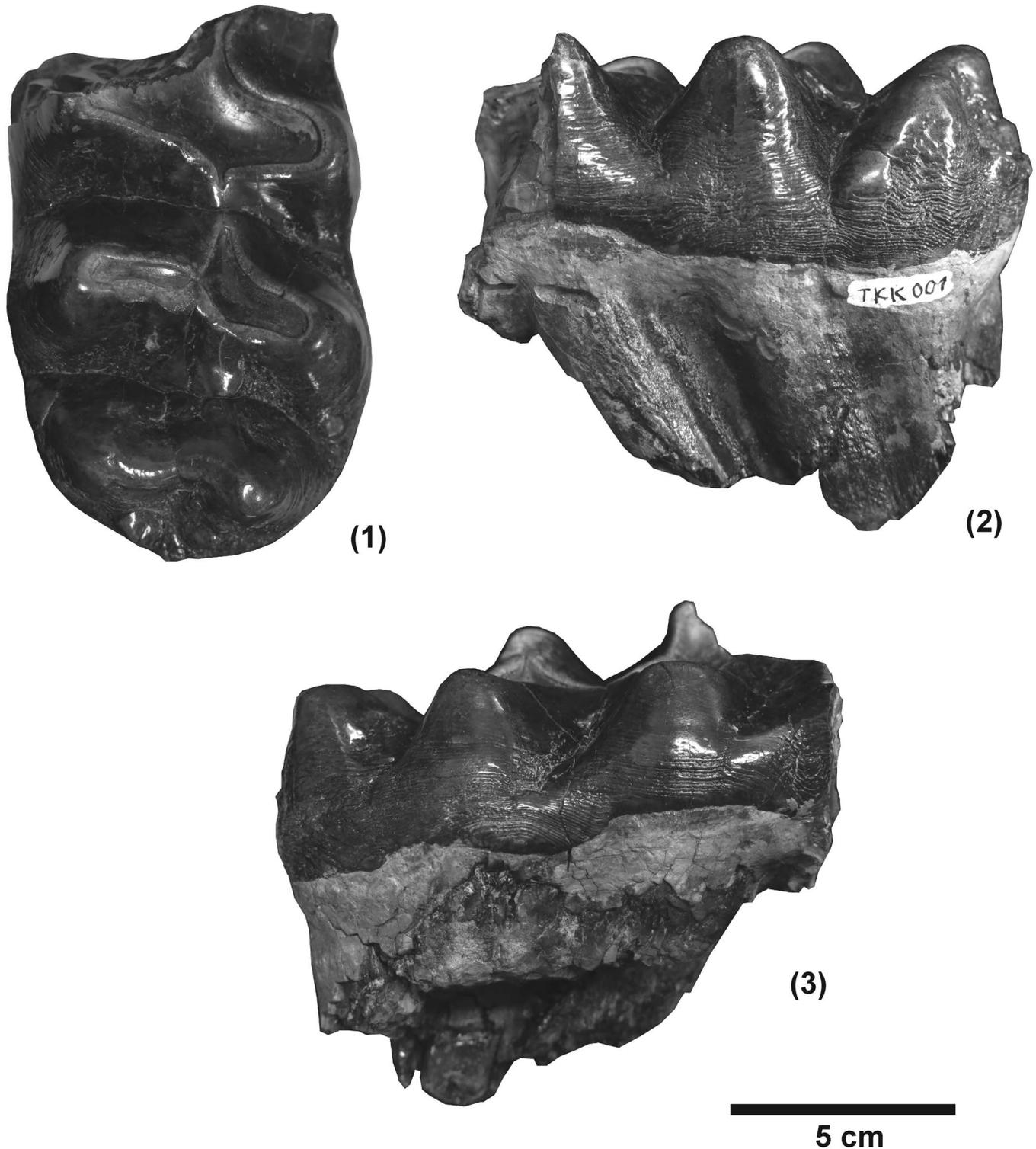


Figure 3. The lower third molar of *Zygodontodon* sp. from Tha Chang sand pit no. 10, NRRU-TKK001: (1) occlusal view, (2) lingual view, (3) buccal view.

There are anterior and posterior crescentoids (acr and pcr) on the pretrite side that show narrow and elongated wear surfaces. The third posttrite half lophid has a main cone and smaller adaxial conelets (clts.po), but conelets are not clearly evident on the pretrite half lophid. The unworn fourth lophid has a main cone and smaller adaxial conelet on the pretrite half lophid while the

posttrite has a large and transversely elongate main cone, however the conelet is furrow-like. Zygodont crests (zc) are present, but not so strong. The cingulids are distinctly reduced. A median sulcus divides the lophids. The talonid (posterior cingulid) is shelf-like and thicker on the pretrite side than on the posttrite side. No cementum is present (Fig. 3).

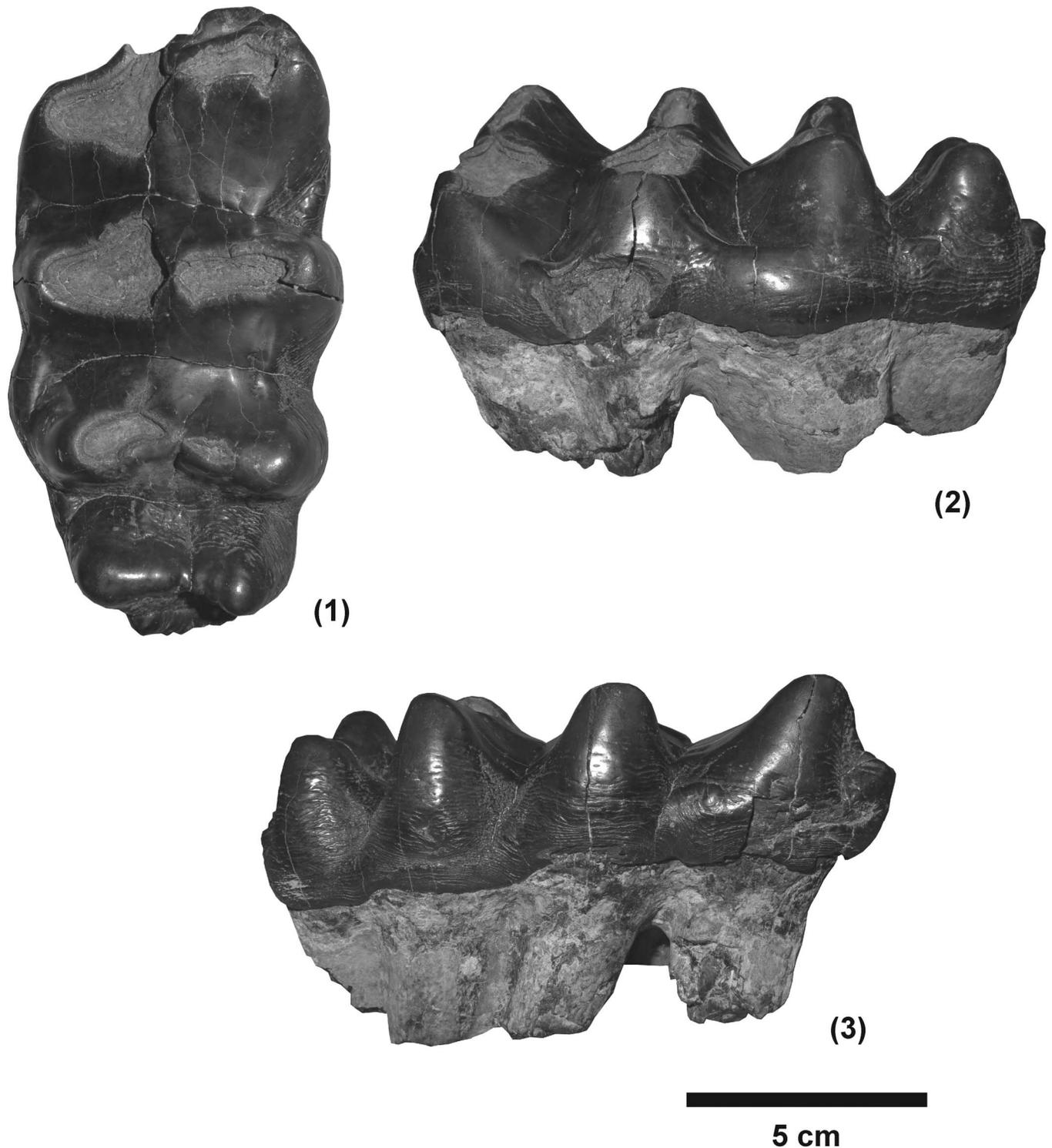


Figure 4. The upper third molar of *Zygodolophodon* sp. from Tha Chang sand pit no. 10, PRY200: (1) occlusal view, (2) lingual view, (3) buccal view.

M3, PRY200. This upper left molar has four lobes, in addition to anterior and posterior cingula. The lingual cingulum is quite strong, and the buccal cingulum is only evident in the vicinity of the first valley. The crowns of the first and second lobes are deeply worn, and the third lobe is also somewhat worn. The crescentoids are present in the pretrite side and arranged in straight lines that run perpendicular to the

anteroposterior axis of the crown, and appear to be yoke-like in this molar. The first and second lobes bear clear zygodont crests. The pretrite and posttrite half lobes are separated by a strong median sulcus. The molar is wider anteriorly than posteriorly. In lateral view, the posterior pretrite crescentoid of the first lobe (pcr1) is well-developed and extends downward to the base of the adjacent valley, where it joins the anterior pretrite

Table 1. Third molars measurement of the zygodont proboscideans (in mm), Rm, Lm = right and left lower molars, RM, LM = right and left upper molars, R = amount of loph(id) (ridge), L = total of molar leangh, W = width of the crown, H = high of the crown, W1 = width of the 1st lophid, Wx = width of the talonid, HI = hypsodonty index, in which the height of individual lophid is expressed as a percentage of the width (H*100/W), WI = width-length index, ratio between the maximum length and the maximum width (width/length/100)), ET = enamel thickness.

No.	Taxon	Specimen	Measurement Referred	R	L	W	H	W1	W2	W3	W4	Wx	HI	WI	ET
NRRU-TKK-001	<i>Zygodolophon</i> sp.	Rm3	owner	(x1)3x	>140*	76.5	42.8+	–	75.2	76.5	69.6	28.1	56+	54.64+	3.2–5.1
PRY-200	<i>Z. sp.</i>	LM3	owner	x4x	152.2	80.8	41.5+	78.7	80.8	79.3	60.4	30	51.36+	53.09	3.8
KNM-LS18244	<i>Losodokodon losodokius</i>	RM3	Rasmussen&Gutierrez, 2009	3x	92.26	53.66	30.7+	51.6	53.6	42.1+	–	–	51.23+	58.16	–
KNM-ME17	<i>Eozygodon morotoensis</i>	LM3	Tassy&Pickford, 1983	3x	110.4	74.4	40.8	71.7	74.4	64.7	–	–	54.84	67.39	–
KNM-ME7545	<i>E.morotoensis</i>	RM3	Tassy&Pickford, 1983	3x	109.3	71.3	40	67.4	71.3	62.6	–	–	56.1	65.23	–
KNM-ME7547	<i>E.morotoensis</i>	Rm3	Tassy&Pickford, 1983	x3x	123.9	67.4	–	61.6	67.4	64.4	–	–	–	54.4	–
DPC9009	<i>Z. aegyptensis</i> (type)	Rm3	Sanders&Miller, 2002	x4x	148.8	55.8	–	–	–	–	–	–	–	37.5	–
DPC12598	<i>Z. aegyptensis</i>	RM3	Sanders&Miller, 2002	x4x	121.1	64.7	43	–	–	–	–	–	66.46	53.43	–
DPC5920	<i>Z. aegyptensis</i>	RM3	Sanders&Miller, 2002	?4?	116	75.6	49	–	–	–	–	–	64.81	65.17	5.8–6.8
	<i>Z. turicensis</i>	Rm3	Tassy, 1977	x4x	157.5	85.5	–	78.5	85.5	85	53	–	–	54.29	–
	<i>Z. turicensis</i>	Lm3	Tassy, 1977	x4x	148	79.5	–	73.5	79.5	79	54	–	–	53.72	–
	<i>Z. turicensis</i>	RM3	Tassy, 1977	x4x	140	84	–	–	84	82	68	–	–	60	–
	<i>Z. turicensis</i>	LM3	Tassy, 1977	x3x	149.5	84	–	84	82.5	82	–	58	–	56.19	–
2280/2	<i>Z. atavus</i> (type)	Rm3	Borissiak, 1936	x4x	163	90	–	–	–	–	–	–	–	55.21	–
2280/2	<i>Z. atavus</i>	Lm3	Borissiak, 1936	x4x	172	95	–	–	–	–	–	–	–	55.23	–
AMNH8137	<i>Z. proavus</i> (type)	RM3	Lofgren&Anand, 2011	4	150.2	95.8	–	87.6	95.8	85.3	60.6	–	–	63.78	–
RAM908	<i>Z. cf. proavus</i>	LM3	Lofgren&Anand, 2011	4 or x3x	127.3	74.4	–	73.8	74.4	66.1	45.8	–	–	58.44	–
RAM908	<i>Z. cf. proavus</i>	RM3	Lofgren&Anand, 2011	4 or x3x	128.2	76	–	76	75.8	67.4	48.3	–	–	59.28	–
F:AM23337	<i>Z. cf. proavus</i>	LM3	Lofgren&Anand, 2011	4	153.5	89.1	–	89.1	84.7	73.3	56.7	–	–	58.05	–
F:AM23337	<i>Z. cf. proavus</i>	RM3	Lofgren&Anand, 2011	4	150.2	92.3	–	92.3	88.8	78.8	61	–	–	61.45	–
PIN2202-4	<i>Zygodolophon gromovae</i>	M3	Tobien et al., 1988	4	182	105	–	–	–	–	–	–	–	57.69	–
PIN2202-5	<i>Z. gromovae</i>	M3	Tobien et al., 1988	4	182	107	–	–	–	–	–	–	–	58.79	–
PIN2202-6	<i>Z. gromovae</i>	RM3	Tobien et al., 1988	4	164	95	–	–	–	–	–	–	–	57.93	–
AMNH-26461	<i>Z. gobiensis</i> (type)	Rm3	owner	x4x	195	87	72	90	–	–	–	–	82.76	44.62	–
AMNH-26476	<i>Z. gobiensis</i>	Rm3	Tobien et al., 1988	4x	160	79	–	–	–	–	–	–	–	49.38	–
IVPP-V5584	<i>Z. gobiensis</i> (<i>Miomastodon tongxinensis</i>)	Rm3	owner	x4x	151.4	74.7	47.5+	67.8	74.7	69.7	51	21	63.6+	49.34	5–7.6
IVPP-V5585	<i>Z. gobiensis</i> (<i>Miomastodon tongxiensis</i>)	RM3	owner	x4	133.5	82.1	50+	81.6	82.1	65.2	41.8	–	60.9+	61.50	5–7.6
IVPP-V4688.1	<i>Z. gobiensis</i> (<i>Z. chinjiensis</i>)	RM3	owner	x4x	177.2	93	63.6	90.8	93	83	70	37	68.4	52.48	–
IVPP-V2487	<i>Z. gobiensis</i> (<i>Z. (Turicius) nemognensis</i>)	RM3	owner	x4x	191.8	91	63.4	87	91+	84.7	75	51.6	69.67	47.45	–
YV0131	<i>Z. gobiensis</i> (<i>Z. lufengensis</i>)	Lm3	Zhang, 1982	x4x	151	74.8	53	65	74.8	73.2	65.5	–	70.86	49.54	–
YV0132	<i>Z. gobiensis</i> (<i>Z. lufengensis</i>)	LM3	Zhang, 1982	x4x	179	93.9	70.3	–	–	–	–	–	74.87	52.46	–
IVPP-no number	<i>Z. gobiensis</i> (<i>Z. jiningensis</i>)	RM3	Chow&Chang, 1974	x4x	135	81.5	41	–	–	–	–	–	50.31	60.37	–
AMNH 19447	<i>Z. chinjiensis</i> (type)	RM3	Osborn, 1929	4x	160	91	52	–	–	–	–	–	57.14	56.88	–
AMNH 19414	<i>Z. metachinjiensis</i> (type)	Rm3	Osborn, 1929	4x	214	85	75	–	–	–	–	–	88.24	39.72	–
GIU	<i>Z. metachinjiensis</i>	LM3	Tassy, 1983	x4	191.3	96	79	92.4	96	94.6	75	–	82.29	50.18	–
IVPP-V2485	<i>Mammut borsoni</i> (<i>Z. shansiensis</i>)	Rm3	owner	x5	190	88.5	56	87	88.5	86	79	51.5	63.28	46.58	–
IVPP-RV77001	<i>Mammut borsoni</i> (? <i>Pliomastodon cf. matthewi</i>)	Rm3	owner	(x1)3x	168*	88.7	58+	–	88.7	85	67.2	36	65.39+	52.80+	5–6.5
THP-00079	<i>M. borsoni</i>	LM3	Tobien et al., 1988	x4x	193	117	54	–	–	–	–	–	46.15	60.62	–
THP-00079	<i>M. borsoni</i>	RM3	Tobien et al., 1988	x4x	197	119	56.8	–	–	–	–	–	47.73	60.41	–
THP-10022	<i>M. borsoni</i>	LM3	Tobien et al., 1988	x4x	170	94	53	–	–	–	–	–	56.38	55.29	–
THP-10031	<i>M. borsoni</i>	LM3	Tobien et al., 1988	x4x	159	92	61	–	–	–	–	–	66.30	57.86	–
THP-18908	<i>M. borsoni</i>	LM3	Tobien et al., 1988	x4x	172	100	64	–	–	–	–	–	64.00	58.14	–
THP-18903	<i>M. borsoni</i>	RM3	Tobien et al., 1988	x4x	174	103	55	–	–	–	–	–	53.40	59.20	–

*Estimate measured.

crecentoid of the second loph (acr2). A similar feature is also present in the valley between the second and the third loph. However, the valley between the third and fourth loph is open. No cementum remains in the valleys.

The pretrite of the first loph is displaced slightly posteriorly relative to the posttrite part. The zygodont crest of the first loph is stronger than those of the other lophs, and continuous with the anterior cingulum. Anterior and posterior pretrite crescentoids (acr1 and pcr1) are present. However, their surfaces are deeply worn. The acr1 is connected to the anterior cingulum.

The second loph is aligned with the transverse axis of the crown, and is deeply worn. An anterior pretrite crescentoid (acr2) is present, and extends downward to the base of the adjacent valley, whereas the posterior pretrite crescentoid (pcr2) is not prominent. The pretrite of the third loph is slightly posteriorly, while the posttrite is straight. The wear surface of the third loph is moderately worn. The posttrite half loph has a rather large main cone and small adaxial conelets (clts.po), which appear furrow-like. However, the morphology of the conelets is not clear in the pretrite half loph because of surface wear. The anterior pretrite crescentoid (acr3) is slightly worn and narrow in shape. The posterior pretrite crescentoid (pcr3) is very weak in this loph. The unworn fourth loph shows two small adaxial conelets (clts.po) on the posttrite side, which appear furrow-like. The main cone is quite large. The pretrite half loph has a large and transversely elongate main cone, and a small conelet near the median sulcus. The anterior crescentoid (acr4) is clearly and extends down to the base of the nearby valley. The talon (posterior cingulum) is shelf-like, and better developed on the pretrite side than on the posttrite side (Fig. 4).

Materials.—The right lower third molar (m3) is stored at the Northeastern Research Institute of Petrified Wood and Mineral Resources, Nakhon Ratchasima Rajabhat University, as NRRU-TKK-001. The left upper third molar (M3) is stored at the Sukhothai Airport Natural History Museum, as PRY-200 (Figs. 2–4).

Remarks.—The lophids of the specimen NRRU-TKK-001 (right m3) are more oblique than the loph of PRY-200 (left M3). This is a generally different pattern between the lower and upper molar, especially in the zygodont proboscideans. The enamel wear surfaces are narrow, transversely elongated and yoke-like (Tobien, 1973b). Both of specimens from Tha Chang have clear zygodont crests. The conelets on the posttrite side (clts.po.) are better developed than those on the pretrite side (clts.pr.). The conelets and half loph(id)s are somewhat less regularly arranged than in the bunodont molars of proboscideans such as *Gomphotherium*. In addition, the mesoconelets of *Gomphotherium* are blunter and more morphologically distinct from the zygodont proboscideans (Tobien, 1973b). The pretrite central conules of bunodonts are arranged in a conule-like pattern, rather than a yoke-like pattern as in the specimens from Tha Chang. These characters above indicate that the Tha Chang specimens are the zygodont proboscideans.

Compared with the oldest zygodont proboscidean, *Losodokodon losodokius*, from the late Oligocene of Losodok (Lothidok), Kenya (Rasmussen and Gutierrez, 2009), and the early to middle Miocene species, *Eozygodon morotoensis*, from

Moroto, Uganda (Pickford and Tassy, 1980; Tassy and Pickford, 1983; Pickford, 2007) that they have three loph(id)s in the third upper and lower molars. The fourth loph(id)s in m3/M3 are absent or poor developed. On the contrary, the Tha Chang specimens have four loph(id)s with the posterior cingula and larger in molar size (Tables 1–3; Fig. 5).

The zygodont crests of the Tha Chang specimens are not strongly developed, in contrast to the condition in *Mammut*. In addition, the lateral cingula of the Tha Chang specimens are less well developed than in *Mammut*, whereas the crescentoids of the Tha Chang specimen are more distinct than in *Mammut*. According to the differentiation between the Tha Chang specimens and the oldest and youngest zygodont proboscideans, *Losodokodon losodokius*, *Eozygodon morotoensis*, and *Mammut*, the dental features such as molar size and well-developed anterior and posterior ridges of Tha Chang specimens indicate that it belongs to *Zygodont*.

Comparison between the Tha Chang specimens and the Egyptian early Miocene zygodont *Zygodont aegyptensis* (see Sander and Miller, 2002, p. 398, fig. 9) reveals that the third and fourth lophids of m3 are strongly convex anteriorly in the Egyptian species but quite straight in the Tha Chang specimen. In lateral view, the lophids of *Z. aegyptensis* are more widely separated than those of the Tha Chang specimens. However, the anterior and posterior pretrite crescentoids of the m3 of *Z. aegyptensis* are clearly in contact with each other according to wear, which is also the case in the Tha Chang specimen. The complete M3 of *Z. aegyptensis* possesses three loph or variably a fourth loph, a thin anterior cingulum composed of numerous tiny tubercles, and a moderate-sized heel; whereas the Tha Chang M3 possesses four lophs and a tiny posterior cingulum. In addition, the lower m3 from Tha Chang is wider but shorter than that of the Egyptian species, whereas the upper M3 from Tha Chang is both wider and longer than its Egyptian counterpart (Tables 1–3; Fig. 5.1, 5.2).

The M3 of *Zygodont cf. proavus*, RAM 908 (see Lofgren and Anand, 2011, p. 1393, fig. 4) from the middle Miocene of the Mud Hills, Mojave Desert, California, North America resembles the Tha Chang M3 in several respects. In *Z. cf. proavus* central conules are not present; however, the wear facet on the protocone extends onto thickened enamel that is present on both anterior and posterior slopes. The posterior and anterior extensions of this wear facet give a false impression that the central conules are only weakly developed. These characters are reminiscent of the Tha Chang M3, but in other important respects this tooth differs from its equivalent in *Z. cf. proavus*. The fourth loph is much less well developed in *Z. cf. proavus* than in the Tha Chang M3. In *Z. cf. proavus*, the first three lophs reduce their transverse dimension anteroposteriorly, unlike in the Tha Chang M3, and an ectoflexus is present on all three interlophs in *Z. cf. proavus* but only on the first interloph of the Tha Chang M3. Moreover, the labial cingulum is better-developed in *Z. cf. proavus* than in the Tha Chang M3. However, the upper molars of *Z. cf. proavus* described by Lofgren and Anand (2011) are smaller than other specimens of the *Z. proavus*. The Tha Chang M3 is longer and wider than RAM908, but narrower than other specimens of *Z. proavus* (Tables 1, 3; Fig. 5.2).

Table 2. The lower third molars (m3) morphology of the Old Word zygodont proboscideans.

Taxa	Dental morphology							
	Dental morphotypes	Pretrite adaxial conelets	Zygodont crests	Crescentoids	Obliquity of lophids (degree)	Cingulids	Forth lophid	Molar sizes and shapes
<i>Eozygodon morotoensis</i>	Gracile	Small or absent	Visible	Visible	High	Well developed in upper molar	Undeveloped	Small
<i>Zygodon aegyptensis</i>	Robust	Rather strong	Visible	Strong and rather blunt	High in two anterior lophids	Well developed	Developed	Small, long and narrow
<i>Z. turicensis</i>	Gracile	Strong	Strong	Strong	Moderate to high	Well developed	Developed	Medium
<i>Z. atavus</i>	?	?	?	?	?	?	?	Large, wide
<i>Z. gobiensis</i>	Robust	Small or absent	Visible	Strong and rather blunt	Low	Reduced	Less Developed	Medium to large
<i>Z. gobiensis (Miomastodon tongxinensis)</i>	Robust	Small	Visible	Visible	Moderate	Reduced	Developed	Medium
<i>Z. gobiensis (Z. lufengensis)</i>	Mixed	Small	Visible	Strong	Rather high	Well developed	Well developed	Large
<i>Z. metachinjiensis</i>	Mixed?	Small	?	?	?	Well developed	Well developed	Large and long
<i>Mammuth borsoni (Z. shansiensis)</i>	Gracile	Rather small	Visible	Visible	Rather high	Reduced	Well developed	Large to very large
<i>M. borsoni</i>	Gracile	Strong	Strong	Visible	High	Well developed	Well developed	Large to very large
Tha Chang specimens	Mixed?	Small	Visible	Visible	Moderate	Reduced	Well developed	Medium

Table 3. The upper third molars (M3) morphology of the Old Word zygodont proboscideans.

Taxa	Dental morphology						
	Dental morphotypes	Pretrite adaxial conelets	Zygodont crests	Crescentoids	Cingula	Forth loph	Molar sizes and shapes
<i>Losodokodon losodokius</i>	Gracile	Small or absent	Visible	Only anterior of first loph	Well developed	Undeveloped	Very small, narrow
<i>Eozygodon morotoensis</i>	Gracile	Small or absent	Visible	Visible	Well developed in upper molar	Undeveloped	Small
<i>Zygodon aegyptensis</i>	Robust	Rather strong	Visible	Strong and rather blunt	Well developed	Developed	Small, long and narrow
<i>Z. turicensis</i>	Gracile	Strong	Strong	Strong	Well developed	Developed	Medium
<i>Z. proavus</i>	Robust	Strong	Visible	Visible	Well developed	Developed	Small to medium
<i>Z. gromovae</i>	Gracile?	Small	Absent?	?	?	Less Developed	Large
<i>Z. gobiensis (Miomastodon tongxinensis)</i>	Robust	Small	Visible	Visible	Reduced	Developed	Medium
<i>Z. gobiensis (Z. Turicius nemongnensis)</i>	Gracile	Strong	Strong in anterior lophids	Visible	Well developed	Well developed	Large and long
<i>Z. gobiensis (Z. lufengensis)</i>	Mixed	Small	Visible	Strong	Well developed	Well developed	Large
<i>Z. gobiensis (Z. jiningensis)</i>	Robust	–	Strong	Strong	Well developed	Developed	Medium
<i>Z. chinjiensis</i>	Robust	Small	Strong	Strong	Well developed	Well developed	Large
<i>Z. metachinjiensis</i>	Mixed	Rather small	Visible	Strong	Well developed	Well developed	Large and long
<i>Mammuth borsoni</i>	?	Strong	Visible	Visible	Reduced	Well developed	Large to very large
(?Pliomastodon cf. matthewi)							
<i>M. borsoni</i>	Gracile	Strong	Strong	Visible	Well developed	Well developed	Large to very large
Tha Chang specimens	Mixed?	Small	Visible	Visible	Reduced	Well developed	Medium

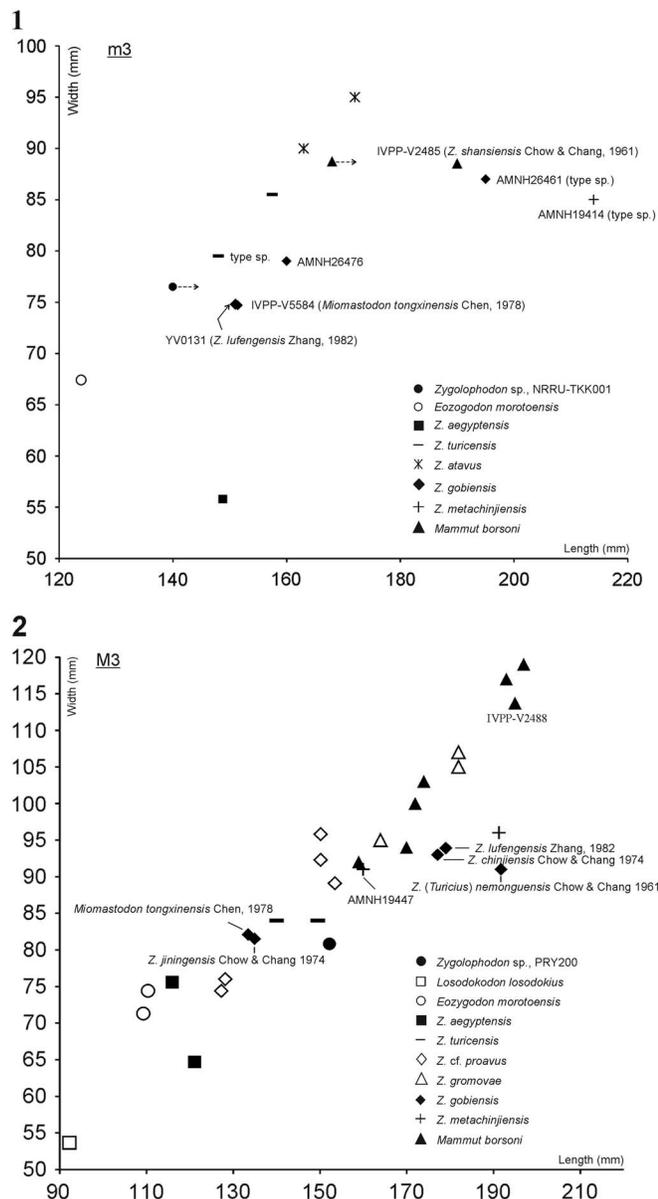


Figure 5. Scatterplot of third molar proportions for various zygodont proboscideans, including *Zygodont* sp. from Tha Chang sand pit no. 10: (1) lower molar, (2) upper molar.

The furrow-like posttrite conelets of the fourth loph(id)s of both Tha Chang specimens resemble the equivalent structures in the middle Miocene European zygodont *Zygodont turicensis* Schinz, 1824. The Tha Chang specimens are only slightly narrower than the equivalent molars of *Z. turicensis* but slightly longer in upper molar and slightly shorter in lower molar (in the lower molar case, the length is probably a bit longer than it estimated) (Table 1; Fig. 5.1, 5.2). However, the zygodont crests and cingula of the Tha Chang specimens are reduced, whereas very strong cingula are present in *Z. turicensis*. In addition, a well-developed lingual cingulum is also present in the upper third molar of *Z. turicensis* from the middle Miocene of Jebel Cherichera, Tunisia (Tassy, 1985, pp. 509–510, fig. 213; Pickford, 2007, p. 30, fig. 2A) and the upper second molars from the Grildain, Ngorora Formation, Member A, Tugen Hills, Kenya

(Pickford, 2007, p. 31, fig. 3). Moreover, the crescentoids of Tha Chang specimens are blunter than those of *Z. turicensis* (see Tobien, 1975, p. 196, fig. 1; Tassy, 1977, fig. 3, p. 659; Tables 2, 3).

A closer inspection of the molars of the zygodont proboscidean “*Mastodon*” *atavus* Borissiak, 1936, from the lower Miocene Djilancik beds of Kazakhstan, will be needed in order to determine whether this specimen is assignable to *Z. gobiensis*, *Z. turicensis*, or neither. However, the symphysis is longer, and the incisors more strongly developed, than in *Z. gobiensis* (Tassy, 1985, fig. 201). These differences seem consistent with the somewhat earlier age (Shanwangian/Orleanian) of the Djilancik site. The shortening of the symphysis and incisors seen in *Z. gobiensis* represents an evolutionary step towards *Mammot*, in which the symphysis and incisors are reduced (Tobien et al., 1988). The m3 of *Z. atavus* is larger and much wider than the Tha Chang m3 (Tables 1, 2; Fig. 5.1).

Previously described Chinese zygodonts show varying degrees of similarity to the Tha Chang specimens. The type specimen of *Zygodont gobiensis* Osborn and Granger, 1932 (AMNH 26461) is a hemimandible with a complete m2 and m3 from the Tunggur locality, Nei Mongol. The m3 of this specimen resembles the Tha Chang m3 NRRU-TKK001 in having small conelets on both pretrite and posttrite sides, a thick talonid on the pretrite, lophids with a low degree of obliquity, weakly developed zygodont crests, a reduced lateral cingulum, and valleys that lack cementum. The m3 of the type specimen of *Z. gobiensis* is larger than the Tha Chang specimen; however, the specimen AMNH 26467 is nearly equal in size to Tha Chang m3. In addition, molar has a narrower crown and the main cone and conelets of the fourth lophid are blunter in *Z. gobiensis* (Tables 1, 2; Fig. 5.1).

Zygodont gromovae Dubrovo, 1970 is represented by an upper M2 and M3 (PIN. no. 2002-5, 2002-6 respectively), from the middle Miocene in age of the Tunggur locality, Nei Mongol. In these specimens, small pretrite conelets are present. Upper M3 has three conelets on the posttrite side. The fourth loph is crest-like rather than conule-like (Tobien et al., 1988). In these characters, the M3 of *Z. gromovae* resembles the Tha Chang M3, PRY200. However, the Tha Chang M3 is smaller than the M3 of *Z. gromovae* and has a better-developed fourth loph (Tobien et al., 1988) (Tables 1, 3; Fig. 5.2). However, the type specimen of *Z. gromovae* is so badly damaged that its M3 is difficult to compare to the Tha Chang M3 in other respects.

The only representative of *Zygodont nemonguensis* Chow and Chang, 1961, an M3 (IVPP-V2487) from Nei Mongol, has four lophs. The fourth loph is as well developed as that of the Tha Chang M3, PRY200. However, the fourth loph is equal in width to the third loph in IVPP-V2487, but clearly narrower than the third loph in PRY200. The talon of IVPP-V2487 is stronger than that of the Tha Chang M3. Nevertheless, the zygodont crest of the first and second posttrite half lophs, the lingual beaded antero-external cingula, and the crescentoids are more prominent in IVPP-V2487 than in PRY200. The pretrite main cone of the fourth loph of PRY200 is larger and more transversely elongate than in IVPP-V2487, and the posttrite half lophs are divided into more conelets. Furthermore, PRY200 is smaller than IVPP-V2487 (Tables 1, 3; Fig. 5.2).

The *Zygodont jiningensis* Chow and Chang, 1974 is an unnumbered M3 from Jining, Nei Mongol. This tooth is unworn,

but the summits of the three most anterior lophs are so badly broken that cusps cannot be distinguished. This specimen has four lophs and a nodular talon. The posttrites are bicuspid, with small adaxial conelets. In these features, the Jining specimen resembles the Tha Chang M3, PRY200. In particular, the bicuspid nature of the posttrite and the presence of small adaxial conelets can be clearly recognized in the fourth loph of PRY200. However, the fourth loph of PRY200 is better developed than that of the Jining specimen. In addition, the pretrite of the fourth loph of the Jining specimen has two subequal larger mammillae separated by two smaller squeezed ones (see Tobien et al., 1988, p. 151, fig. 42), while the main cone of the Tha Chang specimen is large and transversely elongate with small one adaxial conelets presented (Figs. 2, 4.1). The zygodont crests of the Jining specimen are better developed than in the Tha Chang M3, and the molar is shorter (Tables 1, 3; Fig. 5.2).

Miomastodon tongxinensis Chen, 1978 is represented by an m3 (IVPP-V5584) and an M3 (IVPP-V5585), from Gujiazhuangzi, Tongxin, Ningxia. The anterior loph of the upper third molar is strongly worn. The third loph has a small adaxial conelet and a strong anterior conule, but no posterior conule is present. The first and third posttrite half lophs have oblique, oppositely oriented long axes, while the second one is normal to the tooth midline. An antero-external cingulum is present. The pretrite side of the fourth loph has an abaxial main cone and a smaller adaxial conelet. In the above characters, the Tongxin M3 resembles the Tha Chang M3, PRY200. However, the Tongxin M3 differs from the Tha Chang M3 in that the posttrite half lophs are bicuspid, zygodont crests are present only in the first and second lophs, and the fourth loph is the narrowest one. The lower third molar is similar to the Tha Chang m3 NRRU-TKK001 in that the third and fourth lophids bear small adaxial conelets, and the upper and lower molars from Tongxin are similar in size to their counterparts from Tha Chang (Tables 1–3; Fig. 5.1, 5.2). Nevertheless, the pretrite and posttrite of the fourth loph(id)s are bicuspid in both Tongxin molars, whereas the posttrite fourth loph is tricuspid in the Tha Chang specimens.

Zygodontodon chinjiensis was named by Osborn (1929) as *Serridentinus chinjiensis*. The type specimen (AMNH 19447), a right upper third molar (Osborn, 1929, p. 4, fig. 5), bears four ridges and a posterior cingulum. The anterior lophs are each divided into many conelets. We cannot determine whether this character is present in the Tha Chang M3 because of deep wear. However, the fourth loph has a tricuspid posttrite side, and a bicuspid pretrite side. The adaxial conelets are smaller than the main cone, as in the Tha Chang M3. The zygodont crests, crescentoids and lateral cingula of *Z. chinjiensis* are much stronger than those of the Tha Chang M3. The type specimen of *Z. chinjiensis* is much wider and a bit longer than the Tha Chang M3 (Table 1; Fig. 5.2).

Z. chinjiensis from China was described by Chow and Chang (1978), based on two specimens of M3 (IVPP-V4688.1 and IVPP-V4688.2) from the upper Miocene of Xiaolongtan coal mine, Kaiyuan, Yunnan. These Chinese specimens each bear four lophs with posteriorcingulum and have two conelets on the pretrite side. The third and fourth posttrites are similar to the Tha Chang M3 in being tricuspid, but the main cone of the fourth loph pretrite is less transversely elongated than in the Tha Chang M3. The crescentoids are stronger and the size is larger than in the Tha Chang M3 (Tables 1, 3; Fig. 5.2).

Zygodontodon lufengensis from the upper Miocene (Biasatti et al., 2012) of Shihuiba, Lufeng, Yunnan, was described by Zhang (1982). The holotype, left lower m3 (Zhang, 1982, pl. 1, fig. 1), bears four lophids with small a posterior cingulum, and the antero-external and pretrite cingula are quite strong. Zygodont crests are visible on the first and second lophids. The conelets on both the pretrite and posttrite half lophids are small. Hence, this specimen can be referred to *Zygodontodon gobiensis*, (i.e., Tobien et al., 1988) and is similar to the Tha Chang specimens. In addition, the Lufeng m3 is similar in molar size to *Miomastodon tongxinensis* and the Tha Chang specimen, but the M3 of Lufeng specimen is larger than both Tongxin and Tha Chang specimens. The m3 of *Z. lufengensis* shows an advanced character state not seen in *M. tongxinensis* and *Z. gobiensis*, in that the transverse lophids are rather oblique; however, it is also present in the Tha Chang m3 (Tables 1–3; Fig. 5.1, 5.2).

However, Tobien et al. (1988) synonymized many Chinese zygodont proboscideans with *Zygodontodon gobiensis*, including *Zygodontodon gromovae* Dubrovo, 1974, *Z. (Turicius) nemonguensis* Chow and Chang, 1961, *Z. nemonguensis* Yan, 1979 (M3, IVPP2487), *Z. jiningensis* Chow and Chang, 1974 (M3, IVPP-5156), *Z. chinjiensis* Chow and Chang, 1978, *Miomastodon tongxiensis* Chen, 1978, fragments of M1, IVPP-4685.7 and 4685.8, of *Gomphotherium xiaolongtanensis* Chow and Chang, 1978, from the upper Miocene of Xiaolongtan coal mine, Kaiyuan, Yunnan.

In addition, Tobien et al. (1988) transferred some species of *Zygodontodon* to *Mammuth borsoni*, including an upper D4 (IVPP-V4685) of *Zygodontodon* sp. from the lower or middle Pliocene of Anle, Huoxian, Shanxi; M3 and m3 (IVPP-VM867 and IVPP-V2485) of *Z. shansiensis* Chow and Chang, 1961 and M3 (IVPP-V2488) of *Zygodontodon* sp. (Chow and Chang, 1961) from the upper Pliocene or lower Pleistocene of the Yushe Basin, Shanxi; M2 (IVPP-V4689) of *Zygodontodon* sp. (Chow et al., 1978) from the Pliocene of Zhaotong, Yunnan. All of the above taxa and specimens are larger in terms of molar size than the Tha Chang specimens, as well as having stronger zygodont crests and lophids that are more obliquely aligned to the long axes of the teeth (Tables 1–3; Fig. 5.1, 5.2).

Zygodontodon metachinjiensis Osborn, 1929 is represented by a right hemimandible with m2 and m3 (AMNH 19414) from the middle Miocene of lower Chinji Formation, Chinji, Pakistan. The m3 has four lophids, and a low posterior cingulum consisting of many accessories this cingulum. Molar is subhypsodont (75 mm height) and has no cement, and the summits of the lophids each consist of four to five conelets. Tobien (1972) allocated the holotype, lower m2 and m3, of *Z. metachinjiensis* to *Gomphotherium* by used the character of subhypsodonty and relatively large size of m3 that were mentioned by Osborn (1936, p.456). However, there are a few details in this holotype. In 1983, Tassy synonymized the upper M3 of *Z. chinjiensis* and lower m2 and m3 of *Z. metachinjiensis* (Osborn, 1929) to *Z. metachinjiensis*. In this case, after considering the figures of Osborn (1929, figs. 4, 5, 5A and A1) and new material of Tassy (1983a, pl. 2, fig. 2), Tobien et al. (1988) suggested the relations are narrow in their proportions, like the lower and upper second and third molars of *Z. gobiensis*. The pretrite conelets are rather small in *Z. metachinjiensis*,

suggesting this taxon may be closer to *Z. gobiensis* than to *Z. turicensis*. If Tobien et al. (1988) are right; the oldest name for *Z. gobiensis* should be *Z. metachinjiensis* Osborn, 1929. All *Zygodont* species that were synonymized by Tobien et al. (1988) should also be changed. In the Tha Chang m3 NRRU-TKK-001, the transverse lophids are so severely worn that the morphology of the pretrite conelets is generally unclear, except the fourth lophid. In the fourth lophid; however, very small conelets are clearly present on both the pretrite and posttrite sides. The third molars of *Z. metachinjiensis* are much larger, particularly with regard to the length of both the upper and lower molars, than their counterparts from Tha Chang (Tables 1–3; Fig. 5.1, 5.2).

Discussion

In the course of the “proboscidean datum event” (Madden and van Couvering, 1976), which actually comprised multiple proboscidean dispersals from Africa to Asia and Europe, mammutids initially immigrated, in the end of early Miocene, into Europe, and thereafter into Asia and South Asia (Sanders et al., 2010). In Europe, Tassy (1989) identified *Zygodont turicensis* in MN3b sediments in France. In Eurasia and Asia, the records of these taxa in Pakistan, Kazakhstan, and China occur in sediments that date to, or are slightly younger than, MN4 (Tassy, 1996b; Lucas and Bendukidze, 1997). However, material from the Loh Formation in Central Mongolia appears to be late early to early middle Miocene in age, which would make the specimens in question, slightly younger than the first gomphotheres and mammutid immigrants (Göhlich, 2007). However, Mein (1990) thinks that *Zygodont* arrived at Europe coincident with *Gomphotherium* during MN4. If the Loh Formation indicates late early to early middle Miocene in age and considering the opinion of Mein (1990), the initially migration of mammutids is still unresolved.

The family Mammutidae is characterized by a zygodont pattern (yoke-like transverse crests) of the intermediate and third molars. The oldest, most primitive mammutid is *Losodokodon losodokus*, from Kenya dated to the late Oligocene (Rasmussen and Gutierrez, 2009). In Eurasia the Mammutidae is only represented by two genera, *Zygodont* and its descendant *Mammot* (Konidaris and Koufos, 2009). The oldest *Zygodont*, *Z. aegyptensis*, is from the lower Miocene of Wadi Moghara, Egypt (Sanders and Miller, 2002 in Konidaris and Koufos, 2009). The only European *Zygodont* representative is the abundant *Z. turicensis*, whose long stratigraphic range in Europe extends from the middle to the upper Miocene (Konidaris and Koufos, 2009). The “*Zygodont turicensis* group” includes four Eurasian species: the type species *Z. turicensis* Schinz, 1824 from Europe, *Z. atavus* from Kazakhstan, *Z. metachinjiensis* from Pakistan and *Z. gobiensis* from Mongolia and China (Tassy, 1996).

Zygodont has not previously been reported from Southeast Asia. The known *Zygodont* specimens closest to the region are from Lufeng, Yunnan, South China, and were identified as *Z. lufengensis* Zhang, 1982 and *Z. chinjiensis* (Chow et al., 1978; Zhang, 1982). The new specimens from the Tha Chang sand pits are the first record in Southeast Asia. *Z. chinjiensis* and *Z. lufengensis* from Yunnan were assigned to

Z. gobiensis by Tobien et al. (1988) on the basis of dental morphology.

Tassy (1985) and Tobien (1996) noted two dental morphotypes within Mammutidae, robust and gracile, however, the dental morphology in this family is indeed high variable (Tables 2, 3). The zygodont specimens from the Tha Chang sand pits are close in size to the equivalent teeth of *Zygodont gobiensis* (*Miomastodon tongxinensis* Chen, 1978, IVPP-V5584; *Z. gobiensis*, AMNH 26467, Tobien et al., 1988) (both lower and upper molars), *Z. lufengensis* (lower molar) and *Z. turicensis* (both lower and upper molars), but they are smaller than the holotype of *Z. gobiensis*, *Z. metachinjiensis*, and *Mammot borsoni* (Fig. 5.1, 5.2). Tha Chang specimens have small adaxial conelets on both the pretrite and posttrite sides, a feature seen in *Zygodont* specimens from both China and Pakistan. As mentioned above, Tobien et al. (1988) synonymized many species of *Zygodont* with *Z. gobiensis*, implying high variation in the dental morphology of this species. In addition, they suggested that *Z. gobiensis* was more closely related to Pakistan, *Z. metachinjiensis*, which share the small pretrite conelets seen in *Z. gobiensis*, than to *Z. turicensis*. Nevertheless, the essential diagnostic characters of *Z. gobiensis* are the small anterior pretrite conelets on the upper and lower second and third molars, the fact that the lophids are only slightly oblique. Tha Chang specimens share some of these characters, but lack others.

Although the Tha Chang specimens are deeply worn, it is still evident that their crescentoids are less inflated than in the type specimen of *Z. gobiensis*, *Miomastodon tongxinensis*, and *Z. jiningensis* but similar in their degree of inflation to late Miocene *Z. lufengensis* and *Z. chinjiensis*. However, the lophids are less oblique and the zygodont crests less well developed than in *Z. lufengensis* and *Z. chinjiensis*, as in the type specimen and *Miomastodon tongxinensis*. The strongly oblique loph(id)s and zygodont crests are more remarkable in the derived zygodont proboscideans such as *Mammot* (Osborn, 1936; Tobien et al., 1988). The broken specimen of *Z. gromovae* has a loph-like rather than conule-like fourth loph, a point of resemblance to the Tha Chang specimen. In contrast, the fourth loph of the upper M3 of Tha Chang specimen is better developed than in *Z. gromovae*. South Chinese species have small and strongly divided posttrite adaxial conelets, making them more similar to species from the Pakistan (*Z. metachinjiensis*) than those from North China (*Z. gobiensis*, *Miomastodon tongxinensis*, *Z. nemonguensis*, and *Z. jiningensis*). The Tha Chang specimens share specific features with the zygodonts from the Pakistan and Yunnan such as small adaxial conelets, however, they are deeply worn and broken in the anterior loph(id)s and so it is difficult to establish their precise affinities though it is reasonable to designate them as *Zygodont* sp.

The faunal assemblage in the Tha Chang sand pits no. 1 to 9 includes proboscideans, anthracotheres, pigs, rhinos, bovids, giraffids, horses, apes, crocodiles, and tortoises (Nakaya et al., 2002; Chimanee et al., 2004) (Fig. 1), and indicates a middle Miocene to early Pleistocene age. The middle Miocene mammalian fauna consists of amebelodontine gomphotheres (*Protanancus*), *Gomphotherium*, and *Prodeinotherium*. The late Miocene to early Pliocene fauna includes a new orangutan species *Khoratpithecus piriyai* Chimanee et al., 2004, a new

anthracothere species *Merycopotamus thachangensis* Hanta et al., 2008, a new rhino species *Aceratherium porpani* Deng, Hanta, and Jintasakul, 2013 (from the same sand pit that yielded the *Zygodon* specimens, Tha Chang sand pit no. 10), horse *Hipparion*, proboscidean *Stegolophodon* and a primitive species of *Stegodon*. The early Pleistocene fauna includes an advanced species of *Stegodon* (Nakaya et al., 2002, Thasod, 2012). Furthermore, Thasod and Ratanasthien (2005) reported a new species of *Sinomastodon* more derived than *Sinomastodon intermedius* from the Pliocene of China. *Sinomastodon* materials have also been reported from Java (Saegusa, 1995 in van den Bergh, 1999). These specimens were referred to *S. bumiajuensis*, but their skull and dental features resemble those of Chinese *Sinomastodon*. In addition, the molars of *S. bumiajuensis* are more derived than those of Pliocene *Sinomastodon* from Japan and North China, but very similar to *Sinomastodon yangziensis* remains from early Pleistocene cave faunas in South China (van den Bergh, 1999).

Although the *Zygodon* specimens from the Tha Chang sand pits were discovered by sand pit workers and their stratigraphic positions are uncertain, their many dental features are similar to the Yunnan species such as in molar size, four

lophids with small a posterior cingulum, strong antero–external and pretrite cingula, zygodont crests on the first and second lophids, and small conelets on both the pretrite and posttrite half lophids. In addition, the geographical localities are nearby each other. Furthermore, the teeth of zygodont proboscideans from South China and Pakistan are more gracile or mixed between gracile and robust forms than those of northern Chinese species, which are more robust. The Yunnan specimens have been dated to the late Miocene (Biasatti et al., 2012), and those from Pakistan occur in the lower Chinji Formation (about 14–13 Ma) (Osborn, 1929; Chavasseau et al., 2009). The North China species have been dated to the middle Miocene (Tobien et al., 1988), and might be older than the species from Pakistan. Because of similarity to the Yunnan species regarding both dental morphology and geographical locality, thus, the Tha Chang specimens might be late Miocene in age. However, the size and morphological variation of such teeth make stratigraphic conclusions very tentative.

Among the previously described middle to late Miocene proboscideans from northern Thailand are in Mae Moh coal mine (13.3 and 13.1 Ma), Lam Pang Province include *Stegolophodon praelatiden* and *Gomphotherium cf. browni*



- * *Losodokodon losodokius*, late Oligocene, Kenya
- ◆ *Eozygodon morotoensis*, early-early middle Miocene, Uganda, Kenya, Namibia and Egypt
- ▲ *Zygodon aegyptensis*, late early-early middle Miocene, Egypt and Namibia
- *Zygodon turicensis*, middle-late Miocene, Kenya, Tunisia and Europe (widespread)
- ? *Zygodon* ?,
- *Zygodon metachinjiensis*, middle-late Miocene, Pakistan
- + *Zygodon gobiensis*, middle-late Miocene, China and Mongolia
- ▼ *Zygodon atavus*, early middle Miocene, Kazakhstan
- ✦ *Mammot borsoni*, late middle Miocene-Pleistocene, China
- ★ *Zygodon* sp., late middle-late Miocene?, Thailand

Figure 6. Distribution of zygodont proboscideans in the Old World that include the new specimens from Thailand. The oldest zygodont proboscideans have presented in the late Oligocene of Africa and they migrated to Europe and Asia in Miocene (modified data from Tobien et al., 1988; Guan, 1996 in Shoshani and Tassy, 1996; Sanders and Miller, 2002; Pickford, 2007; NOW, 2007; Konidaris and Koufos, 2009; Rasmussen and Gutierrez, 2009).

(Chavasseau et al., 2009). Then, the Chiang Muan coal mine (12.4–12.2 Ma), Prayao Province, has produced *Tetralophodon* cf. *xiaolongtanensis* (Thasod, 2007; Chavasseau et al., 2009). The recognition of *G.* cf. *browni* in northern Thailand implies a degree of biogeographic affinity with Pakistan, whereas the presence of *Tetralophodon* cf. *xiaolongtanensis* in Chiang Muan is a clear link with the fauna of South China. The most widespread taxa in the middle Miocene of Pakistan are the mammutid *Zygodont* *metachinjiensis*, the amebelodont *Protanancus chinjiensis*, the choerolophodont *Choerolophodon corrugatus* and the gomphotherium *Gomphotherium browni* (Tassy, 1983a, 1983b, fig. 7). The first three taxa have apparently not been recorded from the middle Miocene of Thailand, which points to obvious faunal dissimilarities between Thailand and Pakistan (Chavasseau et al., 2009). The middle Miocene localities of North China have yielded a very different fauna dominated by *Zygodont*, the amebelodont *Platybelodon*, and supposedly endemic *Gomphotherium* species (Tobien et al., 1986; Tobien et al., 1988, fig. 7). Thus, the new *Zygodont* specimens in Tha Chang sand pit might indicate a dispersal link between South and East Asian middle and late Miocene proboscideans.

The late Miocene paleoenvironmental record from the Tha Chang sand pits indicates a transition from woodland-dominated to grassland-dominated landscapes (Sepulchre et al., 2010). These results can be correlated to a long-term climatic change that occurred between 8.5 and 6 Ma, leading to a major environmental change with C4 savannas replacing C3 forests and woodlands (Cerling et al., 1994; Sepulchre et al., 2010). However, the late late Miocene new rhino species, *Aceratherium porpani*, from the same sand pit as the *Zygodont* materials, is consistent in its chronological implications with the faunal sample from Tha Chang sand pit no. 8, which includes such taxa as *Khoratpithecus piriyai* and *Merycopotamus thachangensis* (Chaimanee et al., 2004, 2006; Hanta et al., 2005, 2008; Deng et al., 2013). The occipital surface of the Tha Chang rhino is slightly inclined posteriorly or nearly vertical and the cheek teeth are subhypsodont (Deng et al., 2013). Both features indicate a woodland habitat (Zeuner, 1934).

The zygodont proboscidean discovered in Thailand has significant implications for understanding the dispersal of *Zygodont*. The oldest zygodont proboscidean in Africa, *Losodokodon losodokius*, is dated to late Oligocene (Rasmussen and Gutierrez, 2009). The oldest *Zygodont* in Europe is in the late early Miocene, either MN3b or MN4 (approximately 17 Ma) (Drake in Tassy, 1990) while the *Zygodont* materials from Pakistan are in the lower Chinji Formation (approximately 14–13 Ma) (Osborn, 1929; Chavasseau et al., 2009). The North Chinese species are from the middle Miocene (Tobien et al., 1988) and might be older than the species from Pakistan. Finally, the South Chinese species are from the upper Miocene (Biasatti et al., 2012) (Fig. 6). *Zygodont* appears to have dispersed from Africa to Europe in the early Miocene, and become widespread in Asia (especially at middle and high latitudes) in the middle Miocene. *Zygodont* then shifted to low latitude areas such as Thailand in the late Miocene (Fig. 6).

Conclusion

The zygodont proboscidean teeth from the Tha Chang sand pits (no. 10) show the zygodont pattern. The adaxial conelets are small, more closely resembling Chinese specimens of *Zygodont gobiensis* and Pakistan species *Z. metachinjiensis* than the holotype species *Z. turicensis*. Despite deep wear, it is evident that the central conules are less inflated than those of the type specimen of *Z. gobiensis* and *Miomastodon tongxinensis*, but similar to *Z. lufengensis* and *Z. chinjiensis* from the upper Miocene of South China. However, the Tha Chang specimens are badly worn and the m3 is broken anteriorly, making it only to designate these specimens as *Zygodont* sp. This *Zygodont* is the first zygodont proboscidean recorded in Southeast Asia and is likely late Miocene in age.

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