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New Proboscideans (Mammalia) from the middle Miocene of Thailand

OLIVIER CHAVASSEAU[1,2]*, YAOWALAK CHAIMANEE[3], CHOTIMA YAMEE[3], PANNIPA TIAN[3], MANA RUGBUMRUNG[3], BERNARD MARANDAT[1] and JEAN-JACQUES JAEGER[2]

[1]*Institut des Sciences de l'Evolution de Montpellier (ISE-M, UMR-CNRS 5554), Université Montpellier II, place Eugène Bataillon cc64 34095 Montpellier cedex 5, France*
[2]*Institut de Paléoprimatologie et Paléontologie Humaine: Évolution et Paléoenvironnements (iPHEP, UMR-CNRS 6046), Université de Poitiers, 40 avenue du Recteur Pineau, 86022 Poitiers, France*
[3]*Department of Mineral Resources, Paleontology Section, Geological Survey Division, Rama VI Road, 10400 Bangkok, Thailand*

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The proboscidean fauna of the middle Miocene of Thailand consists of five taxa, including four elephantoids and one deinothere. The Thai association is dominated by the genera *Stegolophodon* and *Gomphotherium*. *Stegolophodon* is represented by *S. nasaiensis* and *S. praelatidens*. The latter species, considered invalid and possibly conspecific with *S. latidens*, is re-erected. Its phylogenetic relationships are discussed. The Thai *Gomphotherium* matches with *G. browni* from the middle Miocene of Indo-Pakistan. However, the open nomenclature is employed for the Thai material because it differs from *G. browni* in terms of curvature of the upper tusk. Intraspecific molar size variation observed in *G.* cf. *browni* and *Stegolophodon praelatidens* is attributed to sexual dimorphism. The Thai proboscidean asssemblage is mainly endemic compared with other contemporaneous Asian faunas although the recognition of *Gomphotherium* cf. *browni* denotes faunal affinities with Pakistan. The biostratigraphical implications of the taxa are examined in a regional context. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, **155**, 703–721.

ADDITIONAL KEYWORDS: Asia – biogeography – biostratigraphy – evolution – fauna – Neogene – taxonomy – teeth – Tertiary.

INTRODUCTION

Thailand has yielded a rich vertebrate fauna from the Neogene period. Mammals represent a large fraction of the faunal diversity with approximately 45 sampled taxa, according to Ducrocq *et al.* (1994, 1995). The middle Miocene localities of Thailand are situated in the north-west part of the country (Fig. 1). In this area, extensional forces driven by the motion of the Red river and Mae Ping strike-slip faults caused the formation of multiple continental basins delimited by N–S to SW–NE normal faults (e.g. Morley *et al.*, 2001). These basins are mainly filled by clays, mudstones and sandtones derived from fluviatile, fluvio-lacustrine and lacustrine environments. Clastic deposits are very often interstratified with lignite seams that have been exploited for commercial use. The fossiliferous levels, often lignites, are mainly dated by biochronological studies as middle Miocene in age (e.g. Ducrocq *et al.*, 1994, 1995). The principal fossiliferous localities are situated in the basins of Li, Mae Moh, Chiang Muan and Pong (Fig. 1). In the Li basin, the Mae Long site yielded a micromammal fauna dated as early middle Miocene (Mein & Ginsburg, 1985). Large mammals such as the cervid *Stephanocemas*, the tragulid *Siamotragulus* and the pig *Conohyus* have also been collected (Mein &

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*Corresponding author.
E-mail: olivier.chavasseau@univ-montp2.fr

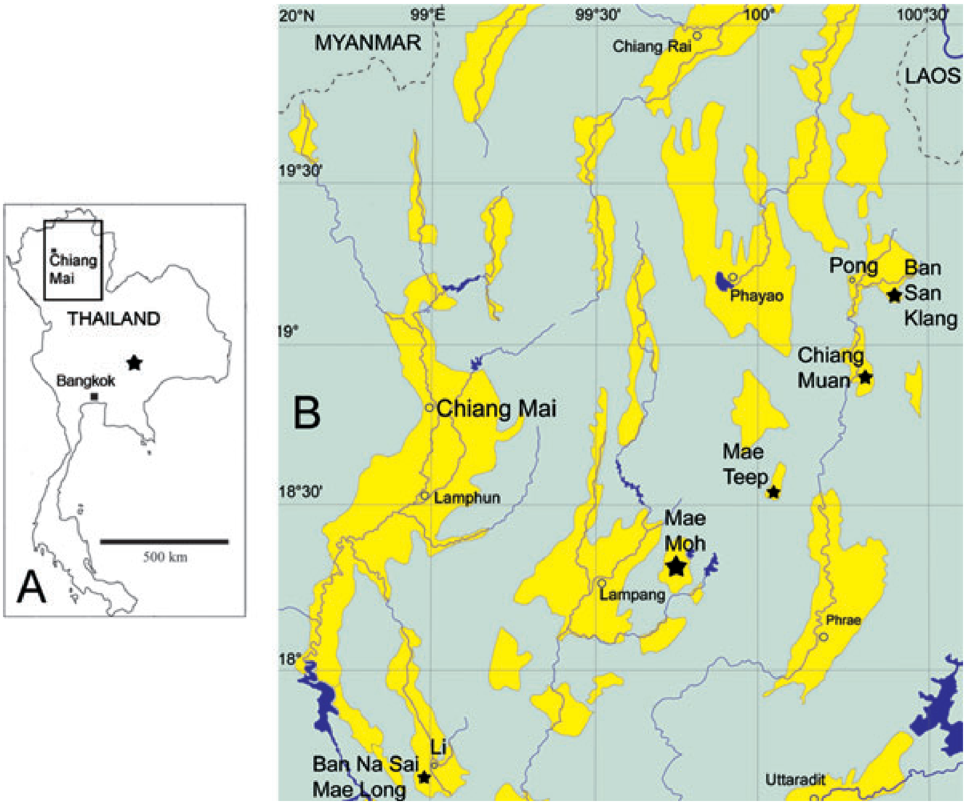

Figure 1. A, map of Thailand showing the main area of study (box). The fossiliferous area of Tha Chang, briefly discussed in this paper, is indicated by a star. B, map of the intermontane basin of north-western Thailand (modified from Uttamo, 2000). The stars indicate the fossiliferous localities mentioned in the text.

Ginsburg, 1997). In the same basin, the locality of Ban Na Sai yielded the proboscidean *Stegolophodon* (Tassy *et al.*, 1992) as well as the anthracothere *Brachyodus*, the rhinocerotid *Gaindatherium* and *Conohyus* (Ducrocq *et al.*, 1994, 1997). The fauna of Ban San Klang, Pong basin, comprises *Siamotragulus, Conohyus* and proboscidean remains attributed to *Gomphotherium* (Ducrocq *et al.*, 1994, 1995). The proboscidean *Deinotherium* (Sickenberg, 1971) plus *Siamotragulus* (Thomas *et al.*, 1990), *Chalicotherium, Brachyodus* and *Gaindatherium* (Ducrocq *et al.*, 1994) were also described from other localities of the Pong basin. The Chiang Muan mine, Chiang Muan basin, yielded hominoid remains (Chaimanee *et al.*, 2003) in addition to, among others, the pigs *Conohyus* and *Parachleuastochoerus* and the proboscidean *Tetralophodon* (Pickford *et al.*, 2004). The fauna of Mae Moh, Mae Moh basin, includes *Gaindatherium* (Ginsburg & Tassy, 1985), the mustelid *Siamogale* (Ginsburg, Ingavat & Tassy, 1983), the amphicyonid *Maemohcyon* (Peigné *et al.*, 2006) and *Stegolophodon* (e.g. Koenigswald, 1959). Koenigswald's description of *Stegolophodon* was the first report of a fossil proboscidean in Thailand.

Recent fieldwork led by a Thai–French team (Department of Mineral Resources, Thailand/ Universities of Poitiers and Montpellier 2, France) in the intermontane basins of Thailand resulted in the collection of additional fossil mammals, particularly at Mae Moh, where collaboration with EGAT (Electricity Generating Authority of Thailand) geologists led to the discovery of numerous well-preserved proboscidean specimens. The Tertiary sequence of Mae Moh or the Mae Moh Group, estimated at 1 km in total thickness, is divided into three formations (Fm.). The lowest is the Huai King Fm., consisting of fluvial and alluvial sandstones, clays and conglomerates. The overlying Na Khaem Fm. comprises mainly claystones and mudstones characteristic of lake and marsh environments. Sandstone levels are rare (Uttamo, 2000; Morley *et al.*, 2001). Gastropod and fish fossils are common in clay and mudstone horizons. The clastic sediments of the Na Khaem Fm. are interstratified with lignite seams named S, R, Q, K and J (from lowest to uppermost). Lignites K and Q are the main fossiliferous levels of the sequence. J is much poorer as is R, the latter containing mostly crocodile and fish remains. The uppermost Huai

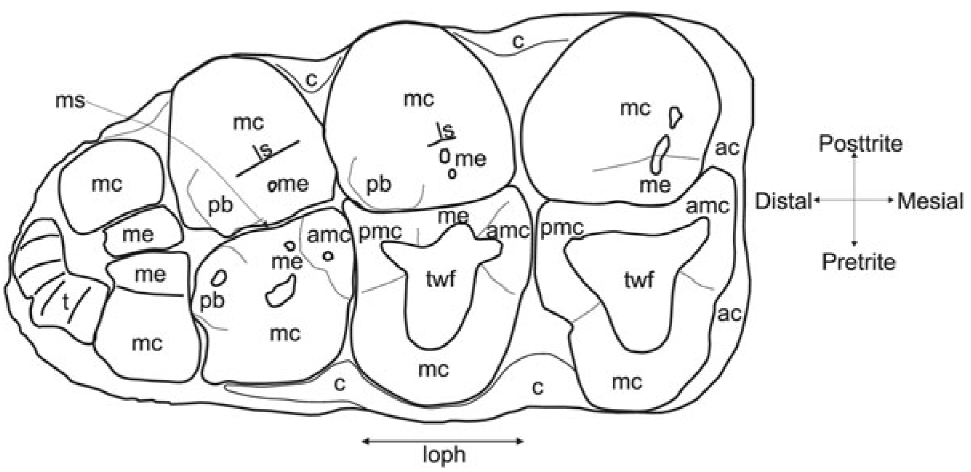

Figure 2. Tooth nomenclature adopted in this article schematized on TF 6266, a right M3/ of *Gomphotherium* cf. *browni*. Abbreviations: ac, anterior cingulum; amc, anterior median (accessory) conule; c, cingulum; ls, lateral sulcus; mc, main cone; me, mesoconelet; ms, median sulcus; pb, posterior bulge; pmc, posterior median (accessory) conule; t, talon; twf, trefoil wear figure.

Luang Fm. is separated from the Na Khaem Fm. by a faint angular unconformity. Claystones, mudstones, siltstones interstratifed with sandstones and conglomerates characterize this formation (Uttamo, 2000). A lignite seam (I) containing mostly trunk fragments is also present.

A large part of the Na Khaem Fm. section is well dated by magnetostratigraphy. Benammi *et al.* (2002) dated the J seam between 12.5 and 12.2 Ma and the K and Q levels between 13.3 and 13.1 Ma. The precision of the chronostratigraphy at Mae Moh renders this locality especially useful for palaeontological studies.

Here we present an update of the proboscidean fauna from the middle Miocene of Thailand in the light of the newly discovered material. For the reasons cited above, this paper focuses on the specimens from Mae Moh. The dental nomenclature adopted here is indicated in Figure 2. All the fossils described and figured are stored at the Department of Mineral Resources, Bangkok. Exceptions include some specimens conserved at the Museum of the Mae Moh mine (the tusks of TF 6267) and two molars from Chiang Muan stored in the fossil collections of the mine.

FAUNA

GOMPHOTHERES

Trilophodont gomphothere

The first taxon of the middle Miocene fauna of Thailand described here is a trilophodont gomphothere. It is mainly documented by fossils from Mae Moh but also occurs in Ban San Klang and probably in Ban Na Sai (Fig. 1). One specimen from Tha Chang, northeastern Thailand, belonging to the private collection of Dr Vidthayanon, is also referable to this species. We discuss briefly the implications of this occurrence below. As mentioned above, Ducrocq *et al.* (1994, 1995) referred the Ban San Klang sample to the genus *Gomphotherium*. Mae Moh specimens originate from lignite levels K and Q. Lignite level R also yielded this gomphothere. This layer is stratigraphically below the base of Benammi *et al.*'s (2002) section dated by them at *c.* 13.5 Ma.

Description: Molars (Fig. 3) – M1 and M2 have three loph(id)s, and M3 four. Molars are characterized by thick unfolded enamel (up to 9 mm), a low and flat crown (height index: 45–60; Table 1), stout main cones, absent posttrite median conules and a clear median sulcus. Anterior lophs are rectilinear. Posterior lophs are often V-shaped owing to posterior shifts of the main cones and/or anterior placement of the mesoconelets.

Upper molars are mainly represented by M3s. There is a thick anterior cingulum. Except for a large anterior conule 1, pretrite median conules are variously developed. They are often absent but can also reach intermediate and large dimensions. When present, the median conules form trefoils together with the pretrite mesoconelet and the main cone but only on lophs 1 and 2. The pretrite trefoil is incomplete on loph 3 most often because of an absent posterior median conule. Posttrite bulges appear sometimes on the posterior side of lophs 1 and 2 and the anterior side of loph 3. The mesoconelets are, similarly to median conules, highly variable. They are mostly small but can reach the size of the main cones. Dissymmetry, expressed by weaker posttrite meso-

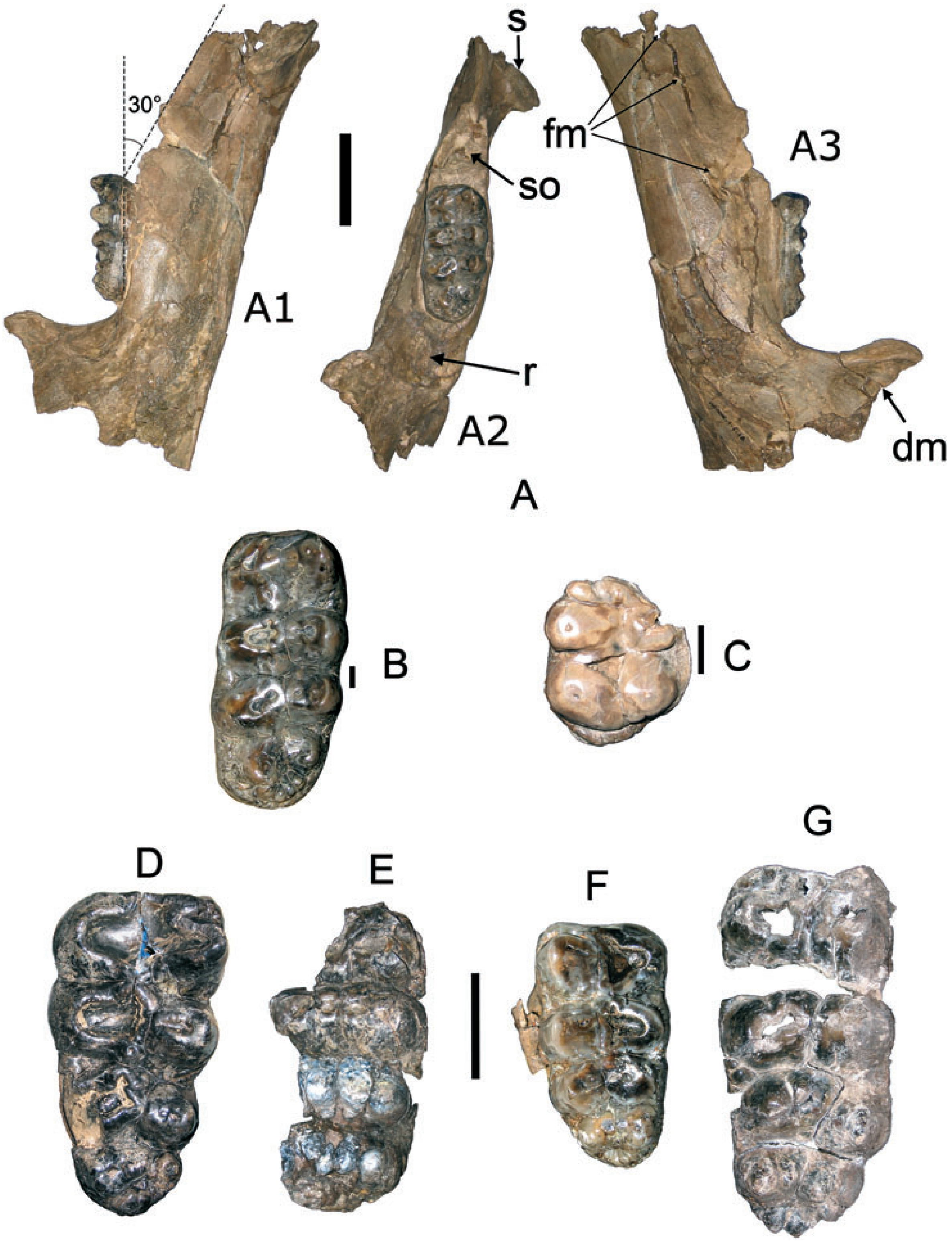

Figure 3. *Gomphotherium* cf. *browni*. A, TF 6266b left hemimandible with M/3: A1, lingual view; A2, occlusal view; A3, labial view. B, TF 6266b: detail of the M/3 in occlusal view. C, TF 6270 right P4/ (occlusal view). D, TF 6267a left M3/ in occlusal view. E, TF 6269 left M3/ in occlusal view. F, TF 6266a right M3/ in occlusal view. G, TF 6268 left M3/ in occlusal view. Abbreviations: dm, deep masseter; fm, foramen mentale; r, retromolar gap; s, symphysis; so, socket of M/2. Scale bars: A = 10 cm, B and C = 1 cm, D–G = 5 cm.

Table 1. Dimensions (in mm) and indices of proboscidean teeth from the middle Miocene of Thailand

Number	Description	L	B	H	BI	HI	LF
Gomphotherium cf. *browni*							
TF 6266a	Right M3/	115.96	63.21	31.1	54.5	49.2	3.45
TF 6266b	Left M/3	130.83	63.09	33.55	48.2	53.2	3.06
TF 6266d	Right upper tusk	730	62.6	77.7	–	–	–
TF 6266e	Left upper tusk	690	71.74	80.78	–	–	–
TF 6266f	Right lower tusk	270	34.15	41.05	–	–	–
TF 6266i	Left M/2	85.54	52.48	–	–	–	3.51
TF 6267a	Left M3/	153	83.13	42.73	54.3	51.4	2.61
TF 6267e	Right lower tusk	330	39.42	50.38	–	–	–
TF 6267f	Right upper tusk	820	77	97	–	–	–
TF 6267g	Left upper tusk	800	90.45	81	–	–	–
TF 6268	Left M3/	176	82.92	37	47.1	44.6	2.27
TF 6269	Left M3/	146.2	73.25	43.58	50.1	59.5	2.74
TF 6270	Right P4/	33.08	30.42	15.61	–	–	–
Stegolophodon praelatidens							
TF 6271f	Left M3/	185	85	45	45.9	52.9	2.7
TF 6271	Left M2/	127	78	–	61.4	–	3.15
TF 6271b	Left M/2	125	69	–	55.2	–	3.2
TF 6271d	Right M/2	124	70	–	56.5	–	3.23
TF 6271a	Left M/3	210	89	46	42.4	51.7	2.38
TF 6271c	Right M/3	200	87	45	43.4	51.7	2.5
TF 6272	Left M/1	88.28	51.08	27.83	57.9	54.5	4.53
TF 6274	Left M?3/	122.88	64.49	33.05	52.5	51.2	4.07
TF 6275	Left M/3	139.53	54.66	35.58	39.2	65.1	3.58
TF 6276a	M/3 right	120.86	46.36	23.57	38.4	50.8	4.14
TF 6276a	M/2 right	> 71.12	42.32	–	–	–	–
TF 6276d	Right lower tusk	> 170	21.62	28.47	–	–	–
TF 6277	Right P4/	39.4	39.97	19.05	–	–	–
TF 6278	Right P/4	36.99	26.39	20.93	–	–	–
TF 6278	Right P/3	25.17	17.83	12.53	–	–	–
TF 6279	P/4 Righ	44.36	36.53	19.4	–	–	–
Stegolophodon nasaiensis							
TF 2648	Right M/3	187	79.46	46.06	42.5	58	2.7
TF 2650	Left M/3	152.6	58.41	34.83	38.3	59.7	3.3
TF 2651	Lower molar frag.	> 85.82	56.06	24.93	–	–	–
Tetralophodon cf. *xiaolongtanensis*							
CMu 2-1	Left M/3	170	70	33	41.2	47.1	2.941
CMu 2-2	Left M2/	> 110	70	38	–	54.3	–

Abbreviations: B, breadth; BI, breadth index = 100 × (breadth/length); H, height; HI, height index = 100 × (height/breadth); L, length; LF, laminar frequency = 100 × (number of lophs/length).

conelets, occurs occasionally. The posttrite mesoconelet is sometimes even absent on loph 3. The fourth loph is smaller than the anterior lophs. It has three to five subequal cusps of medium size. Median cusps are rarely associated with this loph. Talons display two to four small cusps. The roots are posteriorly orientated. Two anterior roots support, respectively, the pretrite half-lophs 1 and 2 and the posttrite half-loph 1, and one posterior root supports the distal lophs.

Lower molars are not abundant in our sample. All of them display pretrite median conules. These are low but stronger than their upper equivalents. Lophids 1 and 2 display asymmetrical trefoils due to larger posterior median conules. Lophid 3 is devoid of median conules on M/1-M/2 and shows only a partial trefoil on TF 6266b, the sole M/3 collected (Fig. 3B). The median cusps are mostly connected to the pretrite main cones on TF 6266b. The mesoconelets are comparatively smaller than the main cones. TF 6266b has a fourth lophid that is narrower and lower than the others. It is composed of four medium-sized equal cusps arranged in an anteriorly pointing V. M/1 or

M/2 display bicuspid or tricuspid talons. TF 6266b possesses, like the corresponding M3/, a talon comprising four small cusps. Lower molars are biradicular with one anterior root under the first lophid and a second one supporting the posterior lophids.

Premolars (Fig. 3C) – The premolars are very poorly known. Only a single incomplete upper P4/ from Ban Na Sai, TF 6270, is assignable to the trilophodont gomphothere. It is bilophodont with a simple quadricuspid bunodont morphology. The posttrite cusps are slightly laterally elongated while pretrite cusps appear rounder in shape. Two faintly individualized conules are visible on the posteromedial side of the posterior main cones. The tooth, with the exception of at the pretrite wall, is surrounded by a cingulum of moderate thickness.

The assignation of this fossil was motivated by the fact that gomphotheres often show P4/ with a simple quadricupid morphology (see Tassy (1985) for *Gomphotherium angustidens*). P4/ of amebelodonts can display similar morphologies. However, there is no evidence that amebelodont proboscideans existed in the middle Miocene of northern Thailand. Stegodontids have usually broader P4/ with well-developed mesoconelets. In addition, a molar fragment displaying blunt and high tubercules recalling TF 6269 (Fig. 3E) has also been found in Ban Na Sai, reinforcing the presence of a gomphothere in this locality.

Mandible (Fig. 3A) – A left fragmentary hemimandible, TF 6266b, was excavated at Mae Moh mine. The mandible preserves an M/3 with the three anterior lophids worn and the unresorbed alveolus of M/2. The latter was recovered beside the mandible and was fully worn. The specimen thus belongs to dental stage 20 of the 23 stages of the scale proposed by Tassy (1985) for *Gomphotherium angustidens*. The corpus is deep, even taking in account the advanced age of the specimen, and nearly constant in height anteriorly to the ascending ramus. The symphyseal region begins at the level of the anterior border of the M/2 alveolus. It is damaged, leaving only a small part of the symphyseal ‘gutter’ and a section of the socket of the left tusk. The ‘gutter’ is delimited anteriorly by a ridge, which posteriorly joins the alveolus of M/2. This ridge is deflected downward at approximately 30° relative to the dentine–enamel contact surface of M/3. In lateral view, the ventral border of the corpus forms an angle of 15° with the neck of M/3. There are three foramen mentale. The anteriormost is situated at the level of the beginning of the tusk socket. The second one is at half-ridge. The posteriormost foramen is positioned at two-thirds of the M/2 alveolus and at 3 cm of the anterior portion of M/3. M/3 is not hidden by the ascending ramus in lateral view, because of the large retromolar space. The angular process and dentary condyle are broken. However, the ascending ramus partially displays the coronoid process. It is high with a markedly bulged anterior border. Its outer side shows a profound insertion of the deep masseter.

Tusks (Fig. 4A–C) – The tusks are mainly documented by individuals TF 6266 and TF 6267, which have associated molars and lower and upper tusks (respective dental ages 20 and 21). The lower tusks are straight in lateral view and straight or faintly curved to the medial side in dorsal view. They are made of concentric dentine covered by a cementum layer. The section is elliptical with a subvertical major axis. No clear longitudinal groove is observable on the dorsal face. The tip is worn dorsally, polished ventrally and exhibits a medial contact facet. The incomplete lower tusk of TF 6266 measures 27 cm in length and shows a small pulp cavity anteriorly.

The upper tusks are straight to slightly concave ventrally in lateral view and show an incurvation towards the external side in dorsal and ventral views. An enamel band is placed entirely on their external side. A large ventral wear facet flattens the section on the anterior portion of the tusk. It extends approximately distally to the half of the tooth on some specimens. The distal extremity of the enamel band is truncated by wear. The section of the upper tusks is elliptical with a maximum diameter parallel to the enamel band. A weak longitudinal groove, discernible on unworn portions, is present at the centre of the ventral side.

Variability: The molars of the trilophodont gomphothere exhibit a strong variability in both size and morphology. The length of M3/s varies from 115 to 176 mm (Table 1). This range of variation represents 53% of the length of the shortest specimen. The coefficient of variation, calculated by the formula ‘(standard deviation/mean) × 100’, is 15% ($N = 8$). Such variability is not uncommon among gomphotheres. Tassy (1985: 362, 1996a: 98) reported a comparable variation in molar size for *Gomphotherium angustidens* at En Péjouan (France). At this locality, the observed range of length represents 39% of the shortest specimen for M/3s and 42% for M3/s. The corresponding coefficients of variation are 10.16% ($N = 13$) and 11.60% ($N = 18$). In addition, important variability in molar size is not restricted to gomphotheres. For instance, the mammutid *Zygolophodon turicensis* from the middle Miocene of Europe shows a range of variation equivalent to ~42% of the shortest specimen for M3/s and ~52% for M/3s (Tassy, 1985; values calculated from figs 203–204). Considering these data, we believe that the disparity of size of the trilophodont gomphothere specimens represents an intraspecific variation. Several authors suspected strong sexual dimorphism to be the cause of

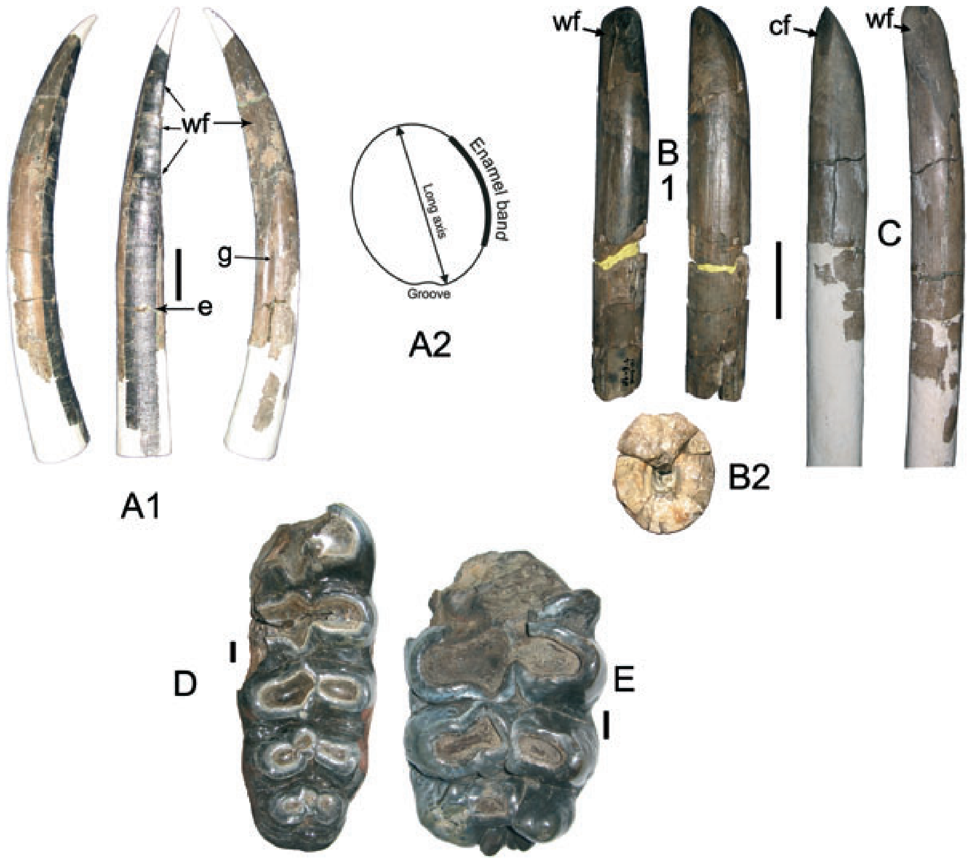

Figure 4. A–C, *Gomphotherium* cf. *browni*. A1, TF 6267f right upper tusk in dorsal, lateral and ventral views (from left to right). A2, schematic representation of the cross-section of a right upper tusk (proximal portion; posterior view). B, TF 6266f right lower tusk: B1, dorsal view (left) and medial view (right); B2, anterior view (not to scale). C, TF 6267e right lower tusk in medial view (left) and dorsal view (right). D, E, *Tetralophodon* cf. *xiaolongtanensis* CMu 2-1: D, left M/3 in occlusal view. E, left M2/ in occlusal view. Abbreviations: cf, contact facet; e, enamel band; g, longitudinal groove; wf, wear facet. Scale bars: A = 10 cm, B and C = 5 cm, D and E = 1 cm.

this variability in mastodonts (Tassy, 1985, 1996a; Göhlich, 1998). We postulate the same hypothesis here even if it cannot be confirmed as our sample is too small to observe a potential bimodal distribution.

As described above, the morphological variation of Thai taxon molars is striking. Nevertheless, these teeth are united by a combination of features such as thick enamel, massive main cones and absence of clear posttrite cusps. Moreover, the occurrence of morphological intermediates corroborates our hypothesis: the variation of the mesoconelets and pretrite trefoils bridge the gap between the two morphological extremes characterized by the associations of stout mesoconelets/absent trefoils and weak mesoconelets/marked trefoils. Finally, taking into account that most of the fossils originate from a 200-kyr interval of the Mae Moh sequence, we interpret the strong variability of the trilophodont gomphothere's molars as being intraspecific.

Comparisons and taxonomy: The proboscidean described above is attributed to the Gomphotheriidae based on the simple bunodonty of its molars. Amebelodont affinities are excluded as the Thai sample does not show either developed posttrite accessory conules on molars or dorso-ventrally flattened lower tusks. This gomphothere does not belong to 'tetralophodont gomphotheres' and stegodontids, which possess at least tetralophodont intermediate molars. The combination of plesiomorphous traits such as the trilophodonty of intermediate molars, the tetrabelodonty, the rectilinear enamel band on the upper tusks and the functional premolars indicates that the Thai material belongs to a species of the primitive genus *Gomphotherium* as defined by Tassy (1985).

Gomphotherium sp. is more derived than the most primitive gomphotheres (sometimes named '*Gomphotherium annectens* group'; see Tassy, 1996b), which display no or only incipient fourth loph and talon on M3/3, and uniformly weaker mesoconelets and median conules. Among the more derived *Gomphotherium* species, it differs from '*G. subtapiroideum*' (middle Miocene, western Europe) by the absence of a ventral longitudinal groove on lower tusks, from *G. angustidens* by its rectilinear lower tusks of elliptical section, the fully lateral enamel stripe on upper tusks, and some mandibular features such as larger retromolar gap at similar dental ages and anterior bulge of the anterior border of the coronoid process, and from *G. steinheimensis* (late middle Miocene to early late Miocene, Germany) by its straight upper tusks. The Thai *Gomphotherium* is distinct from *G. wimani* (middle Miocene; Qinghai province, northern China), which displays molars with coronal cementum and a tendency to choerodonty, from *G. shensiensis* (middle Miocene; Shaanxi province, northern China) which has lost the enamel band on upper tusks, and *G. connexum* (Miocene; Qinghai province), which displays narrower molars with blunter median conules (Tassy, 1985; Tobien, Chen & Li, 1986; Göhlich, 1998).

Gomphotherium browni is a rare taxon from the Chinji Fm. of Pakistan (Tassy, 1983b), dated to the end of the middle Miocene (14.2–11.2 Ma; Barry *et al.* 2002). This species is mainly documented by the holotype, AM 19417, partial skull of a young adult (dental age 17), which preserves left and right M2/-M3/, left upper tusk and a mandible with lower tusks, symphysis, both M/2s and partial M/3s. The molars of AM 19417 are, as those of *G.* sp., mostly primitive by showing a simple bunodonty, blunt main cones, thick enamel and relatively low crown. Note that thick enamel and low crown, judged as apomorphous by Tassy (1983b) in *G. browni*, are considered here as maintained ancestral features as these traits are displayed by primitive elephantoids (e.g. Shoshani, 1996: 164; Sanders, Kappelman & Rasmussen, 2004). The weak or absent pretrite trefoils of upper molars, the reduced fourth loph formed of four to five little cusps on M3/ together with the distinct posterior median conules on M/3 observed on AM 19417 are compatible with the range of variation of the Thai material. The lower tusks of AM 19417 are straight, devoid of a longitudinal groove, and circular or subcircular in cross-section. Mae Moh specimens only differ from them by their slightly more elliptical sections. Finally, the upper tusk of AM 19417 is characterized by a regular ventral concavity, a straightness in ventral/dorsal view, an elliptical cross-section and a lateral enamel band (Tassy, 1983b); O. Chavasseau, pers. observ.). The upper tusks of the Thai sample are dissimilar by being curved to the external side. Furthermore, they are rectilinear in lateral view or faintly curved ventrally, their concavity being predominantly located on the proximal part of the tooth.

The large posterior central conules on lower molars, the multicuspid fourth loph(id) on M3 and the lower tusk traits are derived features shared between *G.* sp and *G. browni*. These characters allow us to hypothesize that these taxa are at least closely related. The differences in the trajectory of upper tusks between *G.* Sp. and *G. browni* might imply that the Thai material is distinct from the Siwalik taxon at the species level. However, it is not certain that these discrepancies do not represent intraspecific variation because few individuals preserving upper tusks are available (one from Pakistan and three from Thailand). Finally, taking into account that the molars and the lower tusks of *G.* Sp. match very well with those of *G. browni*, we judge that conspecificity of the Thai and Pakistani material is more plausible and opt for an identification of the Thai specimens as *G.* cf. *browni*. The specific status of *G.* cf. *browni* will be clarified with the discovery of additional specimens. Systematic palaeontology and referred material of *G.* cf. *browni* are given below.

Order Proboscidea Illiger, 1881
Family Gomphotheriidae Hay, 1922
Genus *Gomphotherium* Burmeister, 1837

Type species: Gomphotherium angustidens Cuvier 1817
Gomphotherium cf. *browni* (Figs 3, 4A–C)

Synonymy:

? Elephantoidea *indet*. – Tassy *et al.*, 1992: 519–21

Gomphotherium sp. – Ducrocq *et al.*, 1994: 152

Referred material: Mae Moh: TF 6266 individual preserving right M3/ (TF 6266a; Fig. 3F), left hemimandible with M/3 (TF 6266b; Fig. 3A, B), atlas (TF 6266c), right upper tusk (TF 6266d), left upper tusk (TF 6266e), right lower tusk (TF 6266f; Fig. 4B), fragmentary occipital condyles (TF 6266g & h) and right M/2 (TF 6266i); TF 6267 individual with left M3/ (TF 6267a; Fig. 3D), right M3/ (TF 6267b), right M2/ (TF 6267c), left M2/ (TF 6267d), right lower tusk (TF 6267e; Fig. 4C), right upper tusk (TF 6267f; Fig. 4A) and left upper tusk (TF 6267g); TF 6268 left M3/ (Fig. 3G), TF 6269 left M3/ (Fig. 3E), M4733a left DP2/, plus a few other specimens stored at the Department of Mineral Resources. Ban San Klang: TF 2649 right M3/, TF 2660 left upper tusk (same individual as TF 2649). Ban Na Sai: TF 6270 right P4/, left upper molar fragment (unnumbered). Tha Chang: CCZ 49 left M3/.

Affinities: The European species *Gomphotherium steinheimensis* displays, like *G. browni* and *G.* cf. *browni*, rectilinear lower tusks devoid of a longitudinal groove with a subcircular or elliptical cross-section. Tassy (1985) hypothesized a *G. steinheimensis* – *G. browni* clade within the genus *Gomphotherium* on the basis of features of the lower tusks. However, convergence might have occurred on the lower tusk characters because the potentially unrelated North American *Gomphotherium productum* also exhibits grooveless lower tusks of circular section (Tassy, 1985). Hence, this phylogenetic relationship remains uncertain especially as the molars of *G. browni*/*G.* cf. *browni* and *G. steinheimensis* do not share obvious synapomorphies.

The Chiang Muan proboscidean

Several gomphothere molars were excavated in the lower lignite member of the hominoid locality of Chiang Muan (Fig. 4D, E). According to Pickford *et al.* (2004), they correspond to a tetralophodont gomphothere, *Tetralophodon* cf. *xialongtanensis*, which is morphologically close to the proboscidean remains described from the locality of Xiaolongtan, southern China. Only third molars are figured by Pickford *et al.* They display either faint 5th lophids or strong talons leaving doubts concerning the tetralophodonty of anterior molars. An isolated M1/ or M2/ (Fig. 4E), as attested to by a posterior contact facet, confirms that the Chiang Muan proboscidean belongs to the tetralophodont grade.

The Chiang Muan gomphothere clearly differs from *Gomphotherium* cf. *browni* by having tetralophodont intermediate molars, a stronger posterior displacement of the pretrite main cone and a weaker talon. It differs in particular from stegodontids of the middle Miocene of Thailand (see further) by having weaker mesoconelets and complete trefoils on anterior loph(id)s.

STEGODONTIDS

This family is represented in the middle Miocene of Thailand by the genus *Stegolophodon*. As mentioned previously, this genus was reported from the localities of Mae Moh (Koenigswald, 1959; Sithiprasasna, 1959; Tassy *et al.*, 1992) and Ban Na Sai (Tassy *et al.*, 1992). In addition, Buffetaut *et al.* (1988) described *Stegolophodon* remains from the site of Mae Teep, Mae Teep basin (Fig. 1). The new stegodontid material described in this paper mainly originates from Mae Moh.

The Mae Moh stegodontid

Stegodontid fossils are present in lignite levels J, K and Q of the Mae Moh section dated between 13.3 and 12.2 Ma (Benammi *et al.*, 2002). We also refer one molar from Tha Chang to this species. This occurence is discussed below.

Description: Molars (Fig. 5A–F) – The molars are reasonably low-crowned (height index = 45–65; Table 1) and formed of bulbous cusps built of moderately thick unfolded enamel (3–6 mm). Wear is mostly visible at the summit of the tubercules, indicating a probable domination of antero-posterior movements during mastication. M1 and M2 are tetralophodont while M3 has five loph(id)s. All loph(id)s are rectilinear or subrectilinear with very slightly anterior mesoconelets. They are most often made of four cusps. The mesoconelets, which are well developed, reach the size of the main cones. The median sulcus is distinct. Lateral sulci are nearly as deep as median sulci. Median conules appear exclusively on the pretrite side. The fifth loph(id) is structurally identical to anterior lophids but narrower and lower. The talon is variable and has from one to three cusps. The configuration of the roots is identical to that of *Gomphotherium* cf. *browni*.

Upper molars are moderately wide (breadth index ~45–50 for M3/; Table 1), and have a straight to faintly convex crown. The mesoconelets are symmetrical. There are no median conules with the exception of an anterior conule and a faint occasional posterior conule on the first pretrite half-loph.

Lower molars have straight to slightly concave crowns. The posttrite mesoconelet is often weaker than its pretrite equivalent or even occasionally absent. Lower median conules are only present on lophids 1–4. Except on the first lophid, anterior median conules are unusual. Posterior conules are massive anteriorly and decrease in size and height posteriorly so that they are minute or absent on lophids 3 and 4. They are placed against the pretrite mesoconelet on lophids 2–4. The organization of the median cusps leads to the absence of a complete trefoil wear pattern on lophid 1.

The presence of a fifth loph(id), the larger mesoconelets, the deeper lateral sulci, the nearly total reduction of upper central conules and the lower crown are features that allow a clear differentiation of stegodontid molars from those of *Gomphotherium* cf. *browni* in the Mae Moh sample.

Premolars (Fig. 5G–I) and deciduous premolars (Fig. 6E, F) – P/3 is bilophodont. The first loph is composed of a large and high protoconid. This cusp appears to be faintly separated into two parts because of very shallow anterior and posterior grooves. Low, round and equally developed hypoconid and entoconid form the second loph. They are separated by a deep sulcus. There is a thin posterior cingulum starting from the hypoconid. Each lophid is supported by a vertical root.

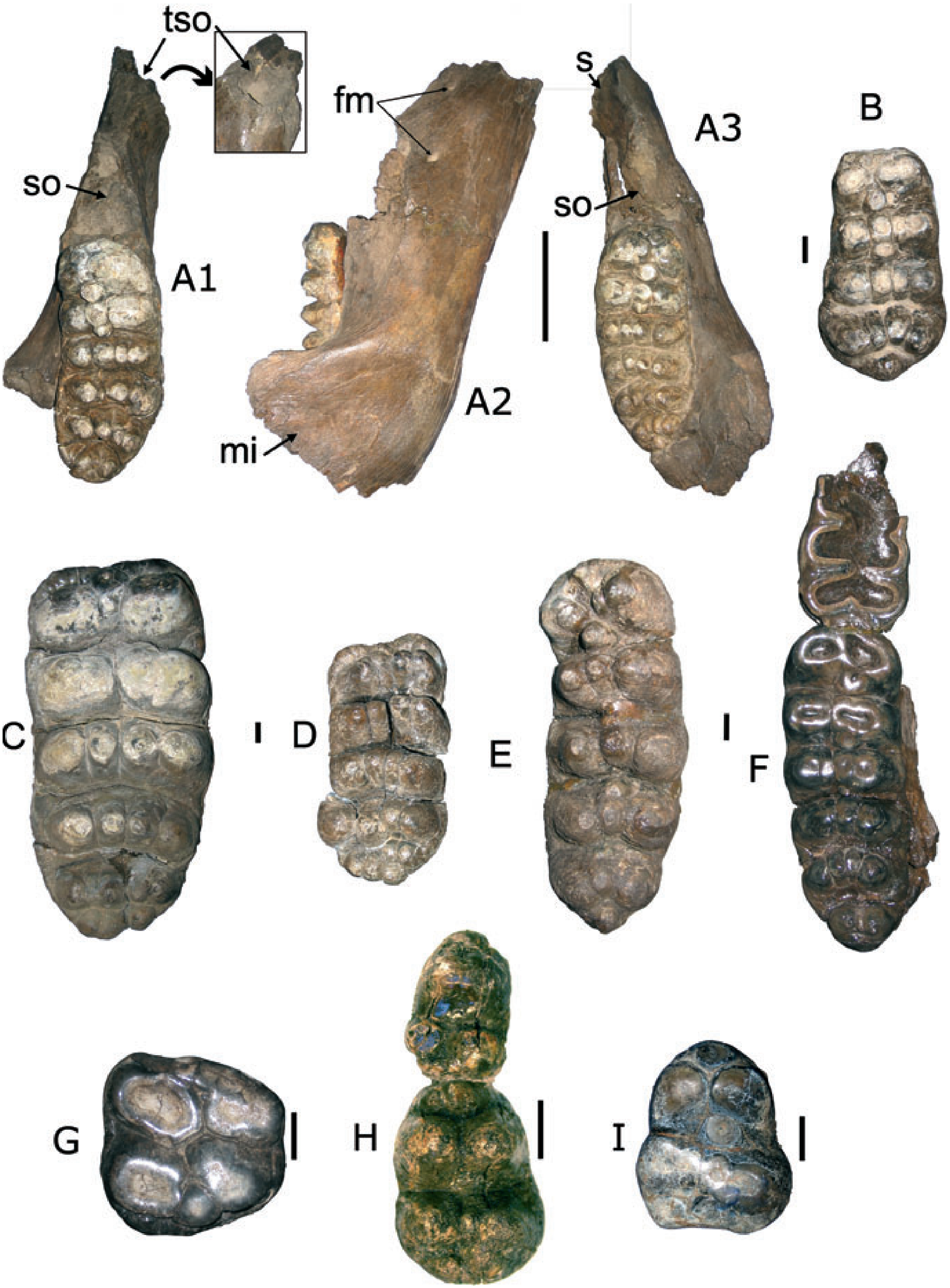

Figure 5. *Stegolophodon praelatidens*. A, TF 6271 left and right hemimandibles with M/3: A1, TF 6271a left hemimandible in occlusal view. Box: lateral view of the anterior portion showing the beginning of the tusk socket; A2, TF 6271c right hemimandible in lateral view; A3, TF 6271c in occlusal view. B, TF 6272 left M/1 or M/2 in occlusal view. C, TF 6271f left M3/ in occlusal view. D, TF 6274 left M?3/ in occlusal view. E, TF 6275 left M/3 (occlusal view). F, TF 6276a, right M/2-M/3 in occlusal view. G, TF 6277 right P4/ (occlusal view). H, TF 6278 right P/3-P/4 in occlusal view. I, TF 6279 right P/4 in occlusal view. Abbreviations as in Figures 3 and 4, plus: mi, masseter insertion; tso, tusk socket. Scale bars: A = 10 cm, B–I = 1 cm.

P/4 is bilophodont. There is a low and thick anterior cingulum from which a central cusp often emerges. The first lophid displays well-separated main cones (protoconid and metaconid), rarely associated with mesoconelets. There is often a massive pretrite posterior conule. The second lophid is lower and wider than lophid 1, the enlargment being mainly localized on the pretrite side. There are typically two stout mesoconelets. Some specimens show weaker mesoconelets or a single pretrite mesoconelet. As in P/3, the posterior cingulum starts from the hypoconid and is usually bicuspid.

P4/ is wide, making its outline close to that of a square. It possesses enlarged main cusps, to which mesoconelets usually are attached. This morphology contrasts with the rectangular P4/ lacking mesoconelets of *Gomphotherium* cf. *browni*. Median conules or displaced mesoconelets on posttrite half-loph 1 and pretrite half loph 2 result in a partial obstruction of the median valley. A triangular posterior cusp is situated between the posterior half-lophs. The anterior cingulum exhibits multiple thick cusplets. Posterior and lateral sides are surrounded by a cingulum.

DP4 is, like M1 and M2, tetralophodont. Most of the specimens are heavily worn. DP/4 increases in breadth posteriorly, with the third lophid being the widest. Median cusps are absent or subsist in interlophids 1 and 2 as posterior pretrite conules. The valleys are narrow. The mesoconelets are placed anteriorly to the main cones on lophid 4. The roots are arranged as in the molars.

DP4/ has a rectangular outline. The lophs are rectilinear and separated by narrow valleys. There are no median conules. The crown is convex.

Tusks (Fig. 6A–D) – The upper tusk remains are fragmentary and were deformed *post mortem*. They are straight or slightly ventrally concave in lateral view and possess a lateral enamel band. The specimens seem to have elliptical sections with a major axis parallel to the enamel band. This morphology is similar to that of *Gomphotherium* cf. *browni* specimens. Thus, the upper tusks can only be identified to taxon if they are associated with molars.

Three fragmentary lower tusks from Mae Moh, two of which are associated with molars, are referred to the stegodontid. TF 6276d preserves only the tip. There is a distinct contact facet which allows an orientation of the tusk. It is a right specimen of ovoid section with a subvertical maximum diameter and a ventrally placed maximum medio-lateral diameter. There is a very weak longitudinal flattening on the medial side. TF 6271g is about 35 cm long. The proximal part of the tusk is nearly complete as shown by the large size of the pulp cavity. In contrast, the tip is broken, rendering the orientation of the specimen problematic. The section is piriform with a weak longitudinal groove that appears as a flattening. There is a slight medio-external curvature that is exaggerated by the damage caused to the specimen. A faint dorsal concavity is also noticeable. TF 6280 is a median portion of tusk of piriform section. The groove is more accentuated than on TF 6271g. The tusk is straight in ventral–dorsal views and weakly concave dorsally. The lower tusks of the Mae Moh stegodontid are differentiated from those of *Gomphotherium* cf. *browni* by their ovoid to piriform sections with a longitudinal flattening/groove, whereas the gomphothere displays elliptical sections devoid of a groove.

Mandible (Fig. 5A) – The mandible of the Mae Moh stegodontid, TF 6271, preserves partial left and right hemimandibles. They are deep and thick, which is not surprising judging by the age of the specimen [stage 19 of the scale constructed by Tassy (1985)] and the large size of M/3. The left hemimandible, TF 6271a, shows a partial view of the anterior portion of the left tusk socket. The alveolus is apparently ovoid with a vertical long axis. The symphysis begins at the level of the anterior root of M/2. An antero-posterior ridge connects the alveolus of M/2 to the symphyseal region. This ridge deflects downward relative to the neck of M/3 at approximately 40°. The ventral border of the corpus forms, in lateral view, an angle of 15° with the cervix of M/3. The left hemimandible preserves part of a massive ascending ramus. The anterior portion of the ramus is vertical and hides the fifth lophid and talon of M/3 in lateral view. The latter feature might be associated with the age of the individual. M/3 was probably not yet functional because it is not entirely out of the dentary and unworn. There is a large masseteric fossa. The right hemimandible, TF 6271c, displays two foramen mentale. The anterior one is tiny and positioned just posterior to the beginning of the tusk alveolus. The posterior foramen, which is larger, is placed ~4 cm posteriorly to the anterior margin of the socket of M/2. The left hemimandible lacks the anterior foramen. TF 6271a & c differ from the mandible of *Gomphotherium* cf. *browni* by fewer f. mentale, absence of a bulge of the coronoid process and slightly more deflected anterior portion of the corpus.

Variability: The stegodontid material from Mae Moh shows great variation in size and morphology, recalling the condition in *Gomphotherium* cf. *browni*. The morphological variation mainly concerns the size of the posttrite mesoconelet and the number and size of the median conules. The Mae Moh sample clearly shows intermediate morphologies that cannot rule out the assignment of all the material to a single species.

The size variation of the Thai stegodontid is even greater than that observed for *Gomphotherium* cf.

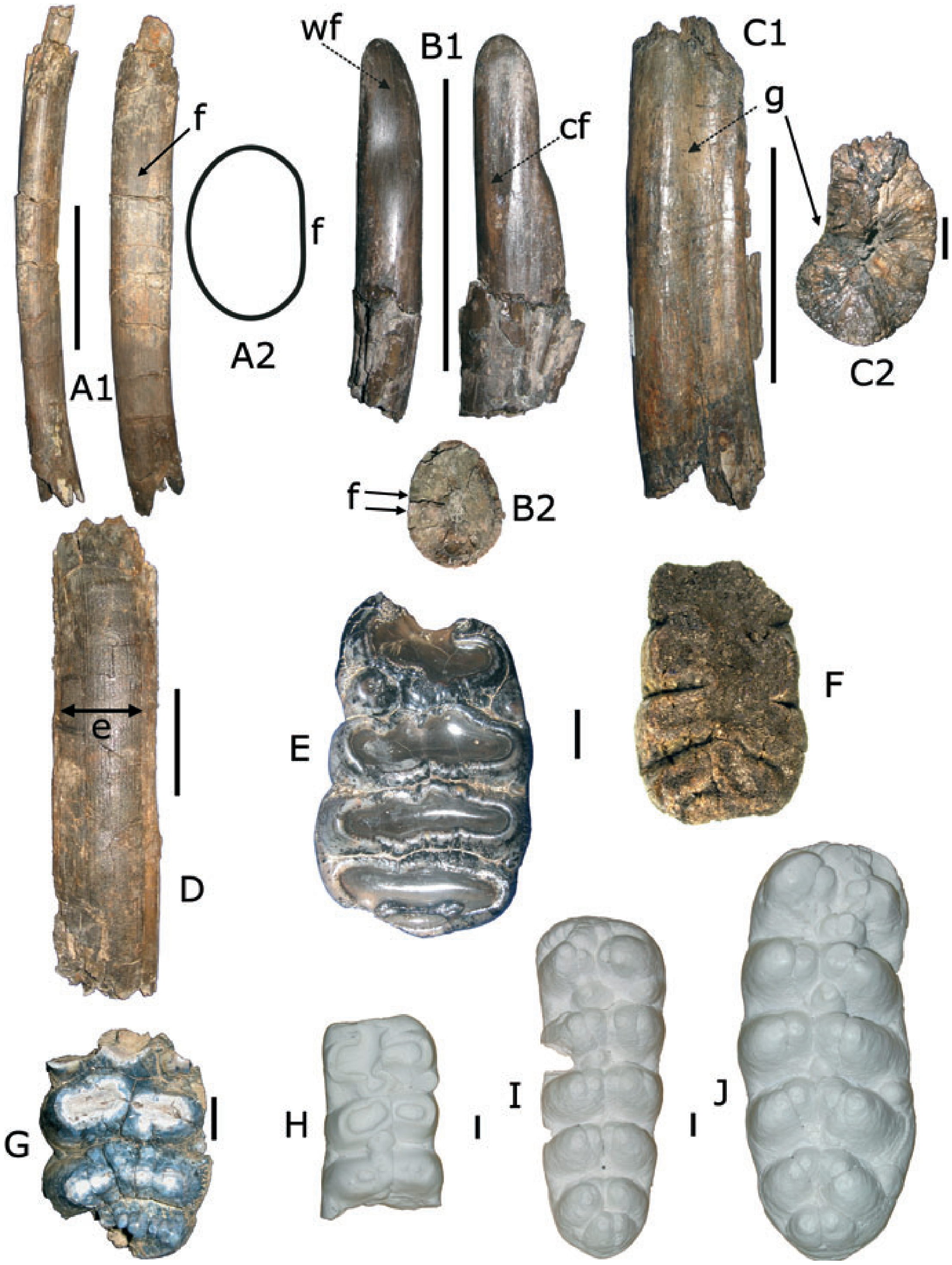

Figure 6. A–F, *Stegolophodon praelatidens*. A, TF 6271g right? lower tusk: A1, dorsal view (left) and medial view (right); A2, schematic cross-section of TF 6271g (anterior view). B, TF 6276d right lower tusk: B1, dorsal view (left) and medial view (right); B2, anterior view of a more proximal fragment of TF 6276d (not to scale). C, TF 6280 fragment of right lower tusk: C1, medial view; C2, anterior view. D, TF 6271h, upper tusk fragment in lateral view. E, TF 6281 right DP4/ (occlusal view). F, TF 6282 right DP/4 (occlusal view). G–J, *Stegolophodon nasaiensis*. G, TF 6283 right DP4/ (occlusal view). H, TF 2651 left lower molar fragment in occlusal view (cast). I, TF 2650 left M/3 in occlusal view (cast). J, TF 2648 right M/3 in occlusal view (cast). Abbreviations as in Figure 4 plus: f, flattening. Scale bars: A, B, C1 and D = 10 cm, C2 and E–I = 1 cm.

browni. It reaches 74% of the smallest specimen's length for M/3. As for the trilophodont gomphothere, we postulate that the variation of size probably denotes a strong sexual dimorphism in this species. Sexual dimorphism might have been common within stegodontids; it is also suspected in *Stegodon sondaari* from the island of Flores (Bergh, 1999: 298).

Comparisons: This taxon has tetralophodont DP4, M1 and M2, which display a simple bunodont morphology. It thus belongs either to gomphotheres or to stegodonts. The presence of stout mesoconelets together with the reduction of the pretrite trefoils due to the absence of anterior central conules indicates that it is a stegodont. Among the Stegodontidae, it belongs to the primitive genus *Stegolophodon* because it retains long lower tusks and apparently an unreduced symphysis, an enamel strip on upper tusks, tetralophodont intermediate molars with few cusps per loph, and premolars.

Koenigswald (1959) erected the species *S. praelatidens* based on a few tooth fragments from the Mae Moh mine. The holotype corresponds probably to a distal part of M/3 (this fragment is too narrow to be an M3/ as initially proposed). Koenigswald hypothesized from dental features that *S. praelatidens* was ancestral to *S. latidens* Clift, 1828, a species described from the Irrawaddy Formation of Myanmar. Ginsburg & Tassy (1985) followed by Tassy *et al.* (1992) judged *S. praelatidens* as invalid and referred Mae Moh's *Stegolophodon* to the Burmese species *S. latidens* under the name *S.* cf. *latidens*. The structure of the first loph of a fragmentary upper molar from Mae Moh, close to that of the lectotype of *S. latidens* was thought by these authors to reveal a probable conspecificity of the Thai and Burmese fossils. The new material discovered at Mae Moh allowed us to make more detailed comparisons than Ginsburg & Tassy (1985) and Tassy *et al.* (1992).

Comparison with Stegolophodon latidens: The lectotype of *S. latidens* (figured in Tobien, 1978) is a maxilla fragment with right M2/-M3/ (M 29713). Here we follow Tassy (1983c: 320) in considering that the other specimens associated with the lectotype by Clift and subsequent authors are of doubtful affinities, both from morphological and from stratigraphic perspectives. As a consequence, we restrict the comparison of Mae Moh material solely to M 29713. M2/ is too worn to display features of phylogenetic interest. M3/ has five lophs. The crown is wide (breadth index = 62; estimated from Tobien's figure). The laminar frequency is high, causing interlophs to be very narrow. There is a remarkable posterior displacement of the main cone on pretrite half-lophs 2–5. It is coupled on loph 2 to an anterior displacement of the pretrite mesoconelet. Interlophs 1 and 2 are obstructed on the pretrite side because mesoconelets 2 and 3 join the posterior median conules of the preceding loph.

Substantial crown width, high laminar frequency, posterior shift of the pretrite main cones, the presence of a pretrite posterior median conule 2 and the obstruction of the two first valleys are not present in the Mae Moh molars. Therefore, we consider that the name *S.* cf. *latidens* is not appropriate for these fossils, *contra* Ginsburg & Tassy (1985) and Tassy *et al.* (1992).

Comparison with Stegolophodon nasaiensis: Tassy *et al.* (1992) described a species of *Stegolophodon*, *S. nasaiensis*, from the Thai Miocene locality of Ban Na Sai. The authors argued that the lower size of the mesoconelets, their anterior placement relative to the main cones on lophids 4 and 5 of M/3, and the persistence of pretrite median conules on M3/ discriminated *S. nasaiensis* from the *Stegolophodon* of Mae Moh.

M3/s from Mae Moh are generally devoid of median cusps. Only a faint posterior median cusp 1 appears infrequently. This contrasts with M4732d from Ban Na Sai (Tassy *et al.*, 1992: 519), which displays both posterior median conule 1 and anterior median conule 2.

TF 2648, 2650 and 2651 and TF 6283 (Fig. 6G–J) are, respectively, unpublished additional lower molars and DP4/ from Ban Na Sai. TF 2648 is a right M/3, in morphology very similar to the M/3 of the holotype of *S. nasaiensis* (M4732a) except slightly stronger mesoconelets and minor differences in the arrangement of the median conules on posterior lophids. TF 2650 is a smaller M/3 with weaker cusps. The mesoconelets are tiny and faintly lower than the main cones. They are symmetrical except on the second lophid where the posttrite mesoconelet is much smaller than the pretrite one. The fourth lophid is nearly rectilinear: the mesoconelets are only faintly anterior to the main cones. Lateral sulci remain oblique in occlusal view. The mesoconelets are anterior to the main cones on the fifth lophid. TF 2651 is a moderately worn broken lower molar with lophids 1–3 preserved. The lophs are organized in a similar way to those of M4732a. TF 6283 is a tetralophodont right DP4/. The second loph shows a pretrite half-loph with a remnant pretrite posterior median conule and a slightly posteriorly shifted main cone. The third loph has five conules, three of which are on the pretrite half-lophid. Numerous anterior median cusps are associated with loph 3. The last loph is composed of several finely divided cusplets.

The larger mesoconelets observed on TF 2648, together with the nearly rectilinear fourth lophid on TF 2650, help bridge a part of the morphological gap between the material from Ban Na Sai and Mae Moh. However, they do not provide a convincing continuum, as Mae Moh's *Stegolophodon* never displays any clearly anteriorly placed mesoconelets on lophids 4 and 5, while its mesoconelets are, even taking TF 2648 in account, always stronger than those of the Ban Na Sai material. This assertion is reinforced by the observation that the Ban Na Sai lower molars share symmetrical mesoconelets as well as a contact on lophids 2–5 between the posterior median conule and the main cone or, as in the case of TF 2648, a cusp slightly individualized from it. In contrast, in Mae Moh's sample, the lower mesoconelets are very often asymmetrical and the posterior median conule is nearly always in contact only with the pretrite mesoconelet. In addition, the DP4/ of Ban Na Sai differs from those of Mae Moh by the conservation of a partial pretrite trefoil on loph 2.

It thus appears that the *Stegolophodon* from Mae Moh is, as stated by Tassy *et al.* (1992), distinct at the species level from *S. nasaiensis*. We agree with Tassy *et al.* (1992) in judging the species of Ban Na Sai as more primitive than *S. praelatidens*.

Other Asian Stegolophodon: The Mae Moh *Stegolophodon* differs from *S. cautleyi* (Neogene, Myanmar) by the absence of median conules on upper molars; from *S. pseudolatidens* (middle Miocene, Japan) by larger mesoconelets and rectilinear posterior lophids on M/3; from the holotype of *S. stegodontoides* and the material associated with this species by Tassy (1983c) under the name *S.* cf. *Stegodontoides* by weaker cusps, absence of supplementary cusps on the pretrite half-lophs, and narrower upper molars; from *S. progressus* (Neogene, Myanmar) by narrower upper molars, absence of median conules and accessory crests in upper molars; and from the other large *Stegolophodon* of the Late Miocene of Yunnan (China), Myanmar and Tha Chang (Thailand) by fewer lophs on M3/3, weaker conules, and small and proportionally narrower molars (Tobien, 1978; Tassy, 1983c; Saegusa, Thasod & Ratanasthien, 2005). The unique specimen of *S. hueiheensis* (middle Miocene, China) is too worn to allow a serious comparison with the Thai material.

These comparisons do not produce any satisfactory match between the Mae Moh *Stegolophodon* and other Middle Miocene species of the genus. Hence, it appears justifiable to re-erect the species created by Koenigswald, *S. praelatidens*. We retain the holotype selected by Koenigswald and propose an emended diagnosis and a new list of referred material (see below).

The Stegolophodon of Mae Teep: Buffetaut *et al.* (1988) described remains of *Stegolophodon* from the locality of Mae Teep. P/4s are close in morphology to some specimens of *S. praelatidens* with an enlarged second lophid, presence of an enlarged median cusp, mesoconelet and bicuspid talon. However, the Mae Moh sample demonstrates that most of these feature are variable. The molar fragment has slightly anteriorly placed mesoconelets. The anterior placement of the mesoconelets is marked in *S. nasaiensis* but absent or occasional and very weak on *S. praelatidens*. As a result, it is difficult to attribute this small fragment to either of the two species. The lower tusks are straight in lateral and dorsal views with a dorsal longitudinal groove. Such morphology is compatible with the observed variation of *Stegolophodon praelatidens*.

The similarities of the Mae Teep P/4 with those of *S. praelatidens* favour an identification as *S.* cf. *praelatidens*. The open nomenclature is conserved in this case as the fragmentary nature of the material renders comparisons uncertain.

Systematics of the Mae Moh Stegodontid

Family Stegodontidae Osborn, 1918
Genus *Stegolophodon* Schlesinger, 1917
Type species: Stegolophodon latidens Clift 1828
Stegolophodon praelatidens Koenigswald 1959

Synonymy:

Stegolophodon sp. – Ginsburg & Tassy, 1985: 18, 20.

Stegolophodon cf. *latidens* – Tassy *et al.*, 1992: 515, 516, 519.

Holotype: TF 251, fragment of M/3 (Koenigswald, 1959, fig. 1)

Type locality: Mae Moh coal mine.

Referred material: Mae Moh: TF 251.1 molar fragments, TF 253.9 posterior part of a left M3/ and upper molar fragment; M4733f left M/3, M4733d first loph of an upper molar, TF 6276 individual with right M/2-M/3 (TF 6276a; Fig. 5F), fragment of left M/3 (TF 6276b), left M/2 (TF 6276c) and right lower tusk (TF 6276d; Fig. 6B); TF 6271 individual with left hemimandible with M/3 (TF 6271a; Fig. 5A1), left M/2 (TF 6271b), right hemimandible with M/3 (TF 6271c; Fig. 5A2/A3), right M/2 (TF 6271d), left M2/ (TF 6271e), left M3/ (TF 6271f; Fig. 5C), right? lower tusk (TF 6271g; Fig. 6A), upper tusk fragment (TF 6271h; Fig. 6D); TF 6272 left M/1 or M/2 (Fig. 5B), TF 6274 left M?3/ (Fig. 5D), TF 6275 left M/3 (Fig. 5E), TF 6277 right P4/ (Fig. 5G), TF 6278 right P/3-P/4 (Fig. 5H), TF 6279 right P/4 (Fig. 5I), TF 6280 right lower tusk (Fig. 6C), TF 6281 right DP4/ (Fig. 6E), TF 6282 right DP/4 (Fig. 6F), plus many other specimens stored at the Department of Mineral Resources. Tha Chang: RIN 804 right M3/ (specimen stored at the Northeastern Research Center and Museum for Petrified Wood and Mineral Resources, Nakhon Ratchasima).

Emended diagnosis: Primitive *Stegolophodon* with four loph(id)s on DP4, M1, M2 and five loph(id)s on M3. Molars with moderate enamel thickness (3–6 mm), brachyodonty (height index = 45–65) and laminar frequency (2.3–4.1 for M3) for a stegodontid. Rare cement deposits in the posterior valleys. Rectilinear loph(id)s made of generally four bulbous cusps of equal size (except often reduced or even absent posttrite mesoconelet on lower molars). Distinct median sulcus and lateral sulci. Lower molars slighty concave with persistent posterior median conules mostly in anterior valleys. Anterior median conules rarely present except on the first loph. Upper molars slightly convex with absent median conules except anterior conule 1 and infrequent posterior conule 1. Probable mainly antero-posterior mastication. At least P/3, P/4 and P4/ conserved. Upper tusks rectilinear or slightly curved ventrally in lateral view with maintained lateral enamel band. Persistant lower tusks generally straight in dorsal and ventral views and slightly concave dorsally. Section ovoid to piriform with a longitudinal flattening or groove. Corpus of the dentary with moderately deflected anterior portion (40°), one or two foramen mentale. Supposedly unshortened symphysis. Massive ascending ramus. Large masseteric fossa.

Differential diagnosis: Stegolophodon praelatidens differs from *S. nasaiensis* and *S. pseudolatidens* by larger mesoconelets and rectilinear posterior lophs; from *S.* cf. *stegodontoides* by smaller size, smaller conules, narrower molars and fewer cusps per loph(id); from *S. latidens* by wider valleys and absence of median conules on upper molars; from *S. progressus* by narrower upper molars, absence of median conules and accessory crests on upper molars; from late Miocene forms of Tha Chang, Myanmar and Yunnan by smaller size, fewer lophs and often weaker cusps on molars.

Affinities: As detailed by Tassy (1983c: 318–322), *Stegolophodon* is problematic because the type species, *S. latidens*, as well as several other species of the genus are defined on fragmentary material of poorly known stratigraphic and geographical provenance. Saegusa *et al.* (2005) attempted to build a classification of *Stegolophodon* mainly based on organization of molar cusps. As emphasized by these authors, the poorly known intraspecific variability of most *Stegolophodon* species limits this approach. Thus, the following paragraph, which discusses the phylogenetic relationships of *S. praelatidens*, essentially expresses hypothesis to be tested in the future.

A local evolution of *S. praelatidens* from *S. nasaiensis* by enlargment of the mesoconelets, acquisition of rectilinear poterior lophs and reduction of the median conules on upper molars is possible but cannot be demonstrated here because these forms do not share obvious apomorphous traits. Contrary to the proposition of Koenigswald (1959), *S. latidens* and *S. praelatidens* probably do not belong to a single lineage: even if the lectotype of *S. latidens* appears more derived than *S. praelatidens* by having broader teeth with higher laminar frequency, it displays central conules on upper molars and a strong posterior shift of the pretrite main cone. These primitive features [see Saegusa *et al.*'s (2005) discussion of the latter trait], not maintained in *S. praelatidens*, render the *S. Praelatidens*–*S. latidens* lineage hypothesis weakly parsimonious. The relationships between *S. praelatidens* and other large *Stegolophodon* of the Late Miocene of southern Asia remain unclear. For instance, *S.* cf. *stegodontoides* exhibits derived upper molars (wide, narrow valleys, blunt cones) that would allow it to be a possible descendant of *S. praelatidens*. Nonetheless, a lower molar of this species (Tassy, 1983c: pl. 7, fig. 6) displays primitive features that are absent or rare on those of *S. praelatidens*, such as the conservation of a pretrite trefoil on lophid 2 and a frequent contact between the pretrite main cone and the posterior median conule. *Stegolophodon praelatidens* and *S.* cf. *stegodontoides* might thus belong to different lineages. Some large *Stegolophodon* of the Late Miocene of Yunnan (China), Myanmar and Tha Chang (Thailand) (see Saegusa *et al.*, 2005) are also potential descendants of *S. praelatidens*. Unfortunately, they are significantly more derived than the middle Miocene species with particularly a 6th loph of M3/3 and extremely reduced lower median conules so that only intermediate forms could reveal a possible lineage.

DISCUSSION AND CONCLUSIONS

The proboscidean fauna of the middle Miocene of Thailand comprises four elephantoids: two stegodontids, *Stegolophodon nasaiensis* and *S. praelatidens*, a trilophodont gomphothere, *Gomphotherium* cf. *browni*, and a tetralophodont gomphothere, *Tetralophodon* cf. *xiaolongtanensis*. We add to this list the rare *Deinotherium* only described from the Pong basin. Never more than two taxa are associated at any one site: *Stegolophodon praelatidens* and *Gomphotherium* cf. *browni* in Mae Moh, *Stegolophodon nasaiensis* and *Gomphotherium* cf. *browni* in Ban Na Sai. The presence of two primitive stegodontids and a

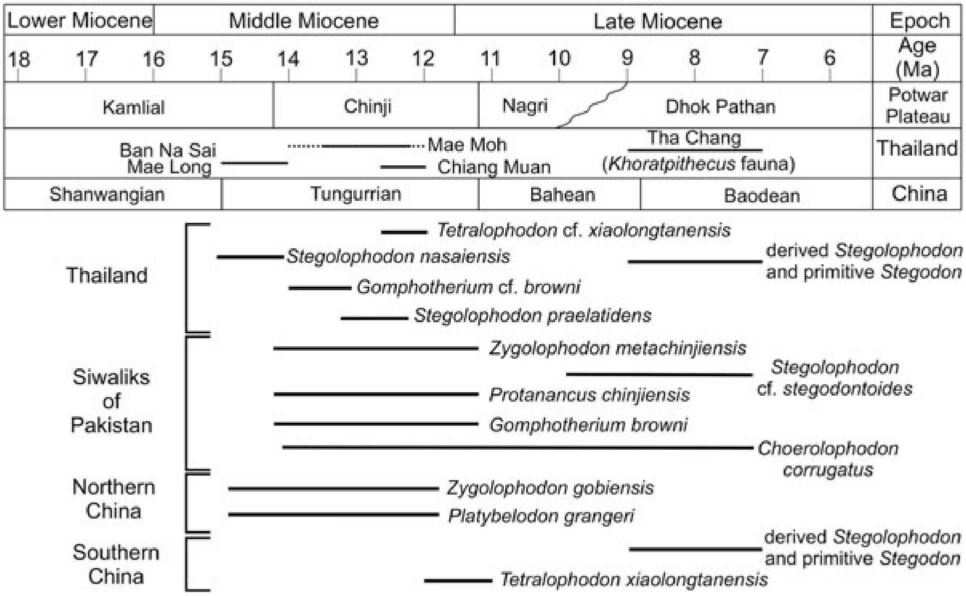

Figure 7. Chronostratigraphic distribution of the main proboscidean species cited in the text. Thailand: age of Mae Moh from Benammi *et al.* (2002) (full line) and P. Coster, M. Benammi, Y. Chaimanee, O. Chavasseau, E.G. Emonet & J.J Jaeger (unpubl. data) (dashed line). Age of Tha Chang (*sensu Khoratpithecus* fauna) from Chaimanee *et al.* (2004). Age of Ban Na Sai, Mae Long and Chiang Muan, this paper. Potwar plateau of the Siwaliks of Pakistan: stratigraphic chart from Barry *et al.* (2002), species ranges from Tassy (1983a, b, c) recalibrated with the scale of Barry *et al.* (2002). China: data from Tobien *et al.* (1986), Qiu (1990), Deng (2006) and Saegusa *et al.* (2005).

tetralophodont gomphothere in the middle Miocene of Thailand reflects that south-east Asia probably played an important role in the early diversification of tetralophodont proboscideans. South-east Asia might have been the centre of origin of the Stegodontidae as mentioned by Saegusa (1996).

The Thai fauna appears endemic when compared with other Asian faunas from the middle Miocene with two stegodontids having been only found in Thailand. The most widespread taxa of Pakistan's middle Miocene are the mammutid *Zygolophodon metachinjiensis*, the amebelodont *Protanancus chinjiensis*, the choerolophodont *Choerolophodon corrugatus* and the gomphothere *Gomphotherium browni* (Tassy, 1983a, b; Fig. 7). The three first taxa are apparently not represented in the middle Miocene of Thailand, which points to obvious faunal dissimilarities. However, the recognition of *G.* cf. *browni* in northern Thailand denotes biogeographical affinities with Pakistan. The presence in Chiang Muan of *Tetralophodon* cf. *xiaolongtanensis* shows clear links with the fauna of southern China. However, the middle Miocene localities of northern China have yielded a very different fauna dominated by *Zygolophodon*, the amebelodont *Platybelodon* and supposedly endemic *Gomphotherium* species (Tobien *et al.*, 1986; Tobien, Chen & Li, 1988; Fig. 7).

The stegodontids might be of potential biochronological interest in southern Asia: *Stegolophodon nasaiensis* is more primitive than *S. praelatidens*, which is itself more primitive than *S.* cf. *stegodontoides* and other late Miocene forms. Ban Na Sai was considered as early middle Miocene in age by Tassy *et al.* (1992): according to them, this locality is stratigraphically below the vertebrate site of Mae Long, dated between 18 and 16 Ma by Mein & Ginsburg (1985). By contrast, Tassy *et al.* (1992) gave a middle to late middle Miocene age to Mae Moh. Later, Ducrocq *et al.* (1994) proposed a 16–14 Ma range for the localities of northern Thailand and placed Ban Na Sai around 16 Ma. We agree with Tassy *et al.* (1992) in considering that the more primitive *Stegolophodon* of Ban Na Sai probably indicates an older age than that of Mae Moh for this locality. However, we believe that the difference in age between these two localities is less substantial than that proposed by Tassy *et al.* (1992) and closer to that estimated by Ducrocq *et al.* (1994). Indeed, both localities yielded the suid *Conohyus thailandicus* (Ducrocq *et al.*, 1997; Chaimanee *et al.*, 2007) and *Gomphotherium* cf. *browni*. In addition, the rodent fauna of Mae Moh, comprising *Neocometes* cf. *orientalis* and *Prokanisamys benjavuni*, resembles that of Mae Long (Chaimanee *et al.*, 2007). The late Miocene *Stegolophodon* are easy to distinguish from the middle Miocene forms with their broader molars, blunter cusps and eventually additional loph(ids). For instance, *Stegolophodon* cf. *stegodontoides*, whose upper molars are clearly more derived than those of the middle Miocene species, is restricted to the Late Miocene deposits of Pakistan (*c.* 10–7 Ma; Fig. 7). The often poorly known anatomy and intraspecific variation of the species of *Stegolophodon*, which handicap the identification of lineages, is a limit to the biochronological use of Stegodontidae. Note that the area of Tha Chang (north-eastern Thailand), known for its late Miocene hominoid-bearing locality (Chaimanee *et al.*, 2004), seems to have recorded *Stegolophodon praelatidens*. This taxon is rare (one molar) and mixed in the collections with specimens of clearly more derived species. Two possibilities arise from this occurrence. The Tha Chang area, which is known to encompass late Miocene to Pleistocene assemblages, yielded a middle Miocene fauna as claimed for instance by Nakaya *et al.* (2002). Another possibility is that *S. praelatidens* had a long stratigraphic range and persisted until the late Miocene. In this case, the biochronological use of this species would be seriously limited. A similar problem is questioned by the rare occurrence in the Tha Chang area of *Gomphotherium* cf. *browni*. Unfortunately, the lack of provenance and stratigraphic control on most of the Tha Chang proboscidean specimens prevent us from solving this issue.

Tetralophodon occurs in Thailand only from the lower lignite level of the Chiang Muan mine. Suganuma *et al.* (2006) proposed an age of *c.* 13 Ma for this stratum. Thus, *Tetralophodon* may have appeared earlier in Asia than in Europe where it is first recorded in the latest middle Miocene (Göhlich, 1998). Considering the data of Suganuma *et al.* (2006), the lower lignite level of Chiang Muan may be contemporaneous with the K and Q levels of Mae Moh, which agrees with the occurrence of *Conohyus* in both sites (Pickford *et al.*, 2004; Chaimanee *et al.*, in press). However, the absence of *Tetralophodon* from Mae Moh, a site where proboscidean fossils are abundant, cannot be justified by sample bias. It is important to note that, despite intensive fieldwork in Mae Moh, no hominoid fossils have been collected. This absence points to possible ecological differences between Chiang Muan and Mae Moh. Nevertheless, the short distance that separates these sites (approximately 100 km) does not encourage us to favour a hypothesis of an ecological bias. A slight difference in age between the two sites [Chiang Muan being probably younger (Pickford *et al.*, 2004)] associated with ecological changes is the hypothesis we favour to explain this faunal discrepancy.

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