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C. R. Palevol 2 (2003) 261–268



Systematic Palaeontology
(Vertebrate Palaeontology)

Occurrence of the anthracotheriid *Brachyodus* (Artiodactyla, Mammalia) in the early Middle Miocene of Thailand

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Received 20 February 2003; accepted 6 May 2003

Presented by Yves Coppens

Abstract

Remains of *Brachyodus* cf. *onoideus* from the Ban Na Sai Basin (Thailand) are described. They correspond to the first occurrence of that genus in South Asia, and might document the latest record of the genus in the Old World. *Sihongotherium* from the Middle Miocene of eastern China is likely a representative of *Brachyodus* that was misinterpreted. **To cite this article:** S. Ducrocq et al., *C. R. Palevol* 2 (2003).

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Résumé

Présence de l'anthracothère *Brachyodus* (Artiodactyla, Mammalia) dans le Miocène moyen de Thaïlande. Des restes provenant du bassin de Ban Na Sai, en Thaïlande, sont décrits et attribués à l'Anthracotheriidae *Brachyodus* cf. *onoideus*. Ce genre existait en Asie du Sud-Est pendant le Néogène, et les fossiles de Ban Na Sai représentent probablement les derniers témoins de cette forme dans l'Ancien Monde. *Sihongotherium sihongense*, un anthracothère du Miocène moyen de Chine orientale, est certainement une espèce de grande taille du genre *Brachyodus*. **Pour citer cet article :** S. Ducrocq et al., *C. R. Palevol* 2 (2003).

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Keywords: Anthracotheriidae; *Brachyodus*; Middle Miocene; Asia

Mots clés : Anthracotheriidae ; *Brachyodus* ; Miocène moyen ; Asie

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Version française abrégée

Introduction

Le Nord de la Thaïlande compte sept localités fossilifères tertiaires ayant livré des restes de mammifères, dont l'étude a conduit à proposer des âges compris entre 16 et 14 Ma pour ces faunes [3, 4]. Parmi ces localités, le sous-bassin de Ban Na Sai [12], situé au sud du bassin de Li (Fig. 1) n'a livré que de grands mammifères : Rhinocerotidae, Suidae, proboscidiens [4, 5, 13]. La présence du genre *Brachyodus* n'y avait été que citée [7], ainsi qu'à Huai Siew (bassin de Pong), sans toutefois qu'aucune description ou figuration n'ait été publiée.

Les Anthracotheriidae sont bien diversifiés dans le Néogène du Sud de l'Asie [10], comme cela avait déjà été mis en évidence par les anciens auteurs [6]. Dans cette note, nous décrivons des restes dentaires (principalement des dents de lait) provenant de Ban Na Sai, pouvant être attribuées au genre *Brachyodus*. Cela nous conduit également à étendre la répartition stratigraphique de ce genre au Miocène moyen en Asie du Sud-Est et à remettre en question le statut taxonomique d'une forme chinoise contemporaine [8]. Enfin, le spécimen attribué à *Brachyodus hui* et décrit dans le lignite oligocène de Chine orientale [14] appartient certainement à un genre plus primitif.

Systématique

Ordre Artiodactyla OWEN, 1848

Famille Anthracotheriidae GILL, 1872

Brachyodus cf. *onoideus* (Gervais, 1859)

Le matériel de Ban Na Sai est constitué principalement de dents déciduales (?M² gauche, D⁴ droite, D⁴ gauche, fragment de maxillaire droit avec D¹–D², D³ droite, D₂ droite, et DI₁ droite). Tous les spécimens appartiennent à un même individu (Fig. 2) et sont déposés dans les collections du Department of Mineral Resources à Bangkok.

Description. D¹ et D² sont biradiculées. D¹ est triangulaire en vue latérale, avec une face labiale plane et une face linguale convexe. La prémolaire présente une crête mésiale et une autre distale, qui toutes deux descendent de l'apex vers la base de la couronne. Un cingulum très faible en longe la face labiale. D² est plus grande, plus massive, avec une partie distale plus large. Deux crêtes mésiales (une labiale et une linguale)

descendent de l'apex pour rejoindre respectivement les bords mésiolabial et mésiolingual de la couronne. La crête distale vient se connecter à un fort épaulement sur le coin distolabial de la dent. La partie postérieure de la dent s'élargit pour former un bassin. D³ présente une structure générale reconnaissable : une cuspidé sur le lobe mésial, une à la jonction entre le lobe mésial et le lobe distal, et deux sur le lobe distal. Les extrémités labiales des vallées transverses ne sont pas oblitérées par des styles distincts, mais plutôt par la jonction des crêtes mésio- et distolabiales des tubercules. La dent est ceinturée par un cingulum faiblement développé. La D⁴ présente une morphologie similaire à celle des molaires supérieures définitives, à l'exception de la crête mésiolinguale du métaconule et d'un cingulum lingual un peu plus forts. La molaire supérieure (M² ?) est typiquement pentacuspidée et sélénodonte, et ses tubercules externes ont une muraille labiale plane. Le protoconule est bien différencié et accolé au protoconne, de sorte que la muraille antérieure de la dent est continue sur ses deux tiers. Le métaconule possède deux crêtes mésiolabiale et distolabiale, et ne montre pas la crête mésiolinguale présente sur la D⁴. La muraille labiale est en « W », avec un parastyle et un mésostyle forts, qui ne forment pas de boucle. Le cingulum labial est étroit à la base des cuspidés labiales, mais il s'élargit et se renforce sur les faces mésiale et linguale de la dent. Les cuspidés sont inclinées lingualement, ce qui rétrécit la surface occlusale.

La D₂ est biradiculée, triangulaire en vue latérale, avec une face labiale convexe et une face linguale concave. Trois crêtes sont visibles : une mésiale, qui descend le long du bord antérieur de la couronne, et deux distales, qui divergent près de l'apex en encadrant une forte dépression, la crête linguale dirigée distolingualement et la crête labiale qui joint la partie postérieure de la couronne. Il n'existe pas de talonide. L'incisive est spatulée, avec son apex légèrement courbé latéralement. La face labiale est convexe, et la face linguale est plane, avec un sillon qui part de la base de la couronne et s'élargit vers son sommet. Il n'y a pas de gonflement à la base de la couronne (Tableau 1).

Discussion

L'âge de 14–15 Ma attribué à la faune de Ban Na Sai est important, car cela correspond à une période

d'échanges fauniques entre l'Afrique et l'Eurasie [4]. Bien que les anthracothères aient été relativement diversifiés en Asie pendant le Néogène, aucun ne peut être rapproché de la forme de Thaïlande. *Telmatodon*, *Gonotelma*, *Hemimeryx*, *Afromeryx* et *Libycosaurus* possèdent des molaires supérieures tétratuberculées, *Parabrachyodus* possède des dents moins sélénodontes et dont les styles des molaires supérieures forment des boucles, et *Sivameryx* présente des styles plus développés et un protoconule réduit. La présence de *Brachyodus* avait déjà été suggérée en Thaïlande [7]. Cependant, *B. onoideus* d'Europe possède des molaires plus larges que longues aux styles et aux cingulum plus développés, alors que les formes africaines *B. depereti*, *B. mogharensis* [11] et *B. aequatorialis* [9] se distinguent par leur plus grande taille, la présence de cément, de styles plus développés et d'un bord labial moins cintré aux molaires supérieures. *B. trofimovi*, du Miocène inférieur du Kazakhstan [1], présente également un cingulum et un protoconule plus faibles, ainsi qu'un métastyle plus développé que chez la forme de Ban Na Sai. *B. onoideus* [2] serait donc la forme la plus proche morphologiquement du taxon de Thaïlande et, en l'absence de matériel supplémentaire, nous référons donc la forme de Ban Na Sai à cette espèce. D'autre part, le genre *Sihongotherium* décrit dans le Miocène inférieur/moyen de Chine orientale [8] semble morphologiquement très proche de la forme de Thaïlande, à l'exception de sa plus grande taille, mais les caractères invoqués par les auteurs pour le distinguer de *Brachyodus* ne sont pas, à notre avis, assez diagnostiques pour justifier l'existence d'un nouveau genre. Pour cette raison, nous considérons qu'en l'absence de matériel supplémentaire, *Sihongotherium sihongense* est une grande espèce asiatique du genre *Brachyodus*.

Le *Brachyodus* de Ban Na Sai représenterait donc la preuve la plus orientale de ce genre en Asie, et le plus récent témoin de cet anthracothère dans l'Ancien Monde. *Brachyodus hui*, de l'Oligocène inférieur de Chine orientale, [14] appartient certainement à un genre distinct, plus primitif. L'identification de *Brachyodus* ne remet pas en question l'âge Miocène moyen attribué à Ban Na Sai, mais elle permet de douter de la validité du genre *Sihongotherium* dans le Miocène inférieur–moyen de Chine. *Sihongotherium sihongense* serait en fait une espèce de grande taille du genre *Brachyodus*.

1. Introduction

The geological survey of continental basins in northern Thailand has led to the discovery of several mammalian assemblages in that area. All localities from northern Thailand occur in a time span ranging from about 16 to 14 Ma [3, 4]. In the southern part of Li basin, the Ban Na Sai Sub-basin is elongated along an east–west axis and located 18 km southwest of Amphoe Li (Fig. 1). Sediments in the Ban Na Sai sub-basin consist mainly of marlstones, calcareous mudstones and claystones, shales and coal beds [12]. The vertebrate fossils have been collected in a 1- to 7-m-thick lignite seam, and no microfauna has been recovered yet from the locality. The large mammals are represented by a rhinocerotid close to *Gaiotherium*, a suid (*Conohyus thailandicus*), a proboscidean (*Stegolophodon nasaiensis*), and an anthracothere [4, 5, 13]. Curiously, anthracothere remains are not very abundant in the Miocene localities of northern Thailand, and the most diversified ungulates are rhinos, ruminants, and suids [4]. The only known anthracotheriid remains have been reported from the Huai Siew locality (Pong Basin) and from Ban Na Sai (Li Basin),

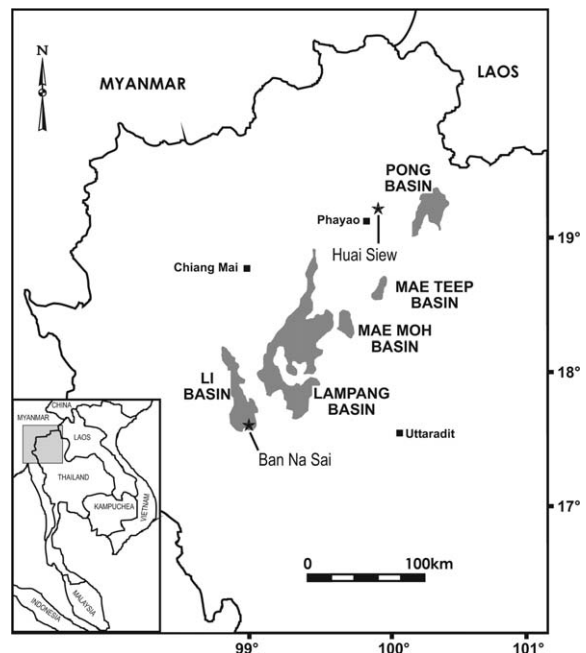


Fig. 1. Location map of Ban Na Sai sub-basin in northern Thailand. Fig. 1. Carte de localisation du sous-bassin de Ban Na Sai, dans le Nord de la Thaïlande.

and they have been attributed to a middle size species of the genus *Brachyodus* [7], but they were never figured or described.

Several cheek teeth belonging to a single juvenile middle-sized anthracothere have been discovered in the lignite beds of the Ban Na Sai locality. Although most of them are deciduous teeth, their morphology is very close to that of known milk teeth of *Brachyodus*. The anthracotheriidae are highly diversified during the Miocene in Asia, as Pickford pointed out [10], but their fossil record occurs mainly in the western part of the continent (India and Pakistan), as Forster Cooper previously demonstrated [6]. The discovery of the Miocene anthracothere in northern Thailand allows us to illustrate, for the first time, remains of *Brachyodus* in the Neogene of South Asia and to extend the geographical and stratigraphical range of that genus to Southeast Asia. It also led us to challenge the taxonomical status of a contemporaneous Chinese form [8]. In addition, the specimen attributed to *Brachyodus hui* from the Early Oligocene of eastern China [14] very likely belongs to a distinct and more primitive genus.

2. Systematic description

Order Artiodactyla OWEN, 1848

Family Anthracotheriidae GILL, 1872

Brachyodus cf. *onoideus* (Gervais, 1859)

Referred specimens: left ?M² (TF 2964), right D⁴ (TF 2965), left D⁴ (TF 2991), fragmentary maxilla with right D¹-D² (TF 2966), right D³ (TF 2992), right D₂ (TF 2993), right DI₁ (TF 2994). All specimens belong to a single individual (Fig. 2), and are housed in the collections of the Department of Mineral Resources in Bangkok.

2.1. Description

Most of the teeth are fresh, with the exception of some worn deciduous teeth. A fragment of maxilla preserves D¹-D². Both teeth are two-rooted and the diverging roots can be seen in labial view. D¹ is a triangular tooth in lateral view, with a rather flat labial face and a convex lingual face. The tooth bears a mesial crest and a distal crest that both run from the apex down to the base of the crown. A very faint cingulum occurs on the labial face of the crown. D² is larger and

more massive with a wider distal part. Its lingual face is strongly convex. Two mesial crests (a labial one and a lingual one) run down from the apex and end on the mesiolabial and the mesolingual corner of the crown, respectively. The distal crest is distolabially directed and connects to a strong shelf on the distolabial corner of the tooth. The distal part of the premolar is basined and forms an enlarged talonid part.

D³ is a classical trilobed tooth, on which only the distolingual cusp is lacking. However, the general structure of the deciduous tooth (one cusp on the mesial lobe, one cusp at the junction between the mesial and the distal lobe, and two cusps on the distal lobe) is easily recognizable. The labial ends of the transverse valleys are not closed by distinct styles, but rather by the junction of the mesio- and distolabial crests of the cusps. The cingulum is weak around the tooth.

D⁴ displays a morphology that is identical with that of the other molars, with the exception of a slightly stronger mesiolingual crest on the metaconule, and of a weaker lingual cingulum.

The upper molar (M²?) is typically five cuspidate and selenodont, and its external cusps have a flat labial wall. The protoconule is well differentiated on fresh teeth, but it is appressed to the protocone, so that the anterior wall is continuous on about the two thirds of the molar width. The metaconule displays only two mesiolabial and distolabial crests, and it lacks the mesiolingual crest that occurs on the D⁴. Although they are fragmentary, the molars display a W-shaped labial wall with strong mesostyle and parastyle that do not form a loop. A narrow labial cingulum occurs at the base of the labial cusps, whereas it is wider and higher on the mesial and lingual faces of the teeth. The lingual cusps are lingually slanted, so that the occlusal plane is rather narrow. The enamel is strongly wrinkled.

The right lower premolar (D₂) has two roots. It is triangular in lateral view, labially convex and lingually concave. This tooth shows three main crests: a mesial one that runs down along the anterior edge of the crown, and two distal ones that diverge near the apex of the tooth, the lingual one running distolingually, and the labial one joining the posterior part of the premolar. A strong depression occurs between these two crests, and no talonid part is visible.

The incisor is small, spatulate, and its apex is slightly bent laterally. The labial face of the tooth is convex and its lingual face is flat with a furrow that

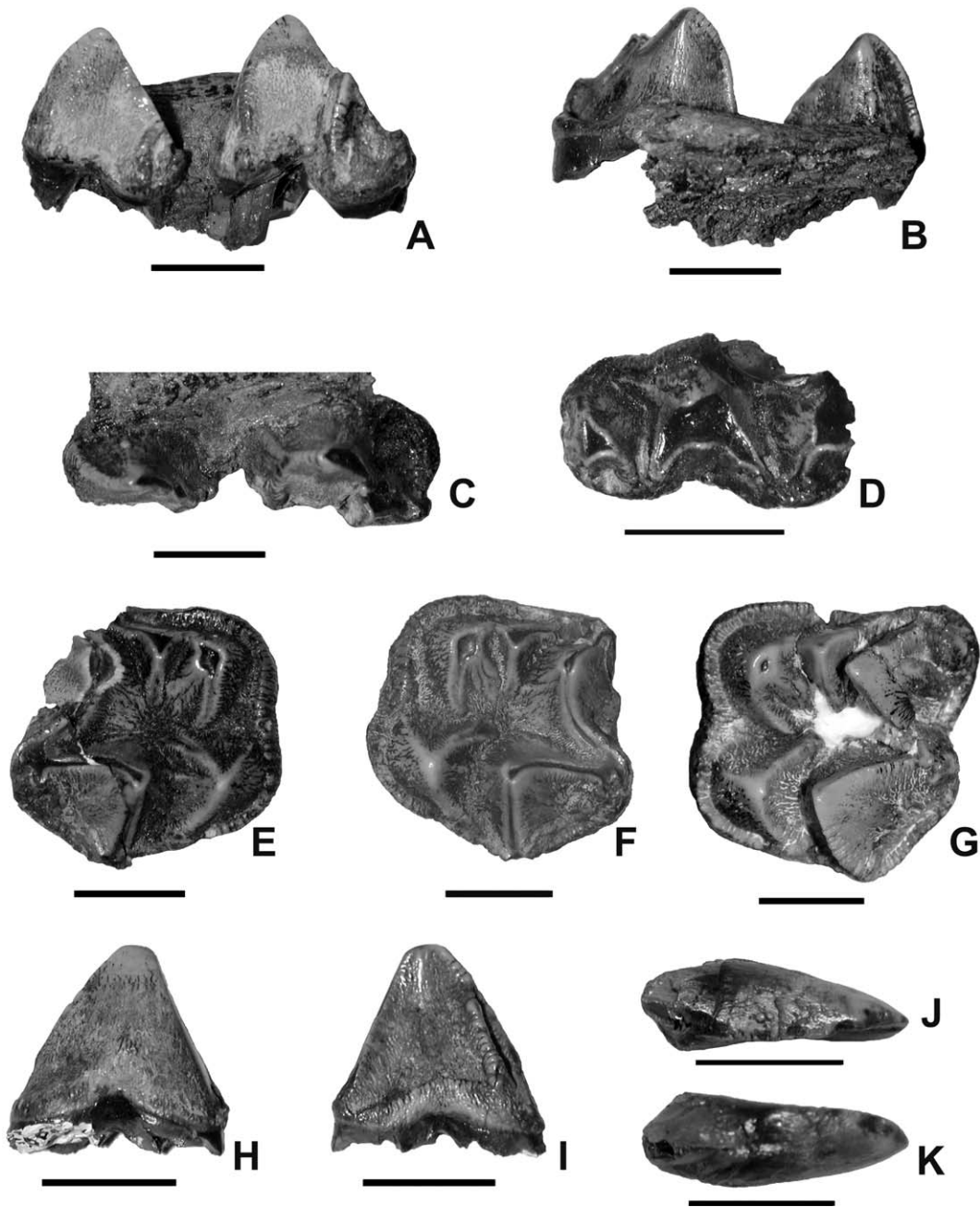


Fig. 2. *Brachyodus* cf. *onoideus* from Ban Na Sai. A–C: Right D¹–D² (TF 2966) in labial, lingual, and occlusal views; D: right D³ (TF 2992) in occlusal view; E: right D⁴ (TF 2965) in occlusal view; F: Left D⁴ (TF 2991) in occlusal view; G: Left ?M² (TF 2964) in occlusal view; H–I: right D₂ (TF 2993) in lingual and labial views; J–K: right DI₁ (TF 2994) in mesial and distal views. Scale bars = 10 mm.

Fig. 2. *Brachyodus* cf. *onoideus* de Ban Na Sai. A–C: D¹–D² droites (TF 2966) en vues labiale, linguale et occlusale ; D: D³ droite (TF 2992) en vue occlusale ; E: D⁴ droite (TF 2965) en vue occlusale ; F: D⁴ gauche (TF 2991) en vue occlusale ; G: ?M² gauche (TF 2964) en vue occlusale ; H–I: D₂ droite (TF 2993) en vues linguale et labiale ; J–K: DI₁ droite (TF 2994) en vues mésiale et distale. Échelles = 10 mm.

runs from the base of the crown and enlarges towards its summit, giving a slightly concave shape to the lingual face. There is no swelling at the base of the lingual face, and the enamel is finely wrinkled (Table 1).

3. Discussion

Anthracotheriids are relatively well diversified in Asia during the Miocene. However, among the anthracotheres from the Siwaliks, several taxa can be easily distinguished from the Thai form by their upper molars, with only four cusps: *Telmatodon*, *Gonotelma*, and *Hemimeryx*. *Parabrachyodus* from Pakistan is about the same size than the Thai form, but it differs from it by its less selenodont teeth, its upper molars with a more loop-like mesostyle and with a protostyle in front of the protoconule. *Sivameryx* also displays distinct loop-like styles, well developed barrels on the labial faces of its labial cusps and a reduced protoconule. Finally, *Afromeryx* and *Libycosaurus* known in the Middle and Late Miocene of Africa, respectively, cannot be referred to the Thai species, mainly by their tetracuspidate upper molars.

Ginsburg [7] stated that *Brachyodus* was present in Huai Siew and Ban Na Sai, but no description or figuration of the Thai fossils was published. *Brachyodus onoideus* is similar to the specimen reported here, but some differences can be observed between both forms. The European species displays a stronger parastyle on its D⁴ and upper molars, a better-developed cingulum surrounding its D³, and a D₂ with a smaller talonid part. Also, in all species of *Brachyodus*, the

upper molars tend to be somewhat wider than long, whereas the only permanent molar we know for the Thai form (TF 2964) is as wide as long. Pickford [11] reported two species of *Brachyodus* in the Lower Miocene of Egypt (*B. depereti* and *B. mogharensis*), and *B. aequatorialis* is known from the Lower Miocene of East Africa [9]. *B. depereti* is much larger, while the upper molars of *B. mogharensis* display cementum in their labial folds, more massive parastyles, and more developed barrels on the labial cusps. Similarly, *B. aequatorialis* has a less waisted labial part between the parastyle and the mesostyle. It is unfortunately difficult to further compare the different species of *Brachyodus*, because most of the Thai material corresponds to deciduous teeth. A new species of *Brachyodus*, *B. trofimovi*, has been described recently from a Lower-Miocene locality from Kazakhstan [1]. However, it is considered as more primitive than the European species, and it clearly differs from the Thai form by its less developed cingulum and protoconule, and by its stronger metastyle. However, by its general morphology and size, the form described here more closely resembles *B. onoideus*, although the latter is slightly larger [2].

Sihongotherium is a genus that has been described by Liu & Zhang [8] from the late Early Miocene or early Middle Miocene of eastern China. This genus is only represented by its lower teeth and no morphological comparison can be made with the Thai material. The Chinese form is much larger than the Thai specimen, but its size is not incompatible with an attribution to *Brachyodus*, as the African species *B. depereti* (see [11]) displays a similar size. In addition, two out of

Table 1

Comparative tooth measurements (in mm) of *Brachyodus* cf. *onoideus* from Ban Na Sai, *B. onoideus* from Europe, and *B. aequatorialis* from Africa. Data from [2] for *B. onoideus* and from [9] for *B. aequatorialis*. Stars indicate estimate measurement.

Dimensions comparées (en mm) du matériel dentaire de *Brachyodus* cf. *onoideus* de Ban Na Sai, *B. onoideus* d'Europe et de *B. aequatorialis* d'Afrique. Données d'après [2] pour *B. onoideus* et [9] pour *B. aequatorialis*. Les astérisques indiquent des dimensions estimées.

	<i>B. cf. onoideus</i>		<i>B. onoideus</i>		<i>B. aequatorialis</i>	
	Max. length	Max. width	Max. length	Max. width	Max. length	Max. width
Right DI ₁ (TF 2994)	5.8	8.8	—	—	—	—
Right D ₂ (TF 2993)	15.9	9.3	19.0	11.6	—	—
Right D ¹ (TF 2966)	14.5	9.2	—	—	—	—
Right D ² (TF 2966)	18.4	12.4	15.9	12.3	—	—
Right D ³ (TF 2992)	24.7*	15.4*	31.9	22.1	19.0	17.0
Right D ⁴ (TF 2965)	24.0	24.5	23.6	27.5	30.0*	22.0
Left D ⁴ (TF 2991)	23.6	23.8	—	—	—	—
Left ?M ² (TF 2964)	28.5	28.7	38.2	42.3	32.0	36.6

three of the characters listed by Liu and Zhang (the large size and a crest that joins both anterior cusps on lower molars that is perpendicular to the long axis of the tooth) that are supposed to distinguish the Chinese form from *Brachyodus* are irrelevant. In *Brachyodus*, the metaconid and the protoconid are connected by a transverse crest (as in most anthracotheres) and therefore this feature cannot be diagnostic. Only the occurrence of a diastema between P₁ and P₂ might be an argument to distinguish the Sihong specimen from *Brachyodus*. However, the shortness of the diastema (10 mm according to Liu and Zhang) and the poorly preserved part of the lower jaw anterior to P₂ in the Chinese specimen lead us to cast some doubts about the exact configuration of the anterior tooth row. In the absence of additional material for that Chinese form, we prefer to consider it as a large Asian species of *Brachyodus*.

The 15–14 Ma age assigned to the Ban Na Sai mammal fauna [4] is important in the palaeobiogeographical story of the Old World, because it followed the collision of the African and Eurasian plates 21 to 18 Myr ago, allowing faunal exchanges between both landmasses. In that frame, a mixture of African and Eurasian mammals characterizes the Asia faunas during the Early Neogene. The age of the Ban Na Sai sub-basin was based on the study of the large mammals (rhinocerotids, suids, and proboscideans), and the comparison of their dental morphology with that of related forms from Europe and Siwaliks. However, the occurrence of *Brachyodus* together with the other mammal taxa in Ban Na Sai does not rule out the conclusions about the age that were previously proposed [3, 4].

4. Conclusions

Brachyodus from Ban Na Sai might represent the most eastern occurrence of that genus in the Old World. The fragmentary lower jaw formerly described in the Early Oligocene of eastern China and attributed to *Brachyodus hui* [14] is markedly smaller and more primitive than all species of *Brachyodus* and very likely belongs to a distinct genus. *Brachyodus* is known during the first half of the Miocene in Eurasia and Africa, and its occurrence in Ban Na Sai might represent the latest record of *Brachyodus* in the Old World. When more material is known, especially per-

manent dental remains, a specific attribution of that Thai form will be possible. We consider that *Sihongotherium sihongense* from the late Early or early Middle Miocene of eastern China (Jiangsu Province) is very likely a large species of *Brachyodus*. The identification of *Brachyodus* does not yield more accurate information about the age of Ban Na Sai mammal fauna, that is regarded as 14–15 Myr old. However, it does not challenge the early Middle Miocene age previously proposed. This anthracotheriid occurred in Southeast Asia during at least the Early–Middle Miocene, and it is likely that the anthracothere remains that have been cited from Huai Siew [7] also belong to the same form, both localities being of about the same age.

Acknowledgements

We thank M. Brunet and M. Pickford, who reviewed the manuscript and provided us with useful comments. This is publication No. 2003-044 of the ‘Institut des sciences de l’Évolution’ de Montpellier.

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