A NEW STUDY OF THE ANTHRACOTHERES (MAMMALIA, ARTIODACTYLA) FROM PONDAUNG FORMATION, MYANMAR: SYSTEMATICS IMPLICATIONS

by

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SUMMARY

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Mots-cles: Taxonomie, *Anthracotherium*, *Anthracokeryx*, *Siamotherium*, *Anthracohyus*, dimorphisme sexuel, Pondaung Formation, South East Asia.

Key-words: Taxonomy, *Anthracotherium, Anthracokeryx*, *Siamotherium*, *Anthracohyus*, sexual dimorphism, Pondaung Formation, South East Asia

ABSTRACT

Anthracotheres from the Pondaung Formation, Myanmar, are considered as one of the most primitive artiodactyl groups and they represent the oldest known record in the world. Thus, the understanding of this group has numerous implications for evolutionary biology and biochronological correlations. However, the systematics of these mammals has been interpreted in different ways, and the main debate focuses on the number of taxa represented in the Pondaung Formation. The revised taxonomy proposed here is mainly based on the relative development of the upper molar W-shaped ectoloph, system of crests and stylar cusps, and on body size. On the basis of these characters, they are classified into four genera including six different species. Two well-known genera, *Anthracotherium* and *Anthracokeryx,* are validated and more precisely diagnosed. *Anthracokeryx* possesses a better developed W-shaped ectoloph, system of crests and stylar cusps than *Anthracotherium*, which displays notable differences with the more derived representatives of this genus. Both of these Pondaung genera show evidence for sexual dimorphism. However, the incompleteness of fossil material fueled a debate concerning the status of two additional Pondaung anthracotheres, *Siamotherium* and *Anthracohyus*. The latter genus is of uncertain affinities, but it has been considered as a hippopotamid ancestor. Despite new material attributed to these two forms, additional discoveries are still required to establish their taxonomic status. The hypothesis that Southeast Asia was the centre of origin of the Anthracotheriidae is supported by the retention of numerous primitive dental characters in these taxa and by the antiquity of the Pondaung Formation, to which an age of 37 My is now generally accepted.

RESUME

Les anthracothères de la Pondaung Formation, Myanmar, sont considérés comme l'un des groupes les plus primitifs d'artiodactyles et représentent les plus anciens connus au monde. Ainsi, la compréhension du groupe a de nombreuses implications sur la biologie évolutive et les corrélations biochronologiques. Toutefois, la systématique de ces mammifères a été interprétée de différentes façons et le principal débat concerne le nombre de taxa représentés dans la Pondaung Formation. La révision taxonomique proposée ici est principalement fondée sur le developpement relatif de l'ectolophe en forme de W des molaires supérieures, le système de crêtes et de cuspides stylaires, et sur la taille du corps. Sur la base de ces caractères, ils sont classés dans quatre genres incluant six espèces différentes. Deux genres bien connus, *Anthracotherium* et *Anthracokeryx,* sont validés avec une diagnose plus précise. *Anthracokeryx* possède un ectolophe en forme de W, un sytème de crêtes et de cuspides stylaires mieux développé qu' *Anthracotherium* qui présente des différences notables avec les représentants plus dérivés de ce genre. Deux de ces genres de Pondaung montrent un dimorphisme sexuel évident. Cependant, le caractère incomplet du matériel fossile a alimenté le débat concernant le statut de deux anthracothères additionnels de Pondaung, *Siamotherium* and *Anthracohyus*. Ce dernier est d'affinités incertaines, mais il a été considéré comme un ancêtre des hippopotames. Malgré le nouveau matériel attribué à ces deux formes, des découvertes additionnelles sont nécessaires pour pouvoir établir leur statut taxonomique. L'hypothèse que l'Asie du sud-est était le centre d'origine des Anthracotheriidae est supporté par la rétention de nombreux caractères dentaires primitifs chez ces taxa et par l'ancienneté de la Pondaung Formation, pour laquelle un âge de 37 Ma est maintenant généralement accepté.

INTRODUCTION

The anthracotheriid artiodactyls represent one of the most abundant groups of mammals collected so far from the late middle Eocene Pondaung Formation in central Myanmar (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Ducrocq, 1999; Ducrocq et al., 2000a; Tsubamoto et al., 2000a, 2003a). The age of this formation was recently established by fission-track analysis of zircon crystals collected from a volcanic ash layer (Tsubamoto et al., 2002) and by study of the remanent magnetized field of sediments (Benammi et al., 2002). Both results converge in attributing an age of 37 Ma to those fossiliferous sediments, which corresponds to the late middle Eocene (Bartonian) of the standard stratigraphical time scale (Berggren et al., 1995). These geochronological assessments of age broadly agree with biostratigraphic results, which are mainly based on the comparable stage of morphological evolution to related taxa, especially the co-occurring genera of the anthracotheriid artiodactyl, *Anthracokeryx* and on amynodontid perissodactyls (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Bender, 1983; Holroyd and Ciochon, 1994, 1995; Ducrocq et al., 1995b, 1997b, 2000a). The anthracotheres have been largely collected in the middle part of the upper member of the Pondaung Formation, which is mainly exposed in the vicinity of the Pangan-Bahin-Mogaung area, Pondaung region in north-western part of central Myanmar (Soe et al., 2002; Soe, 2004). The recent collections of a large amount of new specimens of anthracotheres from this formation have led to renewed investigations of their systematics. In addition, they play an important role in establishing the biochronological correlation charts between the Palaeogene mammal faunas that occur in Asia, especially in China, Thailand, and Baluchistan as well as in Europe, North America and North Africa. They also represent one of the basic clues to reconstruct the palaeoenvironments of mammalian groups. A number of workers have already expressed their interpretations on the various aspects of Pondaung anthracotheres in an attempt to establish the age and correlations with other localities and to locate the places of origins and of initial radiation of the Anthracotheriidae (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Russell and Zhai, 1987; Holroyd and Ciochon, 1991, 1994, 1995; Ducrocq et al., 1995b, 1997b, 2000a; Tsubamoto et al., 2003a).

Anthracotheriid artiodactyls are known from Palaeogene deposits of Europe, North Africa, North America and Asia (Black, 1978; Ducrocq, 1995a, 1999; Kron and Manning, 1998). In Asia, they have been recorded from China, Thailand, Baluchistan and Myanmar, but their occurrences were first documented from the late middle Eocene Pondaung fauna of Myanmar (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Black, 1978; Ducrocq et al., 1997b). The anthracotheres from Myanmar have been primarily recognized by their diverse and primitive dental morphology by comparison with their counterparts in Asia, Europe, North America and North Africa and as the oldest taxa of this group since their original description. Thus, various opinions have arisen amongst scholars interested in the phylogeny of Artiodactyla, especially on the possible ancestors and descendants of anthracotheres. Firstly, some authors consider that anthracotheres have their origins in the Helohyidae. This was concluded from the dental morphology of the moderately specialized anthracothere, *Anthracokeryx tenuis* (formerly *A. ulnifer*) (Pilgrim, 1928, 1940; Colbert, 1938; Coombs and Coombs, 1977a, 1977b). The discovery of *Siamotherium,* a primitive anthracothere from Krabi, Thailand and Pondaung, Myanmar might support a new hypothesis on anthracothere origins. Anthracotheres may have originated directly from diacodexids because *Siamotherium* commonly preserves less apomorphic characters than those of helohyids and the diacodexids stand therefore as the closest sister-group of the Anthracotheriidae (Ducrocq, 1999).

Regarding their descendants, anthracotheres are often cited as potential ancestors of extant hippos (Colbert, 1935; Black, 1978; Gentry and Hooker, 1988; Thewissen et al., 2001), although Pickford (1983, 1989) suggested that hippos evolved from an Old World tayassuid stock. Molecular studies support the idea that Cetacea are deeply nested within Artiodactyla and favour a sister-group relationship between whales and hippopotamid artiodactyls (Gatesy et al., 1996; Gatesy, 1997; Montgelard et al., 1997; Nikaido et al., 1999). In addition, the oldest fossil whales and the cladistic analysis of their morphological characters reveal that cetaceans have evolved from early Artiodactyla (Thewissen and Hussain, 1993; Thewissen et al., 2001; Gingerich et al., 2001; Rose, 2001). *Anthracohyus,* one of the primitive anthracotheriid artiodactyls from the Pondaung Formation remains an enigmatic taxon, but it shows some similarities with primitive hippopotamids in its dental morphology and it is here considered as a possible remote ancestor for hippos (e.g. Gentry and Hooker, 1988).

Comparatively, the anthracotheres from the late Eocene of Krabi are represented by several different taxa: *Anthracotherium chaimanei*, *Anthracokeryx thailandicus*, *Siamotherium krabiense, Bothriogenys orientalis, Atopotherium bangmarkensis* and an Anthracotherinae gen. et sp. indet. but these genera commonly display more derived dental characters than those of Pondaung forms (Ducrocq et al., 1999, 2000a). Anthracotheriid artiodactyls also occur in several areas located in Southern and Eastern China during the middle-late Eocene to early Oligocene. The age of the sediments that have yielded the anthracotheres from China is almost equivalent and/or younger than the Pondaung and Krabi forms (Pilgrim, 1928; Colbert, 1938; Russell and Zhai, 1987; Holroyd and Ciochon, 1991, 1994, 1995b; Ducrocq et al., 1995, 1997b, 2000a; Tsubamoto et al., 2002, 2003a; Benammi et al., 2001, 2002). The author will only consider well documented genera such as *Heothema, Anthracothema* and *Anthracokeryx* and compare them with Pondaung and Krabi forms, because other genera were described from poorly known fossil specimens and their taxonomic status is still debated. But, recent and additional materials documenting the anthracotheres from China progressively enlighten the definition of those taxa and these data can also be provided to improve the biochronological correlation for the sediments bearing those mammalian faunas. *Heothema* from the late Eocene and early Oligocene localities of Southern China is characterized by a moderately developed W-shaped ectoloph, system of crests and labial stylar cusps. This genus includes the following species: *Heothema bellia*, *Heothema media, Heothema nanningensis, Heothema chengbiensis*, *Heothema angnsticalxia* and *Heothema youngi* (Tang, 1978; Zhao, 1981, 1983). Later in 1999, Ducrocq re-evaluated the various species of *Heothema* by comparison with the Krabi forms and with those forms from other areas and then, he discussed on the presence of a paraconid on lower molar of *Heothema*, which represents a distinct character to differentiate *Heothema* from *Anthracotherium* according to Tang (1978) and Zhao (1981, 1983). He stated that it is not a true paraconid and it only represents an anterostylid. Later, he assigned all species formerly referred to *Heothema* to two species in the genus *Anthracotherium*: *H. bellia*, *H. media,* and *H. nanningensis* were combined into *Anthracotherium bellia* and *H. chengbiensis*, *H. angnsticalxia* and *H. youngi* were included in *Anthracotherium chengbiensis* (Ducrocq, 1999). Tsubamoto et al. (2003a) reevaluated these taxa and referred them to *Heothema* on the basis of the following dental characters: more selenodont cusps on upper molars, strong crests on the lingual part of lower premolars, and molariform p4. They recognized a single genus including two species: *H. bellia* and *H. chengbiensis*. *Anthracokeryx gungkangensis* and *Anthracokeryx kwangsiensis* (Qui, 1977; Zhao, 1993) were also described from the late Eocene-early Oligocene Gongkang Formation (Guangxi Province). Both species probably correspond to only one form on the account of their very similar morphology and size. They were subsequently re-classified into a single species, *Anthracokeryx gungkangensis* (Tsubamoto et al., 2003a). *Anthracothema minima* and *Anthracokeryx sinensis* occur from the upper-most Eocene Yuanqu Shanxi, (Xu, 1962; Shi, 1989) and *Anthracokeryx dawsoni* has been recorded from the late Eocene Yuanqu, Shanxi, China (Wang, 1985). Later on, they were also synonymized into a single taxon (*Anthracokeryx sinensis*) after reanalysing dental morphology and tooth size (Tsubamoto et al., 2003a). Although some Chinese taxa have several distinct characters to justify a specific separation, Tsubamoto et al., (2003a) only retained a single taxon, *Anthracokeryx* in light of their generic revision of Pondaung anthracotheres using body size only. The present author prefers to use earlier classifications of these Chinese forms because they display a number of distinct characters that distinguish them from other taxa. A complete upper dentition of *Anthracokeryx birmanicus* was also recently unearthed from the middle-late Eocene Naduo formation of Guangxi, and it shows a well preserved, large, curved outwards and backward upper canine that strongly supports the occurrence of sexual dimorphism in anthracotheriid artiodactyls (Li and Chen, 2001), thereby confirming a much earlier assessment.

The specimens cited in this study have been collected in the Pondaung Formation, Myanmar but they are housed in three different places: in the Geological Survey of India, Kolkata (Calcutta), India (GSI); in the American Museum of Natural History, New York (AMNH); and in the National Museum of Myanmar, Yangon, Myanmar. The new specimens housed in the National Museum of Myanmar are denoted by the acronym of the name adapted from each locality that has yielded the vertebrate fauna. The acronym of the localities and occurrences of Pondaung anthracotheres are shown in fig. (1).

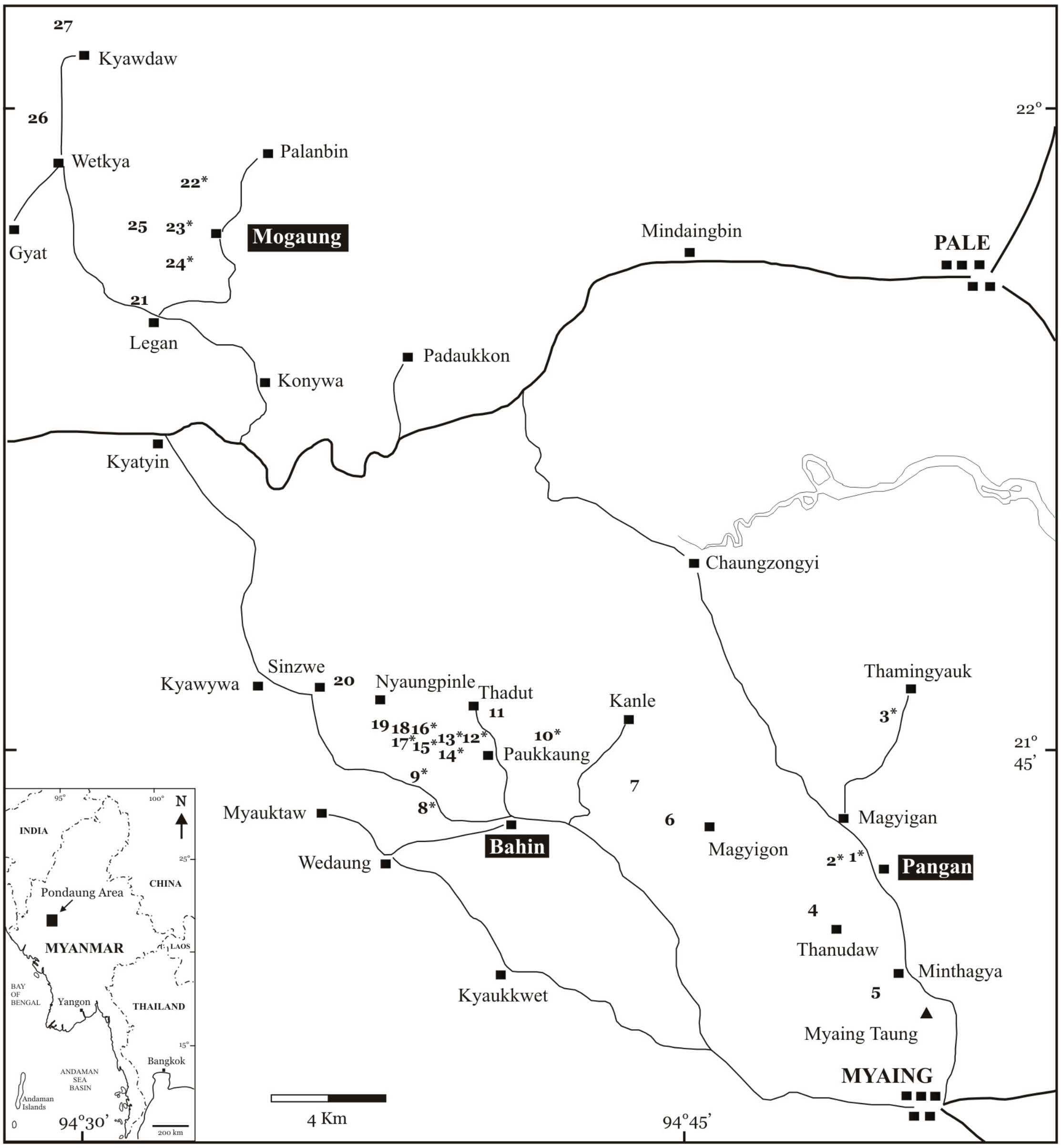

Figure 1.— Map showing the distribution of fossil collecting localities with their abbreviation in Pondaung area, Myanmar. (* fossil primates locality).

Pangan Area

1* - Pangan Kyitchaung (Pgn); 2*- Taungnigyin Kyitchaung (Tng); 3* - Thamineyauk Kyitchaung (Tmk); 4 - Thanudaw Kyitchaung (Tudw); 5 - Myinthagya Kyitchaung (Mta); 6 - Magyigon Kyitchaung (Mggn).

Bahin Area

7 - Kanle Kyitchaung (Kle); 8* - Sakantha Kyitchaung (Ska); 9* - Yarshe Kyitchaung (Yse); 10* - Paukkaung Kyitchaung N 11 (Pkg); 11 - Thadut Kyitchaung (Tdt); 12* - Paukkaung Kyitchaung N 3 (Pkg); 13* - Paukkaung Kyitchaung N 2 (Pkg); 14* - Paukkaung Kyitchaung N 12 (Pkg); 15* - Kyaukpyittar Kyitchaung (Pkg); 16* - Ayoedawpontaung Kyitchaung (Adg); 17* - Sabapondaung Kyitchaung (Spg); 18 - Aini Kyitchaung (Ani); 19 - Nyaungpinle Kyitchaung (Npe); 20 - Sinzwe Kyitchaung (Sze).

REMARK ON PREVIOUS SYSTEMATICS

The study of fossil mammals from the terrestrial Pondaung Formation in central Myanmar begun in the early decades of the 20th Century after the collection of G. de P. Cotter of the Geological Survey of India (Pilgrim and Cotter, 1916). This formation is since well known amongst the scholars because it has yielded rather rich and diverse mammalian communities among which the primitive anthropoid primates have deserved special attention (Pilgrim, 1927; Colbert, 1937, 1938; Szalay, 1970; Ba Maw et al., 1979; Ciochon et al., 1985, 2001; Jaeger et al., 1998, 1999, 2004; Chaimanee et al., 2000; Ducrocq, 2001; Takai et al., 2001, 2003; Egi et al., 2001, 2006; Ciochon and Gunnell, 2002a, 2002b; Gunnell et al., 2002; Shigehara et al., 2002; Marivaux et al., 2003; Kay et al., 2004; Beard, et al., 2005, 2007 in press). The Pondaung Formation has also yielded several primitive forms of various orders of mammals, which have been described and published in various journals or monographs: Artiodactyls (anthracotheriids: Holroyd and Ciochon, 1991; Ducrocq et al., 2000a; Tsubamoto et al., 2003a; anthracobunids: Ducrocq et al., 2000b; helohyids: Holroyd and Ciochon, 1995; Ducrocq et al., 1997a; ruminants: Metais et al., 2000, 2006; Tsubamoto et al., 2003b), Perissodactyls (brontotheriids: Holroyd and Ciochon, 2000; helaletid: Tsubamoto et al., 2000b; eomoropid: Remy et al., 2005: tapiromorph: Metais et al., 2006), Rodents (Dawson et al., 2003; Marivaux et al., 2005), and Creodont (Egi et al., 2004, 2005; Peigne et al., 2007).

In this work, the author study particularly concentrated on the re-examination and re-evaluation of the whole collection of Pondaung anthracotheres, including both new-collected specimens and old collections. Some scholars had previously studied these Pondaung anthracotheres, but their systematic results were conflicting (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Coombs and Coombs, 1977a; Holroyd and Ciochon, 1991; Ducrocq, 1999; Ducrocq et al., 2000a; Tsubamoto et al., 2003a). The author will only consider here the two most recent studies (Ducrocq et al., 2000a; Tsubamoto et al., 2003a) and he will emphasize some inconsistency concerning the generic distinctions that justified his detailed revision. After extensive comparative studies of the Krabi forms, Pondaung anthracotheres, Chinese taxa and some other European taxa, Ducrocq (1999, 2000a) recognized four genera: *Anthracotherium*, *Anthracokeryx, Anthracohyus* and *Siamotherium* among Pondaung anthracotheres. The first two genera include two species and the last two are monospecific. In this classification, some basic characters were used to separate the different taxa: presence of a straight preparacrista and postmetacrista, the position of V-shaped centrocrista, the presence of labial styles and the formation of the W-shaped ectoloph.

Tsubamoto et al., (2003a) recently reclassified the Pondaung anthracotheres and they regrouped all genera into one single taxon, *Anthracotherium* because according to these authors, the dental morphology of the Pondaung anthracotheres displays only subtle differences which fall within the range of interspecific variation. Thus, the *Anthracotherium* from Pondaung includes four species based only on body size differences. Tsubamoto et al., 2003a, also attributed the most primitive and smallest Pondaung anthracotheres, *Siamotherium pondaungensis* (Ducrocq et al., 2000a) that was assessed to the helohyid genus, *Pakkokuhyus* on the basis of occlusal matching of specimens (upper dentition of *Siamotherium* and lower dentary of *Pakkokuhyus*). They noted that *S. pondaungensis*, (Kdw-6), a right maxillary fragment with M2-3 (ref. in Ducrocq et al., 2000a) matched with the specimen of *Pakkokuhyus lahirii* (a right lower jaw with m1-3) that was firstly described by Pilgrim (1928) as *Anthracokeryx? lahirii*. Then, Holroyd and Ciochon (1995) redefined *Pakkokuhyus lahirii,* suggesting that the only difference with anthracotheres was the position of the hypoconulid on m3. In addition, Tsubamoto et al., (2003a) argued on the generic status of an additional uncommon Pondaung anthracotheres, *Anthracohyus* that according to them has no specific characters to differentiate it as another taxon. They referred it to the genus *Anthracotherium* considering that it corresponds to an unusual individual variation of the Pondaung *Anthracotherium.* Accordingly, they paid no attention to the basic dental characters such as development of diastema in anterior dentition and of the W- shaped ectoloph, system of crests and stylar cusps that are generally used to separate and to establish diagnosis among anthracothere taxa (Tsubamoto et al., 2003a). Thus, the present work will demonstrate that the development of W- shaped ectoloph, system of crests and stylar cusps should be used as a set of fundamental characters for the specific differentiation of primitive Pondaung anthracotheres and that these characters should also be prevalent in regard of body size.

As a result, the use of these dental characters leads to present a revised taxonomy of the Pondaung anthracotheres and to recognize four genera including six species. Two valid genera can be established by their relative development of W- shaped ectoloph, system of crests and stylar cusps on upper molars. They are *Anthracotherium* and *Anthracokeryx*, both genera including two distinct species. A right maxillary fragment with M2-3 (Kdw- 6) had allowed recognizing a new taxon, *Siamotherium pondaungensis*, so far considered as the smallest and most primitive Pondaung anthracothere (Ducrocq et al., 2000a). Although a few specimens were recorded in our new collections, they might support the taxonomic position of *S. pondaungensis*. Moreover, *Anthracohyus,* a primitive genus of Pondaung anthracothere, was erected on the basis of its distinct dental characters such as the absence of W- shaped ectoloph and labial stylar cusps, rectilinear centrocrista and less developed system of crests. *Anthracohyus* occurs in Pondaung and Krabi but it is still poorly known because of the insufficient material collected so far from Pondaung. A small number of additional specimens which were presumably referable to this genus have been recently recorded and they might provide further elements to re-examine its phylogenetic position in the order Cetartiodactyla. Unfortunately, the author hasn't examined the distinct cranial characters that have already been taken in account in small-sized Pondaung anthracotheres such as *Anthracokeryx tenuis* (Pilgrim, 1928; Colbert, 1938) because cranial material was not obtained in our recent collections. A number of canine teeth were handily encountered in the recent collections and they can be assigned to each individual taxon judging from their relative size differences recognized in *Anthracotherium* and *Anthracokeryx*. Field occurrences can also help to discriminate the canine teeth configuration in individual species because some specimens were collected in association with distinct dental elements such as upper and lower molar teeth that can be easily organized within a well defined species. But the evidence of sexual dimorphism in the primitive anthracotheres, *Siamotherium* and *Anthracohyus*, is still difficult to demonstrate from Pondaung forms because there have very few numbers of available specimens.

SYSTEMATICS

Molecular studies on the major extant Cetacea and Artiodactyla lineages, which include Ruminantia, Cetacea, Ancodonta, Tylopoda, and Suina indicate that cetaceans are included in paraphyletic artiodactyls. Molecular sequencing studies also support a close relationship of Cetacea and artiodactyls and more specifically with hippopotamids (Montgelard et al., 1997; Nikaido et al., 1999). In addition, morphological and paleontological evidences, which rely mainly on the basis of primitive fossil whales and basal artiodactyls from the early to middle Eocene of Pakistan and India, indicate that Cetacea evolved from early Artiodactyla (Thewissen and Hussain, 1993; Thewissen et al., 2001; Gingerich et al., 2001; Rose, 2001). Montgelard et al., (1997) combined the two genetically related orders, Cetacea and Artiodactyla, into one single taxonomic rank, the Order Cetartiodactyla. The author here follows this combination and he uses the Order Cetartiodactyla in his systematics. Anthracotheres from the Pondaung Formation represent one of the most primitive anthracotheriid artiodactyl groups in East and South Asia (Ducrocq et al., 2000a). They are characterized by a complete dental formula and by a primitive dental morphology: a generally bunodont or bunoselenodont dentition with quadrangular upper molars that display five cusps (paracone, metacone, protocone, metaconule and paraconule) without a hypocone (Ducrocq, 1999). The generic differentiation between Pondaung anthracotheres has been based on dental morphology, especially depending on the development of W- shaped ectoloph, the system of crests and stylar cusps and on the body size. On the basis of these characters, significant differences between those primitive Pondaung taxa, *Anthracotherium*, *Anthracokeryx, Anthracohyus*, and *Siamotherium* (Coombs and Coombs, 1977a; Ducrocq, 1999; Ducrocq et al., 2000a) can be demonstrated. Sexual dimorphism in anthracotheres was recognized by identifying the individual canines compared to those of living artiodactyls analogues as hippos (Law, 1968), muntjac and muskdeers (Li and Chen, 2001). Upper canine of male anthracotheres can be characterized by large, recurved outward, conical, more elongated and with slender outlines and in contrast, the female canines possess a small, straight and short crown (Black, 1978; Kron and Manning, 1998; Ducrocq, 1999; Li and Chen, 2001). Five upper canines teeth might belong to large to medium-sized Pondaung anthracotheres (*Anthracotherium*) and they were allocated to males and females (Plate 1, fig. K, L, M, N and O) judging by their size and morphology. Two canines (Plate 1, fig. L and M) display rather short and nearly straight crowns and are smaller than the other canines (Plate 1, fig. K, N and O). Thus, the two canines (Plate 1, fig. L and M) might be assigned to females; others representing therefore males *Anthracotherium.* The lower canine of the large-sized *Anthracotherium* is characterized by laterally compressed with oval root, mesio-distally situated longitudinal crest but reduced crown, flattened on inner side and is anteriorly procumbent (Plate 1, fig. D and E). In addition, 6 upper canines were encountered among the samples of small to medium-sized Pondaung anthracotheres, *Anthracokeryx,* and their allocation to male or female was made assuming the same principles than those used as in *Anthracotherium* (Plate 1, fig. C, F, G, H, I and J). Some lower canines were also attributed to *Anthracokeryx* in the new collections (Plate 1, fig. A and B). Table 1 and Table 2 provide the measurements of lower and upper dental specimens of all Pondaung anthracotheres. Statistical data for upper and lower molars are also tabulated in Tables 4 and 5. All recorded canines size distributions of Pondaung anthracotheres are also listed in Table 3. Size distributions in each individual are also shown in the scatter diagrams (fig. 3a, 3b). Body weight variation diagram is shown in the fig. 4, and is calculated on lower molar m1 size (length x width) using the formula proposed by Legendre, 1989 and Gingerich et al., 1980. Comparative degree of development of W- shaped ectoloph, system of crests and stylar cusps on upper molar of *Anthracotherium, Anthracokeryx* and *Siamotherium* are shown in Plate 2. An upper case letter stands for upper tooth; a lower case letter stands for lower tooth. Diagrammatic occlusal views of upper molar and lower molar dental nomenclature of the anthracotheres are represented on fig. 2 (after Coombs and Coombs, 1977a).

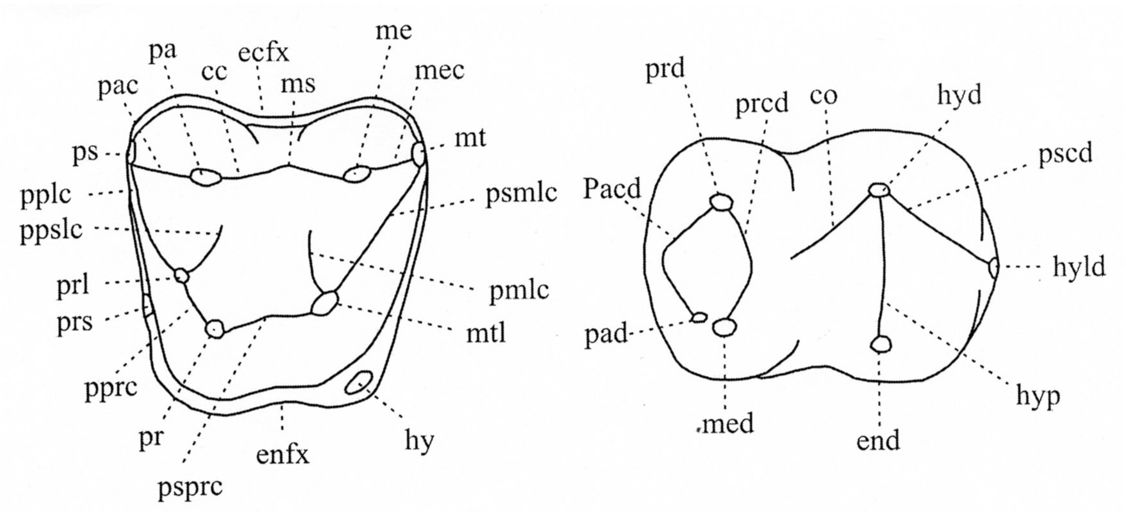

Figure 2.— Diagrammatic occlusal views of upper and lower M1, or M2 of the anthracotheres.

Abbreviations:

cc : centrocrista; co : cristid obliqua; ecfx: ectoflexus; end: entoconid; enfx: entoflexus; hy: hypocone; hyd: hypoconid; hyld: hypoconulid; hyp: hypolophid; me: metacone; mec: metacrista; med: metaconid; ms: mesostyle; mt: metastyle; mtl: metaconule; pa: paracone; pac: paracrista; pacd: paracristid; pad: paraconid; mlc: premetaconule crista; pr: protocone; prcd: protocristid; prd: protoconid; prl: paraconule; prs: protostyle; ps: parastyle; pscd: postcristid; psmlc: postmelaconule crista; psprc: postprotocrista

Order Cetartiodactyla MONTGELARD et al., 1997
Infra-Order Artiodactyla OWEN, 1848
Family Anthracotheriidae GILL, 1872

Genus *Anthracotherium* CUVIER, 1822

Type species: *Anthracotherium magnum* CUVIER, 1822

Diagnosis: See in Ducrocq, 1999, p. 107-108; 110-112

Traditionally, the genus *Anthracotherium* is defined as a medium to large-sized anthracothere with complete dental formula; bunodont or bunoselenodont upper molars with five cusps without hypocone; somewhat selenodont upper molar cusps; well developed W-shaped ectoloph and V-shaped centrocrista; developed parastyle and mesostyle; parastyle projecting labially beyond the general margin of the tooth; mesostyle labially situated beyond outer margin of the upper molar; present and/or absent protostyle; P3 trapezoidal outline in occlusal view; lower molars lack paraconid and increase in size posteriorly; hypoconulids prominent on m1-2. Diastema present in the anterior dentition. Double metacristid occurs on the mesial side of the metaconid. *Anthracotherium* differs from *Anthracokeryx* by its less developed W- shaped ectoloph and V-shaped centrocrista, it's less developed system of crests and stylar cusps, its more bunodont upper molars, the shorter diastema between anterior premolar and by its larger size. Parastyle mesially positioned in *Anthracotherium* while it is mesio-labially directed in *Anthracokeryx*.

Anthracotherium pangan PILGRIM and COTTER, 1916
(Plate 1, figs. E, K, N and O; Plate 2, figs. E, E1 and E2; Plate3; Plate8)

Anthracotherium pangan PILGRIM and COTTER, 1916.
Anthracothema pangan PILGRIM and COTTER, 1916; Pilgrim, 1928; Colbert, 1938.
Anthracohyus rubricae PILGRIM and COTTER, 1916 (in part).
Anthracotherium crassum PILGRIM and COTTER, 1916 (in part).
Anthracothema crassum PILGRIM and COTTER, 1916 (in part), Pilgrim 1928; Colbert, 1938.
Anthracohyus palustre PILGRIM and COTTER, 1916.
Anthracothema palustre PILGRIM and COTTER, 1916, Pilgrim 1928; Colbert, 1938.
Anthracotherium pangan TSUBAMOTO et al., 2003a (in part).

Lectotype: G.S.I. No. B 619, a left maxillary fragment with M2-3 (Colbert, 1938).

Revised Diagnosis:

Large-sized Anthracotherium with body weight ranging between 200 to 400 kg; upper molars with bunodont cusps but rather selenodont metaconule; system of crests weakly marked; straight paracrista and metacrista which together form a weakly developed W-shaped ectoloph; variable V-shaped centrocrista; tiny parastyle and/or mesostyle present; parastyle mesially situated in front of the preparacrista; variable protostyle present; expended premetaconule crista; two bunodont cusps present on P4; P3 triangular outline in occlusal view and slightly straight mesial and distal crests in comparison with longitudinal axis of tooth; shorter diastema present in lower premolar tooth rows.

Discussion:

Differs from A. magnum, A. monsvialense, and A. bugtiense in having: a less developed W- shaped ectoloph; a weakly marked system of crests and stylar cusps; bunodont labial cusps and less selenodont metaconule; mesially situated parastyle; weakly marked protostyle present and P3 with triangular outline in occlusal view; less developed lower premolar cristids, weak labial cingular swelling and a weakly marked hypoconulids on m1-2. Anthracotherium pangan differs also from A. silistrense in having: a less developed W- shaped ectoloph; a weakly marked system of crests and stylar cusps; and a larger body size. A. pangan can be distinguished from A. chaimanei by its less developed labial styles, less selenodont labial cusps and less developed mesial and distal crests of the premolars and small body size. Chinese anthracotheriid taxa, Anthracotherium bellia and Anthracotherium chengbiensis differ from A. pangan by their stronger system of crests, their well-developed labial stylar cusps and by their metastylar cusps on distal cingulum of M3, their more developed W- shaped ectoloph and by the absence of a protostyle. A. pangan can be distinguished from Anthracokeryx by its less developed W- shaped ectoloph and V-shaped centrocrista, its less developed system of crests and stylar cusps, its more bunodont upper molars, shorter diastema between anterior premolar and by its larger size. A mesially situated parastyle present in A. pangan while it is mesio-labially directed in Anthracokeryx. Upper and lower dental specimens of Anthracotherium pangan are shown on Plates 3 and 8, respectively.

Anthracotherium crassum PILGRIM and COTTER, 1916

(Plate 1, figs. D, L and M; Plate 2, figs. D and D1; Plate 4; Plate 9)

Anthracotherium crassum PILGRIM and COTTER, 1916 (in part).
Anthracothema crassum PILGRIM and COTTER, 1916 (in part); Pilgrim 1928; Colbert, 1938.
Anthracohyus rubricae PILGRIM and COTTER, 1916 (in part).
Anthracothema rubricae PILGRIM and COTTER, 1916 (in part); Pilgrim 1928; Colbert, 1938.
Anthracokeryx moriturus PILGRIM 1928; Colbert, 1938.
Anthracotherium crassum TSUBAMOTO et al., 2003a (in part).

Holotype: G.S.I. B. 615, a left maxillary fragment with M2-3.

Revised Diagnosis:

Medium-sized *Anthracotherium* with body weight ranging from 80 to 190 kg; upper molars with rather conical labial cusps; weakly marked protostyle. The relative development of W- shaped ectoloph and system of crests being nearly the same as in *A. pangan* but the V-shaped centrocrista is slightly more developed. *A. pangan* has more distinct cingulum surrounding the mesial, labial and distal portion of the upper molars than *A. crassum*. *A. crassum* can be distinguished from *Anthracokeryx* by the less developed W- shaped ectoloph, less developed system of crests and stylar cusps, more bunodont upper molar and larger body size.

Discussion:

Morphologically, *A. crassum* shows only minor differences with *A. pangan*, but size is a very distinct character to differentiate them. In addition, *A. crassum* possesses reduced protostyle and more conical labial cusps than *A. pangan* and it's labially directed postparacrita and premetaconule-crista form a slightly developed V-shaped centrocrista. *A. pangan* has a more distinct cingulum surrounding the mesial, labial and distal portion of the upper molars than *A. crassum. A. crassum* can be distinguished from *Anthracokeryx* by the less developed W- shaped ectoloph, less developed system of crests and stylar cusps, more bunodont upper molar and large body size. The body size of *A. crassum* is smaller than *A. pangan* but larger than *Anthracokeryx. A. crassum* differs from *A. chaimanei* by its body size because the weight of *A. chaimanei* ranges from 400 to 450 kg. Also, *A. chaimanei* has a mesiodistally compressed triangular P3 that has pre-and postprotocrista running more diagonally while on *A. crassum,* P3 is mesiodistally elongated with pre and postprotocrista running mesiodistally. *A. crassum* shows a weaker selenodonty and a weaker development of stylars cusps than *A. chaimanei*. The characters differences between the Chinese taxa, *Anthracotherium bellia*, *Anthracotherium chengbiensis,* and *A. crassum* are nearly the same as those stated in *A. pangan*. Some newly collected upper and lower dental specimens of *Anthracotherium crassum* are shown in the Plate 4 and Plate 9, respectively.

Genus *Anthracokeryx* PILGRIM and COTTER, 1916

Type species: *Anthracokeryx birmanicum* PILGRIM and COTTER, 1916

Revised Diagnosis:

Small to medium-sized anthracothere; somewhat crescentic upper molar lingual cusps; compressed paracone and metacone; distinct parastyle, moderately developed mesostyle which does not protrude beyond the labial margin of the tooth; protostyle presents but tiny; weakly marked or absent metastyle; system of crests well developed, slightly oblique preparacrista; moderately developed W- shaped ectoloph and V-shaped centrocrista; bifurcated premetaconule crista; P4 bears two cusps with a larger and rather crescentic labial one and a conical lingual one; post canine diastema present but rather short especially between p1 and p2; long and nearly horizontal symphysis; strong double metacristid on lower molar and moderately marked hypoconulid on m1 and m2; anteriorly procumbent lower canine.

Anthracokeryx birmanicum PILGRIM and COTTER, 1916

(Plate 1, figs. B, C, I and J; Plate 2, figs. C, C1 and C2; Plate 5; Plates 10-11)

Anthracokeryx birmanicum PILGRIM and COTTER, 1916 (in part); Pilgrim 1928; Colbert, 1938.
Anthracokeryx hospes PILGRIM, 1928; Colbert, 1938.
Anthracohyus choeroides PILGRIM and COTTER, 1916 (in part).
Anthracotherium birmanicum TSUBAMOTO et al., 2003a (in part).

Holotype: GSI B. 621, right maxilla with P3-M3.

Revised Diagnosis:

As for genus.

Discussion:

Differs from *Anthracotherium* in having more developed W- shaped ectoloph and V-shaped centrocrista; more selenodont upper molar cusps; more developed parastyle and mesostyle; sometimes tiny metastyle and protostyle present and smaller body size. Differs from *Anthracokeryx tenuis* in having: tiny or incipient protostylar cusps on mesial cingulum, rather straight preparacrista, and comparatively less developed W-shaped ectoloph and larger body size. *Anthracokeryx birmanicum* can be distinguished from *A. thailandicus* by its more selenodont upper molars, its shorter diastema and nearly horizontal symphysis. The lower canine of the Pondaung *Anthracokeryx* is somewhat more procumbent anteriorly than that of *A. thailandicus*. *A. birmanicum* differs from *A. sinensis* in having a rather straight preparacrista, less developed W-shaped ectoloph, metaconule and protocone less selenodont and larger size. *A. birmanicum* is different from *A. gungkangensis* by its less developed selenodonty of upper molar cusps, its conical protocone and its crescentic labial cusp of P4. *A. birmanicum* differs from *A. dawsoni* by its crescentic labial cusp of P4 and smaller size. The body weight distributions of *Anthracokeryx birmanicum* ranges from 20 kg to 60 kg. Plates 5, 10 and 11 represent some newly collected specimens of *Anthracokeryx birmanicum* from Pondaung Formation.

Anthracokeryx tenuis PILGRIM and COTTER, 1916

(Plate 1, figs. A, F, G and H; Plate 2, figs. B, B1 and B2; Plates 12-14)

Anthracokeryx tenuis PILGRIM and COTTER, 1916; Colbert, 1938.
Anthracokeryx birmanicus PILGRIM and COTTER, 1916 (in part).
Anthracokeryx bambusae PILGRIM, 1928; Colbert, 1938.
Anthracokeryx myaingensis PILGRIM, 1928; Colbert, 1938.
Anthracokeryx ulnifer PILGRIM, 1928; Colbert, 1938.
Anthracotherium tenuis TSUBAMOTO et al., 2003a (in part).

Holotype: GSI B. 625, a left maxillary fragment with M1-2, and GSI B. 626, a left mandibular fragment with m1 and posterior part of dp4.

Revised Diagnosis:

Small-sized anthracothere with selenodont upper molar cusps; parastyle as prominent as in derived *Anthracotherium* species; mesostyle well marked but not protruding beyond the labial margin of the tooth; protostyle absent, tiny metastyle sometimes present; moderately developed W-fold ectoloph and V-shaped centrocrista; somewhat crescentic labial cusp and conical lingual cusp on P4; longer symphysis, and short diastema present between anterior cheek teeth especially between p1, p2 and canine, respectively. The body size has been estimated between 10 kg and 20 kg for minimum and maximum weight, respectively.

Discussion:

A. tenuis is a small-sized and abundant species among the anthracotheres collected from the late middle Eocene Pondaung formation (Table. 1, 2 and figures shown in Plate 6, 12, 13 and 14). *A. tenuis* differs from the *A. birmanicum* by its smaller size, its labially directed preparacrista, absence of its protostylar cusp and more developed W- shaped ectoloph. It differs from other Pondaung *Anthracotherium* in having a more developed W- shaped ectoloph, V-shaped centrocrista, and all labial stylar cusps, but it shows a tiny metastyle and a small body size. *A. tenuis* differs from *Anthracokeryx thailandicus* in having more selenodont labial cusps, a weaker metastyle, longer and nearly horizontal symphysis and diastema. Body weight of *A. thailandicus* is almost the same as the maximum body size of *A. birmanicum*, which is therefore 3 times larger than that of *A. tenuis*. The lower canine of *A. tenuis* is somewhat more procumbent anteriorly than that of *A. thailandicus*. *A. tenuis* shares similar dental morphology with Chinese *Anthracokeryx* species but the latters have larger body size. *A. tenuis* also differs from *Siamotherium* in having more developed W- shaped ectoloph, V-shaped centrocrista, and all labial stylar cusps but it shows tiny metastyle and short diastema present between anterior cheek teeth.

Genus *Siamotherium* SUTEETHORN et al., 1988

Type species: *Siamotherium krabiense* SUTEETHORN et al., 1988.

Revised Diagnosis:

Small anthracothere with very bunodont upper molars displaying five conical cusps; a weak cingulum occurs at the mesial and distal part of the upper molar; parastyle present but very weakly marked; tiny mesostyle sometimes present; rather crescentic labial cusps on P4; P3 without lingual cusp; tooth row without diastema; rounded and rather vertical lower canine; absence of paraconid on lower molar; p3 smaller or same sized than p4; heel of m3 short, narrow and monocuspidate.

Siamotherium pondaungensis DUCROCQ et al., 2000a

(Plate 2, fig. A)

Pakkokuhyus lahirii TSUBAMOTO et al., 2003a (in part).

Holotype: Kdw- 6, a right maxillary fragment with M2-3,

Revised Diagnosis:

Small primitive anthracothere; differing from type-species in having a quadrangular crown, bunodont upper molar cusps but somewhat selenodont metaconule; more bunodont protoconule; no stylar cusps; no trace of W- shaped ectoloph; straight paracrista and metacrista (no V-shaped centrocrista); less developed system of crests; a rather weak cingulum occurs on the mesial and distal part of the upper molars.

Discussion:

Differs from Pondaung *Anthracotherium, Anthracokeryx* in having a much smaller body size, and more primitive dental characters such as more bunodont upper molar cusps and weakly marked systems of crests, absence of V-shaped centrocrista, of W-fold ectoloph and of nearly all stylar cusps. Differs from *Anthracohyus* in having a much smaller size, less selenodont metaconule, absence of protostyle and posterior lobe not protruding lingually. *S. pondaungensis* can also be distinguished from *S. krabiense* by its smaller size, its more bunodont upper molar cusps, its somewhat less developed lingual cingulum and parastyle, its absence of protostyle, mesostyle and metastyle, its rectilinear centrocrista (no V-shaped centrocrista) and by its more bunodont paraconule (Plate 2, fig. A). Differs from *Probrachyodus, Bothriogenys,* and *Ulausuodon* of South Asia by the absence of distinct stylar cusps especially parastyle and mesostyle, conical labial cusps, not laterally compressed, and more bunodont lingual cusps. Tsubamoto et al., (2003a) re-examined the generic status of *S. pondaungensis* and designated it as a junior synonym of *Pakkokuhyus lahirii* (helohyid) instead of a primitive anthracothere. But, the presence or absence of paraconid on lower molar, which is used as the basic character to differentiate the families Helohyidae and Anthracotheriidae, has not been taken into account in their final conclusions.

Genus *Anthracohyus* PILGRIM and COTTER, 1916

Type species: *Anthracohyus choeroides* PILGRIM and COTTER, 1916

Revised Diagnosis:

As for species.

Anthracohyus choeroides PILGRIM and COTTER, 1916

(Plate 7)

Holotype: GSI B 603, a left isolated M3 ,

Revised Diagnosis:

Medium-sized anthracothere; bunodont upper molar with conical cusps but rather large and selenodont metaconule; no labial stylar cusps and a small protostyle occur on the mesial cingulum; rectilinear centrocrista (no V-shaped centrocrista), absence of W-shaped ectoloph; less developed system of crests and absence of postprotocrista; occurrence of moderately developed mesial, distal and labial cingulum but absence of lingual cingulum; the posterior lobe more protruding lingually than the anterior one; mesiodistally shorter buccal margin than the lingual one on upper molars; P4 bears two conical cusps. The labially slanted lingual wall is high and shows a strong slope.

Discussion:

Differs from all *Anthracotherium* and *Anthracokeryx* in having the absence of W- shaped ectoloph and labial stylar cusps, rectilinear centrocrista (no V-shape centrocrista), less developed system of crests, mesial and distal cingulum and labial conical cusps of P4 (Plate. 7). *Anthracohyus* is clearly distinguished from *Siamotherium* by its larger body size, its large selenodont metaconule, it's lingually protruding posterior lobe and by the presence of a protostyle. *Anthracohyus* further differs from other anthracotheres by its rectilinear centrocrista, absence of mesostyle, loss of postprotocrista, and large metaconule. *Anthracohyus* exhibits the distinct derived dental characters of rectilinear centrocrista, absence of mesostyle, loss of postprotocrista, and large metaconule. These characters are analogous to share derived characters of *Hippopotamus* and match the characters stated by the cladistic analysis of Gentry and Hooker (1988). *Anthracohyus* definitely stands as a primitive unique taxon amongst the Pondaung anthracotheres by those characters in present new taxonomy and these characters also support the hypothesis that modern hippos were nested within the anthracotheres, especially with *Anthracohyus*.

a

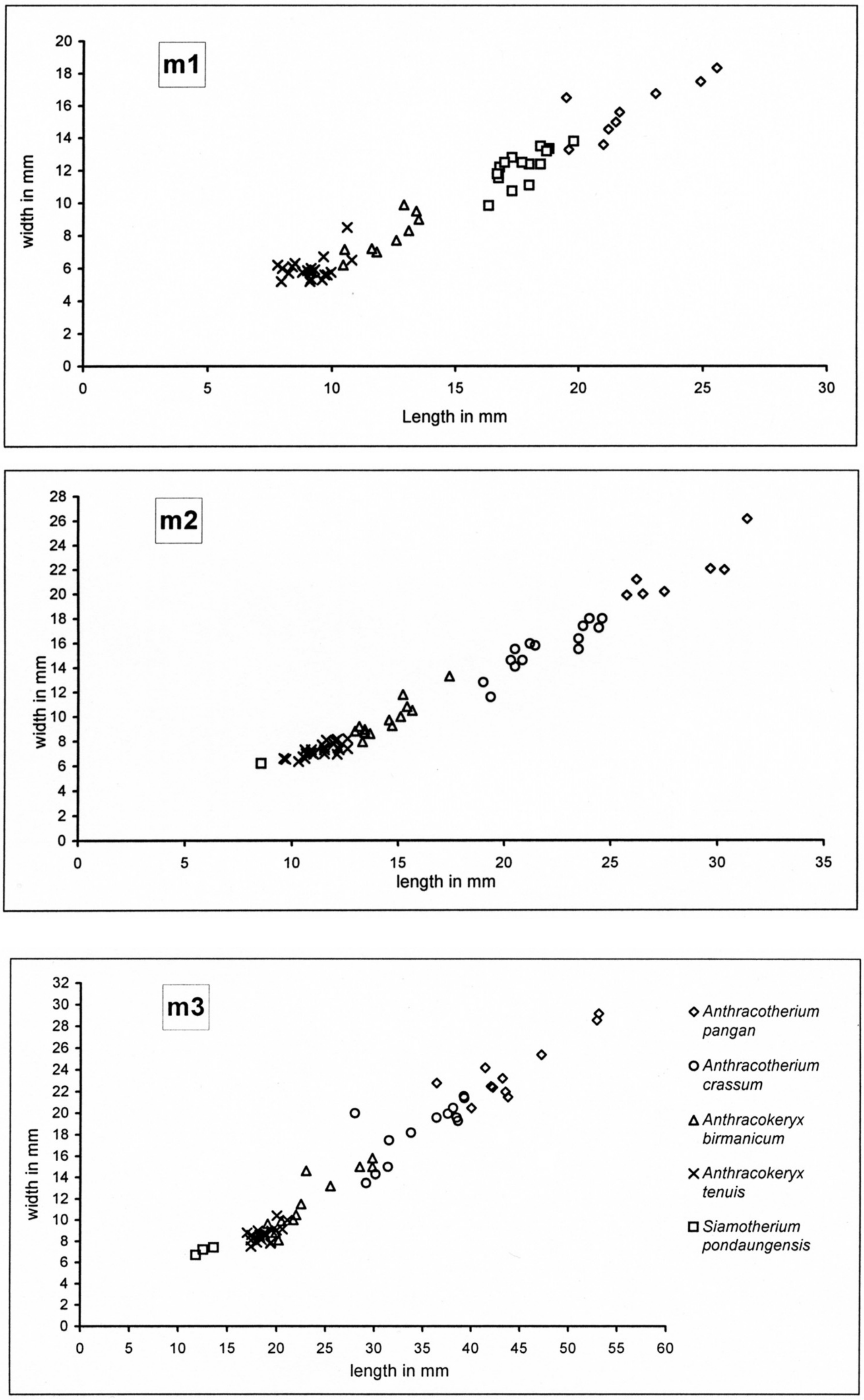

Figure 3a.— Scatter diagrams for lower molars (a) and upper molars (b) of the Pondaung anthracotheres.

b

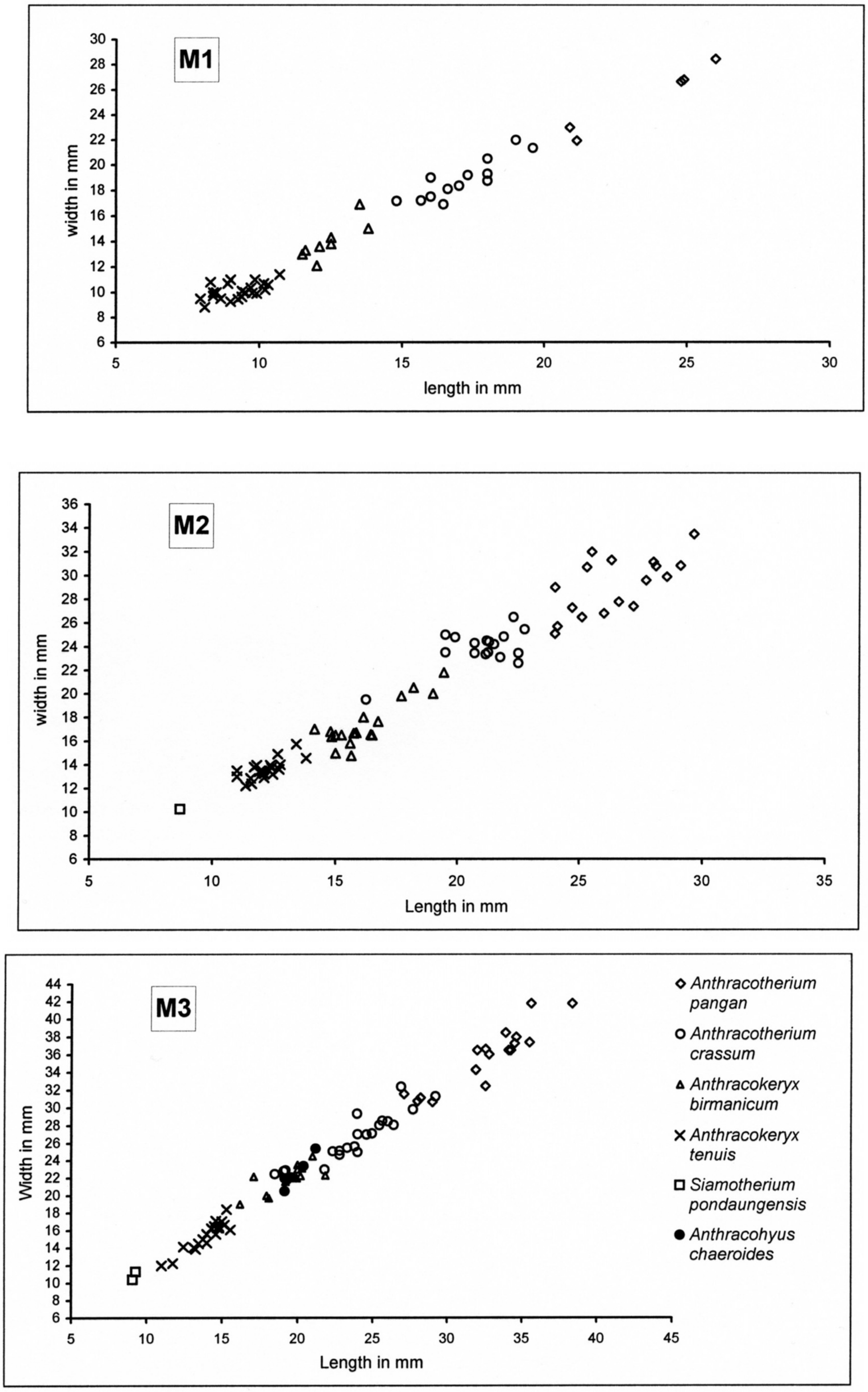

Figure 3b.— Scatter diagrams for lower molars (a) and upper molars (b) of the Pondaung anthracotheres.

CONCLUSIONS

The present effort is a clarification of the taxonomic status of anthracotheres from the late middle Eocene Pondaung Formation (Central Myanmar). Cranial elements have not been encountered in our new collections so far and the systematics of Pondaung anthracotheres is therefore mainly based on the morphology of the teeth associated with body size. *Anthracotherium* corresponds to the largest and medium-sized Pondaung anthracotheres and differs from *Anthracokeryx* in having weak or absent stylar cusps, straight preparacrista and postmetacrista, less developed W- shaped ectoloph and V-shaped centrocrista. *Anthracokeryx* differs from the more derived *Anthracotherium* in the following respects: smaller in size, parastyle distinct but generally less prominent, developed mesostyle not protruding beyond the general labial margin of the tooth, moderately developed W- shaped ectoloph and V-shaped centrocrista, expanded premetaconule crista, P3 with triangular outline in occlusal view and m2 hypoconulid large. Present study can also conclude that sexual dimorphism may occur amongst the individual genera of *Anthracotherium* and *Anthracokeryx* judging by the configuration of their canine teeth.

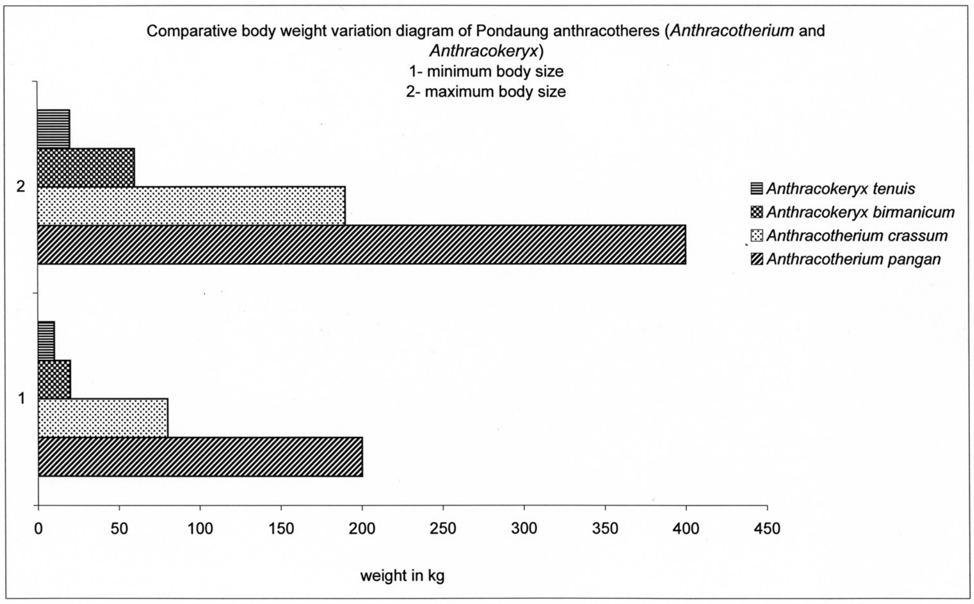

Figure 4.— Comparative body weight diagrams of Pondaung anthracotheres (*Anthracotherium* and *Anthracokeryx*).

According to this new taxonomy, the smallest Pondaung anthracothere, *Siamotherium pondaungensis* could represent the most primitive anthracothere from South East Asia because of its retention of typical primitive dental characters such as: the less developed system of crests and cingulum, rather more bunodont paraconule as well as straight centrocrista and absence of W-ectoloph and stylar cusps. Paraconid, one of the primitive dental characters occurring on the lower molar of artiodactyls, stands as a fundamental element for the differentiation between *Pakkokuhyus lahirii* and *Siamotherium pondaungensis*. "*P. lahirii*" from the Pondaung Formation has no paraconid on its lower molars and also, the character considered as important in the classification of Holroyd and Ciochon (1995) was the position and shape of the heel of hypoconulid on m3 that is one of the most common characters of the Pondaung anthracotheres (Ducrocq et al., 1997a, 2000a). Thus, those characters cannot be used to attribute the smallest Pondaung anthracotheres, *S. pondaungensis,* to a new group. The author concludes therefore that it is one of the valid genera of anthracotheriids artiodactyls in his new Pondaung anthracothere's taxonomy. He could also insist on those characters mentioned for *Siamotherium,* that are closely related to those of Diacodexidae suggesting that Diacodexidae might have been the ancestral group of anthracotheres (sensu stricto Ducrocq, 1999). *Anthracohyus*, an uncommon taxon of Pondaung anthracotheres, has a set of distinctive derived dental characters: rectilinear centrocrista, absence of mesostyle, loss of postprotocrista, and large metaconule and these characters represent the links especially on the relationships between the Anthracotheriidae and the Hippopotamidae as previously stated in the cladistic analysis completed by Gentry and Hooker (1988). Anthracotheriidae shares a set of several derived dental characters with Hippopotamidae. They are closely linked by a downturned dentary angle, by various mesostylar developments, by obtuseness of the upper molar distobuccal corner, by a lingual shift in the orientation of its upper molar preparacrista and postmetacrista, by having the upper molar paraconule extended distobuccally. For those reasons, the author strongly supports the widely accepted hypothesis that *Anthracohyus* is potential ancestor of *Hippopotamus* but, additional well preserved fossil specimens need to be recovered to strengthen this phylogenetic hypothesis.

The Pondaung anthracotheriid artiodactyls, *Anthracohyus, Siamotherium*, *Anthracokeryx* and *Anthracotherium* are more primitive than the other taxa recorded from East and South East Asia, especially by the development of their W- shaped ectoloph, system of crests and selenodonty of upper molar cusps. The primitive dental characters of anthracotheriid artiodactyls indicate that they originated in South East Asia especially from the Pondaung area, Myanmar. Moreover, some anthracotheres from Thailand and China possess more derived characters than those of Pondaung and the age of the Pondaung Formation bearing the Anthracotheriidae is slightly older than anthracotheriid bearing localities from Thailand and China. The fission track and magnetostratigraphic results confirm the late middle Eocene age of the Pondaung Formation, which indicates that the Pondaung Formation is slightly older than the other Paleogene mammalian localities having yielded anthracotheriid artiodactyls in Asia. The author can thus conclude with good confidence that the radiation centre of the Anthracotheriidae was located in South Asia, and more probably in South East Asia and that they migrated from South Asia to Africa during the late Eocene Epoch and to Europe during the lowermost Oligocene, soon after Stehlin's “Grande Coupure” (Ducrocq, 1993; 1995a).

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Table (1)

Taxon	Sp. N°	P / 3		P / 4		M / 1		M / 2		M / 3	
		L	W	L	W	L	W	L	W	L	W
Anthracotherium pangan	Bhn-1049	23	9.9								
	Bhn-1512			20.65	12.3						
	Bhn-1515	22.8	9.5								
	Kle-2					21.2	14.55				
	Kle-9	21.95	8.8								
	Kmi-1									42	22.5
	Lgn-3	20.4	9.75								
	Lma-50					19.6	13.3				
	Lma-51			19.6	13.3						
	Mgg-204									42.2	22.4
	Mta-15					21	13.6				
	Npe-28					25.55	18.35				
	Npe-35							27.5	20.2		
	Npe-45									40	20.5
	Pgn-4									41.4	24.2
	Pkg-162					23.1	16.75				
	Pkg-163			22	18.85						
	Pkg-206			19.15	11.35						
	Pkg-212			20.6	11.3						
	Pkg-213					24.9	17.5				
	Pkg-244	19.05	9.15								
	Pkg-354			19.15	9.7						
	Spg-1	22.5	11.5								
	Tmk-8			19.9	11.5						
	Tmk-10							31.35	26.2		
	Tmk-66									52.9	28.6
	Tmk-77							26.5	20		
	Tmk-97					21.65	15.6				
	Tmk-142	19.9	10.25								
	Tudw-23	20.1	9.45								
	Tudw-28									43.75	21.5
	Tudw-31							25.75	19.9		
	Tudw-296	20	10								
	Tudw-300			20.85	12.5						
	Tudw-315			18.3	11						
	Tudw-413									43.5	22
	Yse-5							29.65	22.1		
	Yse-52									43.2	23.25
	B-607									53.1	29.2
	B-617			19.4	12.6	19.5	16.5	26.2	21.2	36.4	22.8
	B-620									47.2	25.4
	B-745	24.1	12.7	21.6	14.1	21.5	15	30.3	22		

Table 1.— Measurements (in mm) of the lower dental material of Pondaung anthracotheres from GSI, AMNH and National Museum of Myanmar.

Table (1) continued

		P / 3		P / 4		M / 1		M / 2		M / 3	
Taxon	**Sp. N°**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
Anthracotherium crassum	Bhn-39					17.3	10.75				
	Bhn-44							19	12.8		
	Bhn-56							24	18	39.25	21.4
	Bhn-57							20.5	14.1		
	Bhn-64									38.45	19.6
	Bhn-77					18.45	13.5				
	Bhn-96			17.7	12.65						
	Bhn-105					18.45	12.4				
	Bhn-896			16.1	8.65						
	Bhn-1053					18	12.4				
	Bhn-1057							23.5	16.35	36.4	19.6
	Bhn-1516			18.4	11.35						
	Kdw-140							21.2	15.95	33.75	18.2
	Kdw-142	18.2	7.25								
	Kmi-34					18	11.1				
	Kle-1							20.3	14.6		
	Mgg-20							24.45	17.25		
	Mta-17									37.55	19.95
	Mta-31	19.9	9.7	18.5	11.5	17.7	12.5				
	Pgn-3					19.8	13.8				
	Pgn-172	15.55	8.15								
	Pgn-187			15.45	9						
	Pkg-25					18.8	13.35				
	Pkg-101					16.35	9.85				
	Pkg-103					16.8	12.2				
	Pkg-139									29.15	13.5
	Pkg-209			16.1	8.5						
	Pkg-220			17.6	7.45						
	Pkg-379	16.5	9								
	Sze-1							19.35	11.6		
	Tdg-19			16.55	9						
	Tmk-5							20.85	14.6		
	Tmk-89									31.4	15
	Tudw-12			17.15	8.15						
	Tudw-37									38.6	19.3
	Tudw-278							21.45	15.8		
	Tudw-287			18.1	11.2						
	Tudw-295	18.65	7.4								
	Tudw-361					16.75	11.55				
	Tudw-362	17.65	7.75								
	Yse-6									30.1	14.3
	B-612					16.7	11.8	23.7	17.4		
	B-613									38.1	20.5
	B-614	20.9	10.4								
	B-751	20.2	9.7	20.2	11.4	17.3	12.8	24.6	18	39.2	21.6
	AMNH-20011	16.5	7.5	16.5	9	17	12.5	20.5	15.5	31.5	17.5
	AMNH-20029									28	20
	AMNH-32522					18.7	13.2	23.5	15.5		

Table (1) continued

		P / 3		P / 4		M / 1		M / 2		M / 3	
Taxon	**Sp. N°**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
Anthracokeryx birmanicum	Adg-1			13	7.55						
	Bhn-25							14.55	9.7		
	Bhn-29					13.5	9				
	Bhn-34							15.65	10.5		
	Bhn-45			13.35	7.15						
	Bhn-54	16	7.65	14.5	7.8						
	Bhn-59			15.8	8.15						
	Bhn-1517							14.7	9.25		
	Bhn-1523									19.9	8.8
	Kmi-38					12.6	7.7				
	Lgn-12			12.45	7.2						
	Mgg-13					10.45	6.2	13.3	7.95		
	Mgg-17							13.4	8.7		
	Mta-16	16.3	6.8								
	Npe-29							12.95	8.8		
	Npe-43									22	10.5
	Pkg-6					10.5	7.15				
	Pkg-28			11.3	5.7	11.8	7	13.15	9.2	19.1	9.65
	Pkg-29			10.95	5.15	11.6	7.2	13.4	8.95	20.5	9.9
	Pkg-150							15.1	10		
	Pkg-203	16.7	6.3	14.6	7.55						
	Pkg-258			13	6						
	Pkg-371									29.8	15
	Pkg-385							13.5	9.65		
	Pkg-386							15.4	10.8		
	Pkg-388									25.5	13.2
	Spg-34			11.85	5.8			13.65	8.6	21.7	10
	Tudw-26									22.5	11.5
	Tudw-30									23	14.6
	Tudw-135	11.2	5.4								
	Tudw-293	13.1	7.25								
	Tudw-318					13.1	8.3				
	Tudw-336			13	7.25						
	Tudw-375									20.2	8.1
	Yse-51			16.2	6.95						
	B-605			13.9	7.9	13.4	9.5	17.4	13.3	29.8	15.8
	B-767			12.3	6.8	12.9	9.9	15.2	11.8		
	AMNH-20015									28.5	15

Table (1) continued

Taxon	Sp. N°	P / 3		P / 4		M / 1		M / 2		M / 3	
		L	W	L	W	L	W	L	W	L	W
Anthracokeryx tenuis	Bhn-12							10.3	6.35		
	Bhn-15					9.6	5.3				
	Bhn-30							12.6	8.2		
	Bhn-35									18.1	9
	Bhn-42							12.1	8.15	20.05	10.4
	Bhn-1056							10.9	7.05	20.6	9.15
	Bhn-1513							10.5	6.75		
	Bhn-1519			9.6	4.75						
	Bhn-1520									18.8	8.7
	Bhn-1546	10.4	4.3								
	Kdw-7							12.15	7.45		
	Kdw-8									19.4	7.8
	Kdw-153							12	8.05	20	9.05
	Kle-36					10.8	6.5				
	Lgn-6			10.6	5.4						
	Lgn-7									18.45	8.15
	Lma-42									18.25	8.6
	Mgg-16							12.6	7.4		
	Mta-30					9.2	5.75	10.9	7.3		
	Npe-16									17.4	7.5
	Npe-18					8.8	5.75				
	Npe-44			10	5			11.5	7.3	18	7.9
	Npe-44b	9	4	9.5	5	10.6	8.5	11.5	7.5		
	Pgn-184									17	8.8
	Pkg-7									19.5	9
	Pkg-9					9.95	5.75				
	Pkg-12							10.6	6.6		
	Pkg-27					8.25	5.7	10.6	7.3	18.8	8.8
	Pkg-100							10.65	7		
	Pkg-123							9.6	6.6		
	Pkg-124			9.6	4.75	7.95	5.2	9.7	6.55		
	Pkg-146			12.5	5.9						
	Pkg-165					9.15	5.35				
	Pkg-176							12.1	6.95		
	Pkg-204									19.45	7.9
	Pkg-218	11.9	5.3								
	Pkg-376			9.5	5						
	Pkg-378					7.8	6.2				
	Pkg-384			10.15	5.2	9	5.85	11	6.95	17.45	8.6
	Sgk-3	11.6	4.85								
	Tmk-78					9.65	6.7				
	Tmk-135			11.1	5.4						
	Tmk-138	11.5	5								
	Tudw-281					9.15	5.75				
	Tudw-325	10.9	4.2	11.5	5.2	9.3	5.9			18.3	8.4
	Tudw-326			11.5	5.35	9.15	6	11.95	7.8	18.8	8.6
	Tudw-376					9.8	5.6				
	B-626					9.7	5.6				
	B-627							12.2	7.3	17.4	8.1
	B-755	11.7	4.3	11.2	5.5	8.5	6.3	11.6	8.1	21.1	10
	B-759							11.5	7		

Table (1) continued

		P / 3		P / 4		M / 1		M / 2		M / 3	
Taxon	**Sp. N°**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
Anthracokeryx tenuis	B-760					9.1	5.2				
	B-761	11.5	4.5								
	AMNH-20017	10.5	5	9.5	5.5	8	6	11.5	7.5	19.5	9
	AMNH-20017					8.4	6.1	11.4	7.7		
Siamotherium pondaungensis	Bhn-906							8.55	6.2	11.8	6.7
	Tmk-83									13.6	7.4
	Tudw-327									12.55	7.2

Table (2)

		P 3 /		P 4 /		M 1 /		M 2 /		M 3 /	
Taxon	**Sp. N°**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
Anthracotherium pangan	Bhn-68									27.1	31.6
	Bhn-69							26.6	27.8		
	Bhn-70									29	30.7
	Bhn-74			16.45	18.05						
	Bhn-102			17.9	18.25						
	Bhn-184	17.2	12								
	Bhn-1504	19.45	15.4								
	Bhn-1518			15.7	21			24.7	27.3	32.55	32.5
	Bhn-1525			20	24.35						
	Bhn-1543			15.95	19.95						
	Bhn-1550	20	14								
	Kdw-144									28.2	31.15
	Kle-3							24	25.1		
	Kle-5							29.1	30.85		
	Kle-35	20	16.2								
	Kle-39							25.1	26.5		
	Kmi-11					26	28.45				
	Lgn-9									32.8	36.05
	Lgn-10							25.5	32		
	Lgn-11			15.5	21.25						
	Lma-49			15.7	19.9						
	Mgg-22									34.25	36.5
	Mgg-23									35.5	37.4
	Mggn-5			15.9	21.2						
	Mta-13	20.5	16.2								
	Mta-29									38.35	41.8
	Npe-36	18.7	14								
	Pgn-6									28	30.8
	Pgn-153							27.7	29.6		
	Pgn-160			15.3	20.9						
	Pkg-4							28.55	29.9		
	Pkg-215							26	26.8		
	Pkg-372					22	30				
	Tmk-18							26.3	31.3	35.6	41.8
	Tmk-65							28	31.15		
	Tmk-68					21.15	21.95				
	Tmk-70	23.2	18.85								
	Tmk-71			17.55	21.6						
	Tmk-76							29.65	33.5		
	Tudw-45									34.6	38
	Tudw-46									34.1	36.5
	Tudw-47					24.9	26.8				
	Tudw-179					20.9	23				
	Tudw-285									32.55	36.65
	Tudw-311			16.6	19.6						
	Tudw-313	20	16								
	Tudw-319					24.8	26.65				
	Tudw-359	22.45	17.5								
	Yse-46			13.45	18						
	Yse-50							24.1	25.7		
	B-608	24.5	20.3								
	B-609									31.9	34.3
	B-610							25.3	30.7		
	B-616			15.8	19.8						
	B-618	24.1	19.7								
	B-619							27.2	27.4	34.1	36.5

Table 2 .— Measurements (in mm) of the upper dental material of Pondaung anthracotheres from GSI, AMNH and National Museum of Myanmar.

Table (2) continued

		P 3 /		P 4 /		M 1 /		M 2 /		M 3 /	
Taxon	**Sp. N°**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
Anthracotherium pangan	B-748	21.5	21.2	16.1	21.4						
	B-750							28.1	30.8	34.5	37.3
	B-752									33.9	38.5
	AMNH-32526							24	29	32	36.5
Anthracotherium crassum	Bhn-62			12.6	15.7	15.65	17.2	20.7	23.45		
	Bhn-63									22.35	25.1
	Bhn-76					16.6	18.1				
	Bhn-895							19.9	24.8	23.95	29.35
	Bhn-1502			12.2	15.25						
	Kdw-15									25.45	28.05
	Kdw-141							21.9	24.85		
	Kdw-145					14.8	17.15				
	Kle-35	20	16.2								
	Kmi-2							22.5	23.45		
	Mgg-240									22.8	25.15
	Mta-32					19.6	21.35				
	Mta-33									25.65	28.55
	Npe-37			14.4	15.8						
	Pgn-169									19.1	22.8
	Pgn-170									19.3	21.8
	Pgn-171									19.2	22.9
	Pgn-185					19	22				
	Pkg-5							22.75	25.45		
	Pkg-15			14	16.25						
	Pkg-30							22.5	22.6	23.8	25.65
	Pkg-140									21.8	23
	Pkg-141							21.75	23.1		
	Pkg-147					18	20.5				
	Pkg-178							21.15	23.35		
	Pkg-180									26.4	28.1
	Pkg-184							16.25	19.5	18.5	22.45
	Pkg-214			14.6	17	17	18.35	21.5	24.2		
	Pkg-216							21.2	24.5		
	Pkg-387							20.7	24.3		
	Sze-15							22.3	26.5	27.7	29.85
	Tdg-14	15.8	12.3								
	Tng-1									22.8	24.7
	Tng-6									23.3	25.5
	Tmk-67					18	19.3				
	Tudw-25					16.45	16.9				
	Tudw-42					18	18.75				
	Tudw-301									24.6	27
	Tudw-302									24.95	27.15
	Tudw-303							21.25	23.5		
	Tudw-304	16.65	12.75								
	Tudw-360			13.4	16.9						
	Yse-43			12	16.05						
	Yse-48									24	27.05
	B-604	15.4	11.7								
	B-611			14.8	18.4						
	B-615							21.3	24.4	26.9	32.4
	B-763									29.2	31.3
	[illegible]					[illegible]	[illegible]				

Table (2) continued

Taxon	Sp. N°	P 3 / L	P 3 / W	P 4 / L	P 4 / W	M 1 / L	M 1 / W	M 2 / L	M 2 / W	M 3 / L	M 3 / W
Anthracokeryx birmanicum	Adg-3									21.85	22.3
	Bhn-41							16.15	18		
	Bhn-53							16.45	16.55		
	Bhn-61	13.6	8.65								
	Bhn-1552					13.5	16.9				
	Kdw-146									19.7	22.05
	Kdw-147			11	13.9						
	Npe-13							15.25	16.5		
	Npe-40					12.5	13.8	15	16.5		
	Npe-41			8	10	11.5	13	19	20		
	Pkg-1			9.15	12.25	11.6	13.3	14.15	17	17.1	22.15
	Pkg-102					12	12.1	15.6	15.8		
	Pkg-148							15.85	16.7		
	Pkg-152			11	13.45						
	Pkg-166									20.2	22.25
	Pkg-169									20	23
	Pkg-189			10.7	13.65						
	Pkg-369							18.2	20.5		
	Sgk-1							15.65	14.75	18.1	19.7
	Spg-17									20.3	23.1
	Spg-18							15.75	16.65		
	Spg-23			11.25	14.65						
	Spg-53	14.1	10.1	10.4	12.5	13.8	15	17.7	19.8	19.2	21.6
	Spg-56							16.75	17.65		
	Spg-67	17	9	11.5	14						
	Spg-68							16.5	16.5		
	Tmk-69							15	14.95		
	Tmk-87					12.1	13.6				
	Tmk-93			10	14.45						
	Tmk-137	14.9	10								
	Tmk-167									21	24.5
	Tmk-171			11.2	11						
	Tng-4							14.85	16.35		
	Tudw-286			10.25	14						
	Tudw-291							19.45	22.35		
	Yse-44									19.95	22
	Yse-47	14.9	11.6								
	B-621	13.4	9.9	9.2	12	12.5	14.3	14.8	16.8	16.2	19
	AMNH-20015									20	23.5

Table (2) continued

Taxon	Sp. N°	P 3 / L	P 3 / W	P 4 / L	P 4 / W	M 1 / L	M 1 / W	M 2 / L	M 2 / W	M 3 / L	M 3 / W
Anthracokeryx tenuis	Bhn-17					10.3	10.6				
	Bhn-19					10.15	10.7				
	Bhn-21					8.65	9.5				
	Bhn-22									13.75	15
	Bhn-23	8.25	7	7.25	8.4						
	Bhn-24									13.45	14.5
	Bhn-26					8.4	9.7				
	Bhn-28							11.6	12.4	13.25	13.9
	Kdw-9					9.75	9.95				
	Kdw-10					9.5	10				
	Kdw-12							11.55	12.85		
	Kle-29	10.5	9.5								
	Kle-38			7.35	9.4	8.1	8.8				
	Kmi-32					10.2	10.2				
	Kmi-33									11.75	12.25
	Kmi-78							11.9	13.4		
	Mta-22	10.55	6.8								
	Mta-23			8.6	9.75						
	Mta-24					9.85	11	12.75	14	15.55	16.1
	Mta-25							12.7	13.6		
	Mta-26									15	17.05
	Npe-17									12.45	14.15
	Npe-20					9.25	9.45				
	Npe-21					9.39	9.65				
	Npe-30							11.8	13.95	14.8	16.45
	Npe-44c	9.2	6.5	8	10	9	11	11	13.5		
	Pkg-2									14	15.6
	Pkg-13					9.7	10.35				
	Pkg-14					9	9.25				
	Pkg-31							12.1	13.25		
	Pkg-107									14.3	16.25
	Pkg-151					7.95	9.5				
	Pkg-205							13.8	14.55		
	Pkg-366	7.5	4.2								
	Pkg-368			9.5	11						
	Pkg-384									11	12
	Sgk-2							12.35	13.95		
	Spg-21			8.15	9.25	9.4	10.1				
	Spg-55							13.8	14.55		
	Tmk-85									14.8	16.3
	Tmk-86							13.4	15.75		
	Tmk-88			8.4	10.45						
	Tmk-94	10.85	7.1								
	Tmk-133	11.3	7								
	Tmk-144									14	14.6
	Tmk-173							12.4	13.75		
	Tng-3									13.15	14.05
	Tudw-317							12.65	14.9	15.3	18.4
	Tudw-321							12.45	13.2		
	Tudw-322							11.35	12.2		
	Tudw-358									15.15	16.65
	Tudw-373	10.35	6.6					12.00	13.25		

Table (2) continued

Taxon	Sp. N°	P 3 / L	P 3 / W	P 4 / L	P 4 / W	M 1 / L	M 1 / W	M 2 / L	M 2 / W	M 3 / L	M 3 / W
Anthracokeryx tenuis	B-625			7.4	7.8	9.9	9.9				
	B-756			9.2	10.4	8.9	10.7	12.3	13.5		
	B-756	11.2	7.4	8.4	10.9	8.3	10.8	11.7	13.8	14.6	17.1
	AMNH-20017	11.5	7.5	8.2	10	8.5	10	11	13	14.5	16.5
	AMNH-20017					8.4	10	12	13.5	14.7	16.3
Anthracohyus choeroides	Bhn-1505	17.75	18.35								
	Mgg-77			9.85	13.55						
	Tmk-6									19.6	22.1
	Tmk-9									19.15	22
	Tmk-12	12	9.75	10	13.25						
	Tmk-84									19.15	20.5
	Tmk-133	11.30	7.00								
	Tmk-134	11.00	6.75								
	Tmk-136			11.10	15.30						
	Tmk-174									20.4	23.4
	B-603									21.2	25.4
Siamotherium pondaungensis	Kdw-6							8.7	10.25	9.3	11.3
	Yse-1									9.1	10.4
	Pkg-389	9.6	7.45	8.8	10.5						

Table (3)

Taxa	Lower canine		L	W
Anthracotherium pangan	Tudw-41	Left	17.80	7.55
	B-746		17.20	13.70
Anthracotherium crassum	Kle-30	Right	12.50	8.20
	Lma-47	Right	11.90	8.30
	Pkg-22	Left	12.30	7.25
	Tmk-143	Left	10.65	6.50
	Tudw-414	Right	12.00	9.50
	B-753		18.30	15.40
Anthracokeryx birmanicum	Bhn-86	Right	11.30	7.35
	Bhn-897	Left	10.00	6.10
	Kmi-3	Right	10.00	5.20
	Tdt-3	Right	9.35	6.65
	Tmk-96	Right	11.40	6.65
	Tmk-130	Left	10.50	7.30
	Tudw-288	Right	9.30	6.50
Anthracokeryx tenuis	Bhn-1521	Right	9.30	5.15
	Kmi-79	Left	4.15	2.85
	Lma-48	Right	8.10	5.80
	Pkg-18	Left	5.50	3.45
	Pkg-210	Left	5.75	3.80
	Pkg-259	Right	7.55	2.65
	Pkg-372	Left	9.50	8.00
	Pkg-392	Right	8.90	3.40
	Tdg-27	Right	8.25	5.00
	Tdt-4	Left	8.80	5.65
	Tmk-146	Right	5.85	4.70
	AMNH-20017		8.50	6.00

Table 3.— Measurements (in mm) of the canine teeth of Pondaung anthracotheres from National Museum of Myanmar.

Table (3) Continued

Taxa	Upper Canine		L	W
Anthracotherium pangan	Bhn-84	Left	14.45	11.60
	Pgn-24	Right	22.50	9.60
	Pkg-168	Right	13.20	11.70
	Tmk-58	Right	24.30	13.15
	Tmk-75	Left	14.15	12.00
	Tmk-111	Left	16.65	12.90
	Tudw-355	Right	16.85	12.90
Anthracotherium crassum	Bhn-1522	Right	12.00	8.00
	Kdw-131	Right	12.50	7.70
	Kle-10	Left	13.90	9.80
	Pkg-256	Left	11.80	8.90
	Tmk-92	Right	11.15	9.70
	Tmk-139	Right	12.90	10.60
	Tmk-140	Right	11.70	11.55
	Wka-33	Right	12.45	11.65
Anthracokeryx birmanicum	Bhn-1545	Left	11.80	8.15
	Kle-32	Right	10.00	6.80
	Kle-33	Right	9.80	6.80
	Npe-42	Right	10.00	7.00
	Pgn-188	Right	9.35	7.35
	Pkg-21	Right	9.50	6.85
	Pkg-208	Left	9.90	8.60
	Pkg-211	Left	10.40	7.10
	Tmk-4	Left	11.20	8.80
	Tmk-74	Left	11.20	8.80
	Tmk-151	Left	9.40	8.30
	Tudw-11	Right	9.60	7.85
	Tudw-289	Left	10.25	6.80
Anthracokeryx tenuis	Kdw-143	Left	6.00	3.80
	Lgn-2	Left	6.95	5.40
	Pgn-150	Left	8.95	6.60
	Pgn-173	Right	7.55	6.10
	Pkg-48	Right	8.10	5.80
	Pkg-217	Left	7.55	5.35
	Pkg-255	Right	8.40	5.90
	Pkg-373	Left	8.00	5.00
	Pkg-391	Left	4.20	4.60
	Spg-35	Right	7.10	4.95
	Spg-36	Right	9.40	6.15
	Tmk-168	Right	9.00	6.00
	Tudw-366	Left	4.50	3.35
	Yse-63	Right	8.20	5.20
	AMNH-20017		13.00	6.00

Table 4.

(St. Dev. = Standard deviation, C. V. = coefficient variation)

m1

Taxa		Sample	Maximum	Minimum	Mean	St. Dev.	C.V.
Anthracotherium pangan	lm1	8	25.55	19.5	22.30	2.06	9.24
	wm1	8	18.35	13.6	15.98	1.59	9.95
Anthracotherium crassum	lm1	15	19.8	16.35	17.74	0.97	5.47
	wm1	15	13.8	9.85	12.25	1.09	8.90
Anthracokeryx birmanicum	lm1	9	13.5	10.45	12.24	1.12	9.15
	wm1	9	9.9	6.2	7.99	1.26	15.77
Anthracokeryx tenuis	lm1	17	9.95	7.95	9.04	0.63	6.97
	wm1	17	6.1	5.3	5.76	0.39	6.77

m2

Taxa		Sample	Maximum	Minimum	Mean	St. Dev.	C.V.
Anthracotherium pangan	lm2	7	31.35	25.75	28.18	2.23	7.91
	wm2	7	26.2	19.9	21.66	2.20	10.16
Anthracotherium crassum	lm2	14	24.6	19	21.92	1.96	8.94
	wm2	14	18	11.6	15.53	1.89	12.17
Anthracokeryx birmanicum	lm2	12	17.4	12.95	14.37	1.32	9.18
	wm2	12	13.3	7.95	9.73	1.51	15.52
Anthracokeryx tenuis	lm2	21	12.6	9.6	11.31	0.90	7.95
	wm2	21	8.2	6.35	7.3	0.56	8.9
Siamotherium pondaungensis	lm2	1			8.55		
	wm2	1			6.2		

m3

Taxa		Sample	Maximum	Minimum	Mean	St. Dev.	C.V.
Anthracotherium pangan	lm3	10	53.1	36.4	44.12	5.47	12.4
	wm3	10	29.2	20.5	24.04	2.90	11.9
Anthracotherium crassum	lm3	13	39.25	28	34.73	4.20	12.09
	wm3	13	21.6	13.5	18.50	2.67	14.43
Anthracokeryx birmanicum	lm3	9	29.8	19.1	22.81	3.81	16.7
	wm3	9	15.8	8.1	11.48	2.90	25.26
Anthracokeryx tenuis	lm3	17	21.1	17.4	19.05	1.04	5.46
	wm3	17	10.4	7.5	8.71	0.74	8.5
Siamotherium pondaungensis	lm3	3	13.6	11.8	12.65	0.90	7.11
	wm3	3	7.4	6.7	7.10	0.36	5.07

Table 4.— Statistical data for Pondaung anthracotheres lower molars.

Table 5.

(St. Dev. = Standard deviation, C. V. = coefficient variation)

M1

Taxa		Sample	Maximum	Minimum	Mean	St. Dev.	C.V.
Anthracotherium pangan	lM1	5	26	20.9	23.55	2.35	9.98
	wM1	5	28.45	21.95	25.37	2.76	10.88
Anthracotherium crassum	lM1	12	19.6	14.8	16.95	1.31	7.73
	wM1	12	21.35	16.9	18.61	1.37	7.36
Anthracokeryx birmanicum	lM1	5	13.8	11.6	12.40	0.85	6.85
	wM1	5	15	12.1	13.66	1.09	7.99
Anthracokeryx tenuis	lM1	20	10.7	7.95	9.31	0.77	8.27
	wM1	20	11.4	9.25	10.14	0.58	5.72

M2

Taxa		Sample	Maximum	Minimum	Mean	St. Dev.	C.V.
Anthracotherium pangan	lM2	16	29.65	24	26.55	1.86	7
	wM2	16	33.5	25.1	29.31	2.40	8.19
Anthracotherium crassum	lM2	16	22.75	16.25	21.00	1.62	7.71
	wM2	16	26.5	19.5	23.88	1.54	6.45
Anthracokeryx birmanicum	lM2	14	19.45	14.15	15.96	1.35	8.46
	wM2	14	21.8	14.75	17.09	1.84	10.77
Anthracokeryx tenuis	lM2	19	13.8	11	12.28	0.77	6.27
	wM2	19	15.75	12.2	13.64	0.87	6.38
Siamotherium pondaungensis	lM2		8.7				
	wM2		10.25				

M3

Taxa		Sample	Maximum	Minimum	Mean	St. Dev.	C.V.
Anthracotherium pangan	lM3	18	38.35	27.1	32.72	2.98	9.11
	wM3	18	41.8	30.7	35.81	3.39	9.47
Anthracotherium crassum	lM3	22	29.2	18.5	23.72	2.87	12.1
	wM3	22	32.4	21.8	26.43	2.92	10.05
Anthracokeryx birmanicum	lM3	11	21.85	16.2	19.17	1.65	8.61
	wM3	11	23.5	19	21.69	1.48	6.82
Anthracokeryx tenuis	lM3	19	15.55	11.75	14.16	1.00	6.85
	wM3	19	18.4	12.25	15.62	1.45	9.28
Siamotherium pondaungensis	lM3	2	9.3	9.1	9.20	0.14	1.52
	wM3	2	11.3	10.4	10.85	0.64	5.9
Anthracohyus choeroides	lM3	4	21.2	19.15	19.78	0.97	4.9
	wM3	4	25.4	20.5	22.50	1.93	8.58

Table 5.— Statistical data for Pondaung anthracotheres upper molars.

PLATE 1

Assessment of the lingual view of lower and upper canines of Pondaung anthracotheres. They are categorized by the relative size associated with field data. Scale bars represent 5 mm.

Anthracokeryx tenuis:

A: left lower (Pkg-18);

F: left upper (Lgn-2);

G: right upper (Spg-36);

H: left upper (Kdw-143).

Anthracokeryx birmanicum:

B: right lower (Bhn-86);

C: right upper (Pkg-21);

I: left upper (Tudw-289);

J: left upper (Tmk 74).

Anthracotherium crasssum:

D: left lower (Pkg-22);

L: right upper (Tmk-92);

M: right upper (Wka-33).

Anthracotherium pangan:

E: left lower (Tudw-41);

K: left upper (Bhn-84);

N: right upper (Pkg-168);

O. left upper (Tmk-75).

PLATE 1

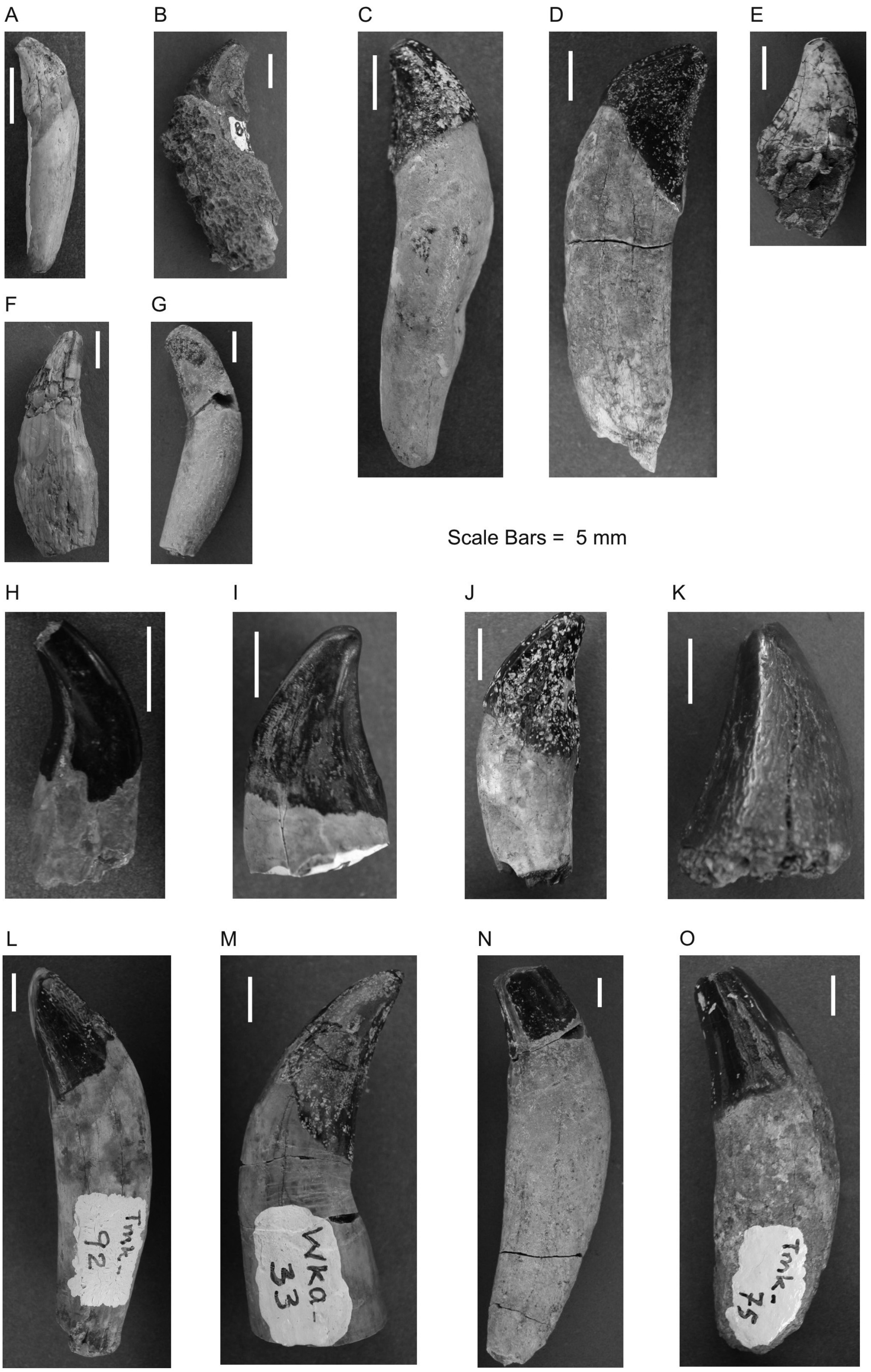


PLATE 2

Relative development of W-ectoloph, system of crests and stylar cusps on upper molar of the Pondaung anthracotheres. Scale bars represent 10 mm and indicate above teeth row, respectively.

Siamotherium pondaungensis:

A: right maxillary fragment with M2-3 (Kdw- 6).

Anthracokeryx tenuis:

B: left M1 (Kdw-9);

B1: left M2 (Mta-24);

B2: Left M3 (Bhn-22).

Anthracokeryx birmanicum:

C: right M3 (Kdw-146);

C1: left M2 (Tudw-291);

C2: left M1 (Tmk-87);

Anthracotherium crasssum:

D: left maxillary fragment with M2-3 (Bhn-895);

D1. left M1 (Pkg-147);

Anthracotherium pangan:

E: right M3 (Mgg-22);

E1: right M2 (Pkg-4);

E2: left M1 (Tudw-319).

PLATE 2

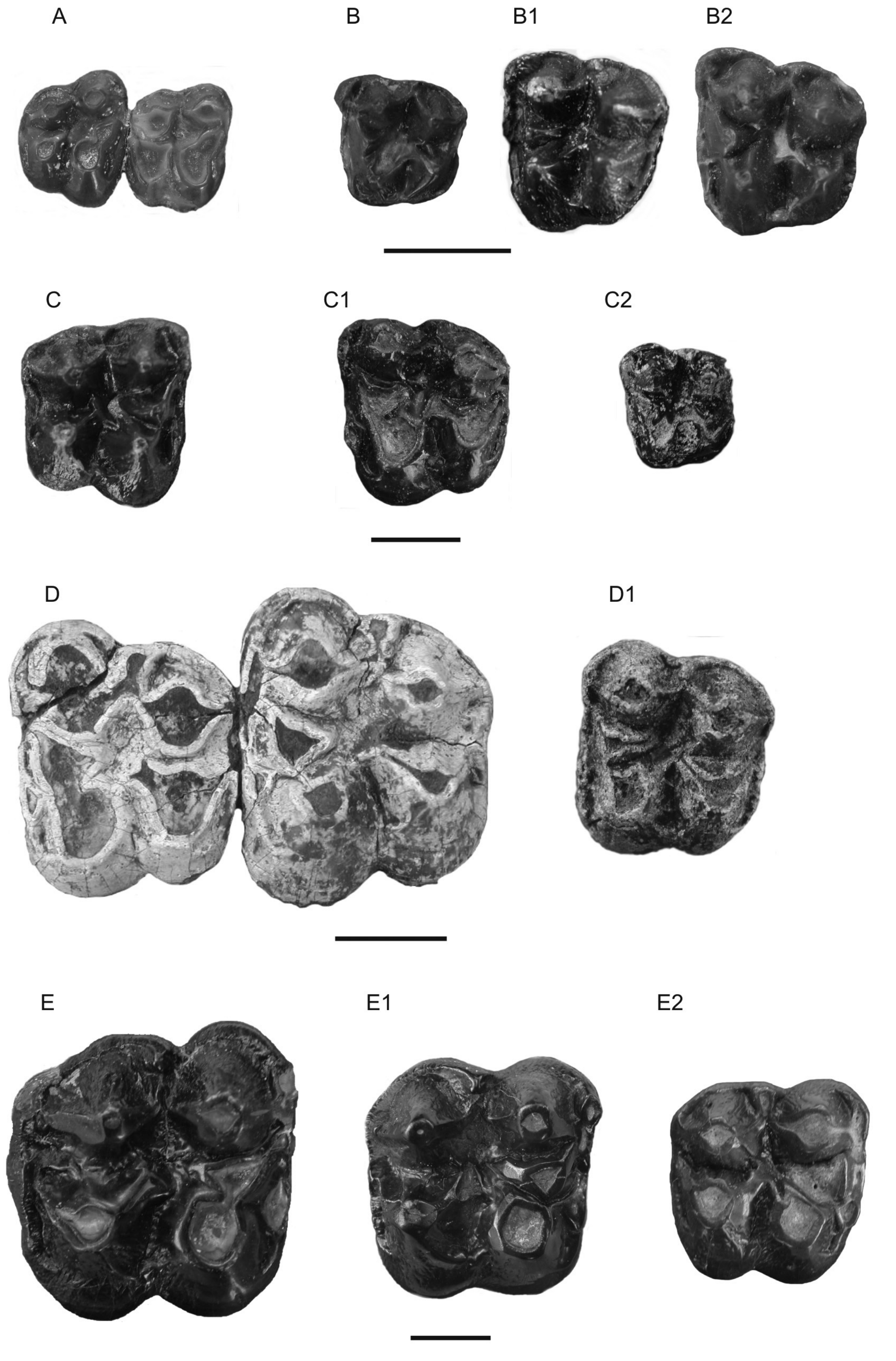


PLATE 3

Upper teeth of *Anthracotherium pangan* in occlusal views.

A: right M3 (Mta-29);
B: right M3 (Mgg-23);
C: right M3 (Pgn-6);
D: left M3 (Tudw-285);
E: left M3 (Kdw-144);
F: right M3 (Bhn-68);
G: right M3 (Lgn-9);
H: left M2 (Tmk-65);
I: right M2 (Tmk-76);
J: right M2 (Bhn-69);
K: right M2 (Lgn-10);
L: left M2 (Pgn-153);
M: left M1 (Tmk-68);
N: right P4 (Mggn-5);
O: left P3 (Tmk-70);
P: right P3 (Tudw-359);
Q: left P4 (Bhn-102);
R: left P4 (Yse-46);
S: right P4 (Bhn-74);
T: right P4 (Lgn-11);
U: right P4 (Tudw-311)

PLATE 3

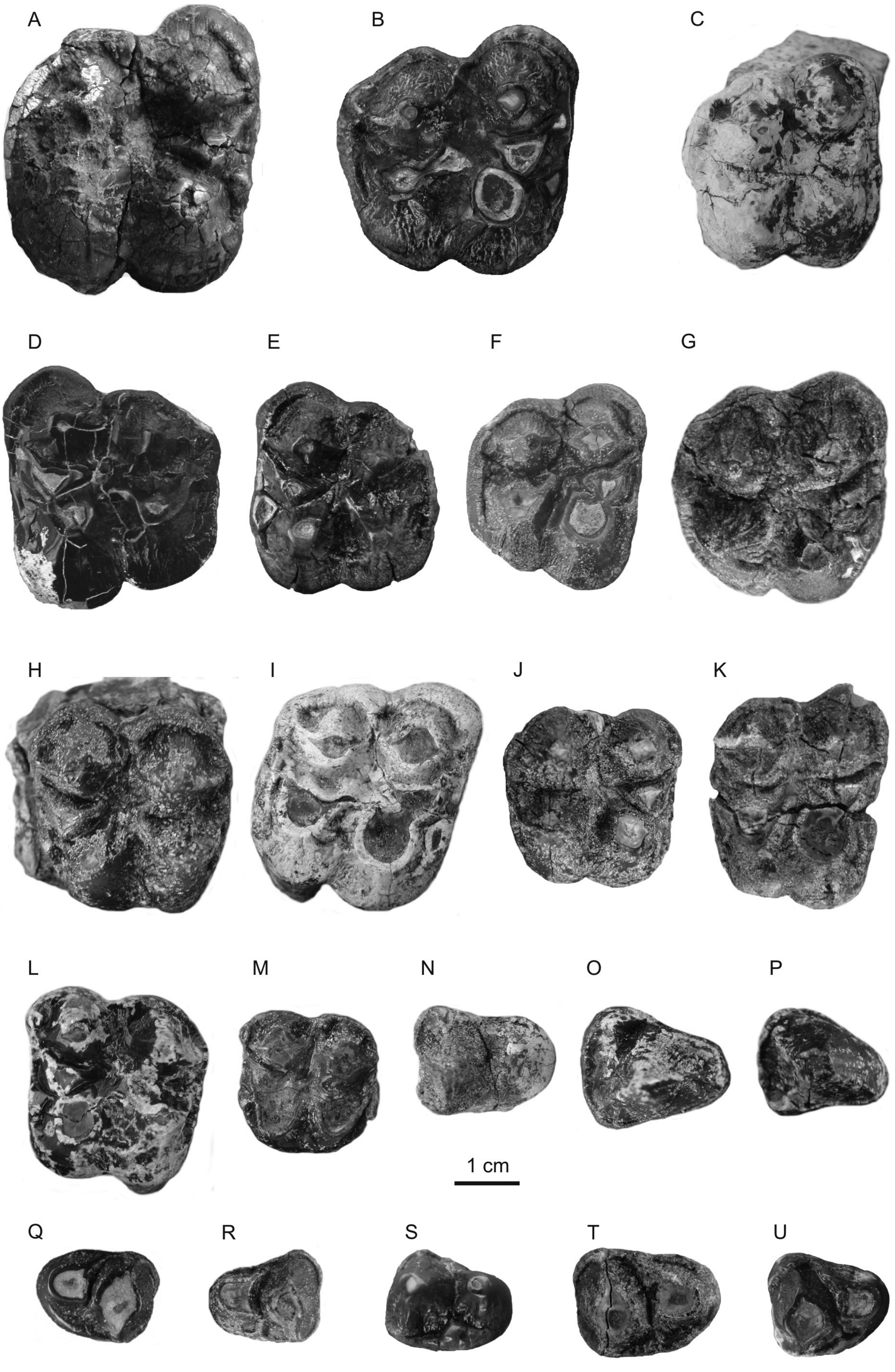


PLATE 4

Upper dentitions of *Anthracotherium crassum* in occlusal views.

A: right maxillary with distal half of M2-3 (Yse-48);

B: right M3 (Pgn-169);

C: right M3 (Tudw-301);

D: left P3 (Tudw-304);

E: left maxillary with M2-3 (Pkg-184);

F: left M2 (Kdw-141); G. left M3 (Tudw-302);

G: right P4 (Pkg-15); I. left M3 (Pkg-180);

J: right maxillary with distal half of M2-3 (Pkg-30);

K: left P4 (Yse-43); L. right P4 (Tudw-360);

M. left M3 (Pkg-140); N. left M3 (Pgn-170);

O: left M3 (Pgn-171);

P: left P4 (Bhn-1502).

PLATE 4

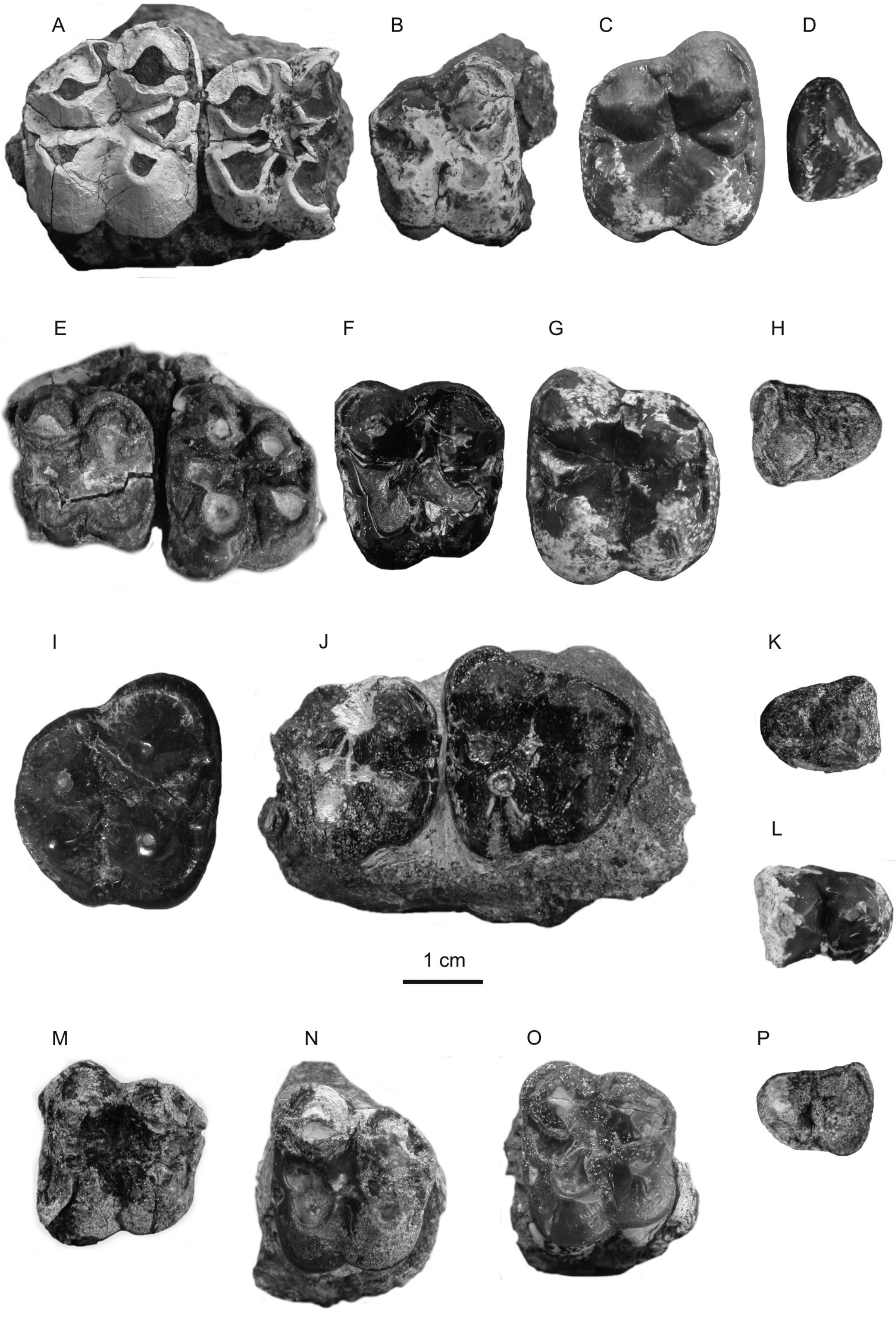


PLATE 5

Upper dentitions of *Anthracokeryx birmanicum* in occlusal views.

A: left maxillary with P4 and M1-3 (Pkg-1);

B: right P3 (Yse-47);

C: right P3 (Bhn-61);

D: right M3 (Kdw-146);

E: right M3 (Pkg-166);

F: right M3 (Spg-17);

G: left M1 (Tmk-87);

H: left M3 (Pkg-169);

I: left M2 (Bhn-41);

J: left P4 (Tudw-286);

K: right P4 (Pkg-189);

L: left P4 (Kdw-147);

M. left M3 (Pkg-148).

PLATE 5

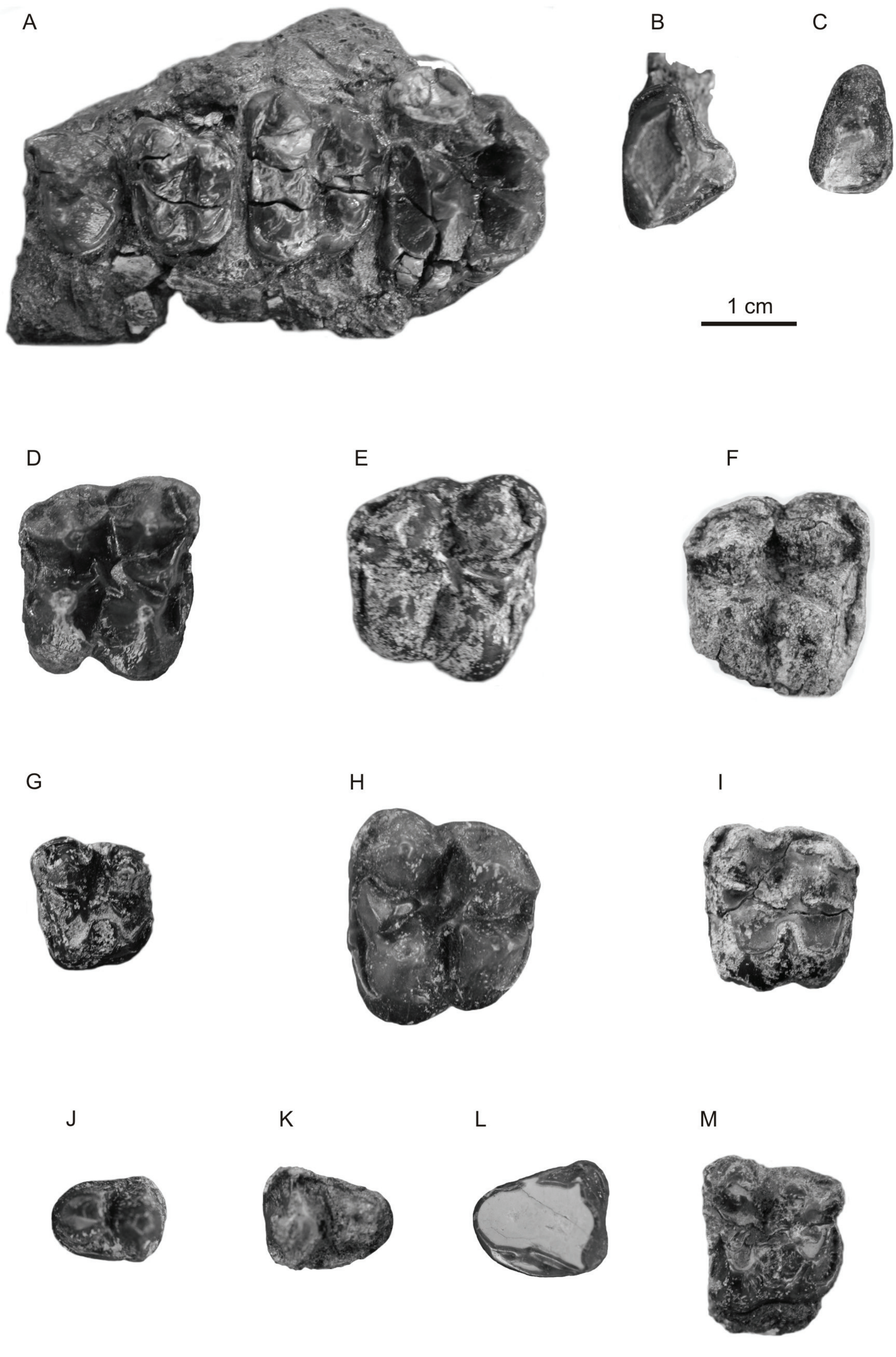


PLATE 6

Upper dentitions of *Anthracokeryx tenuis* in occlusal views.

A: right maxillary with dP3-4 and M1 (Bhn-19);

B: left maxillary with dP4 and M1 (Bhn-17);

C: left P3 (Tudw-373);

D: left maxillary with M2-3 (Bhn-28);

E: left maxillary with M2-3 (Npe-30);

F: left P4 (Mta-22);

G: right M3 (Bhn-24);

H: left maxillary with M1-3 (Mta-24);

I: right maxillary with P3-4 (Bhn-23);

J: right M3 (Pkg-31);

K: right M3 (Mta-26);

L: right M2 (Mta-25);

M: left maxillary with P4-M1 (Spg-21);

N: left M1 (Pkg-14);

O: left M2 (Pkg-13);

P.: left M3 (Kdw-9).

PLATE 6

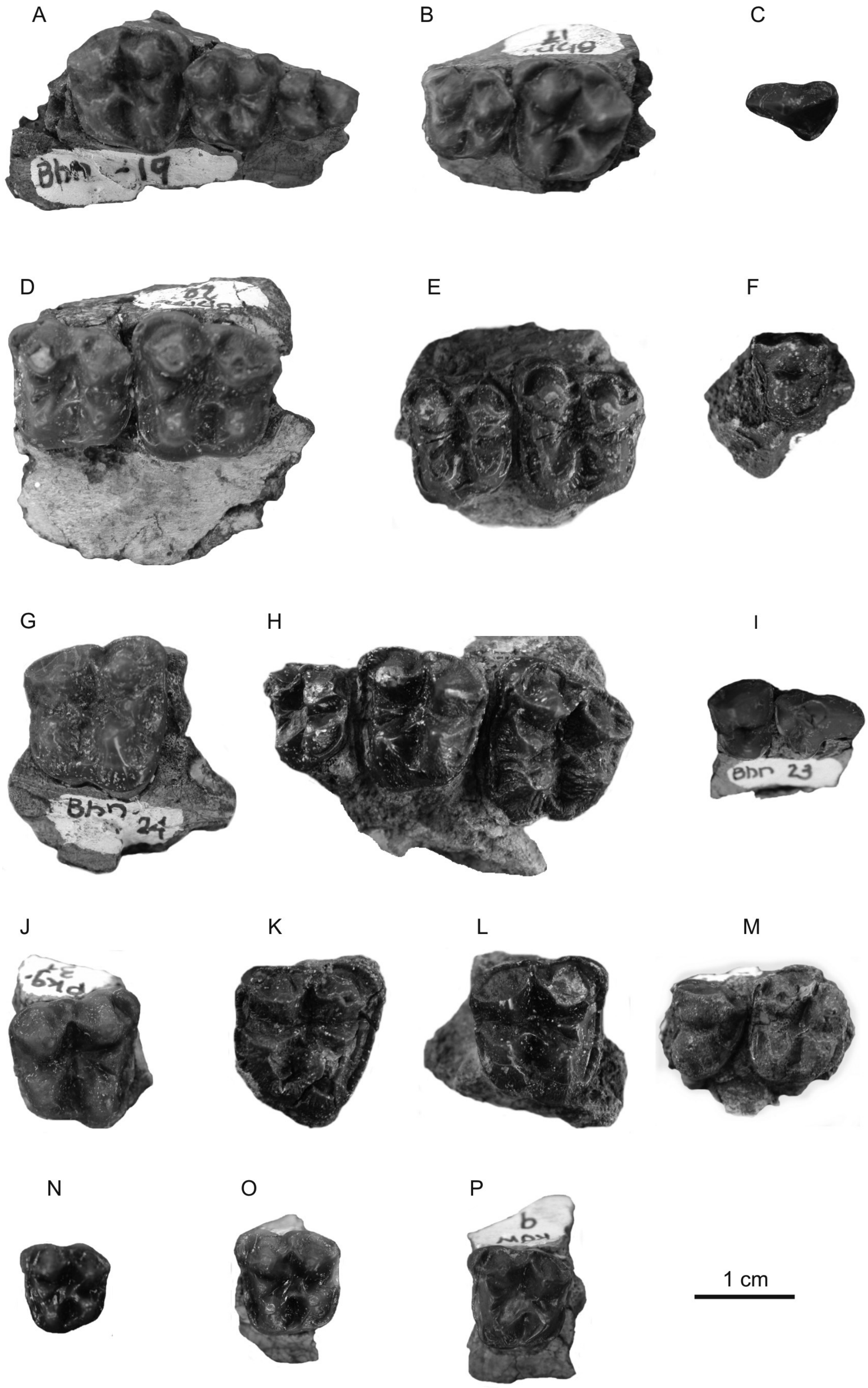


PLATE 7

Upper teeth of *Anthracohyus choeroides* in occlusal views.

A: left M3 (Tmk-6);

B: right M3 (Tmk-9);

C: right M3 (Tmk-84);

D: left P3-4 (Tmk-12);

E: right P4 (Tmk-136);

F: right P4 (Mgg-77).

PLATE 7

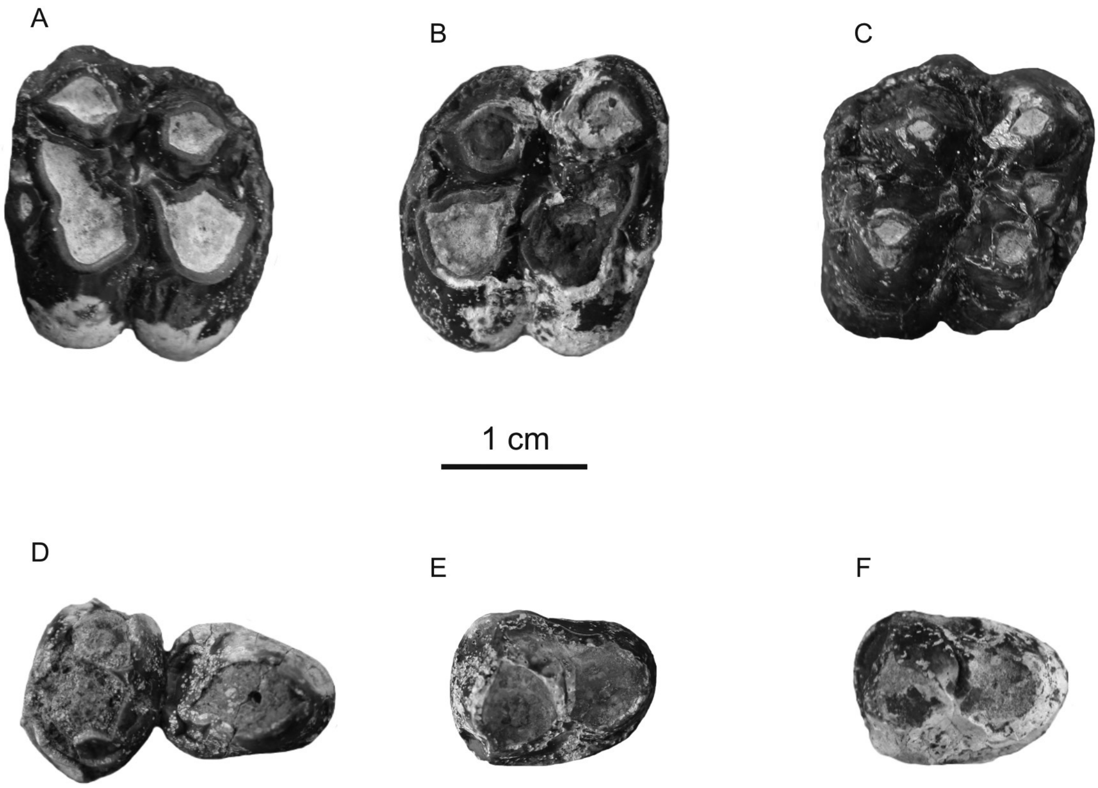


PLATE 8

Lower dentitions of *Anthracotherium pangan* in occlusal views.

A: right p3 (Kle-9);

B: right p3 (Bhn-1515);

C: right p4 (Bhn-1512);

D: left m1 (Tmk-97);

E: left m1 (Pkg-162);

F: right m1 (Npe-28);

G: left m2 (Tmk-77);

H: right m3 (Kmi-1);

I: right m3 (Tmk-66);

J.: right m3 (Pgn-4).

PLATE 8

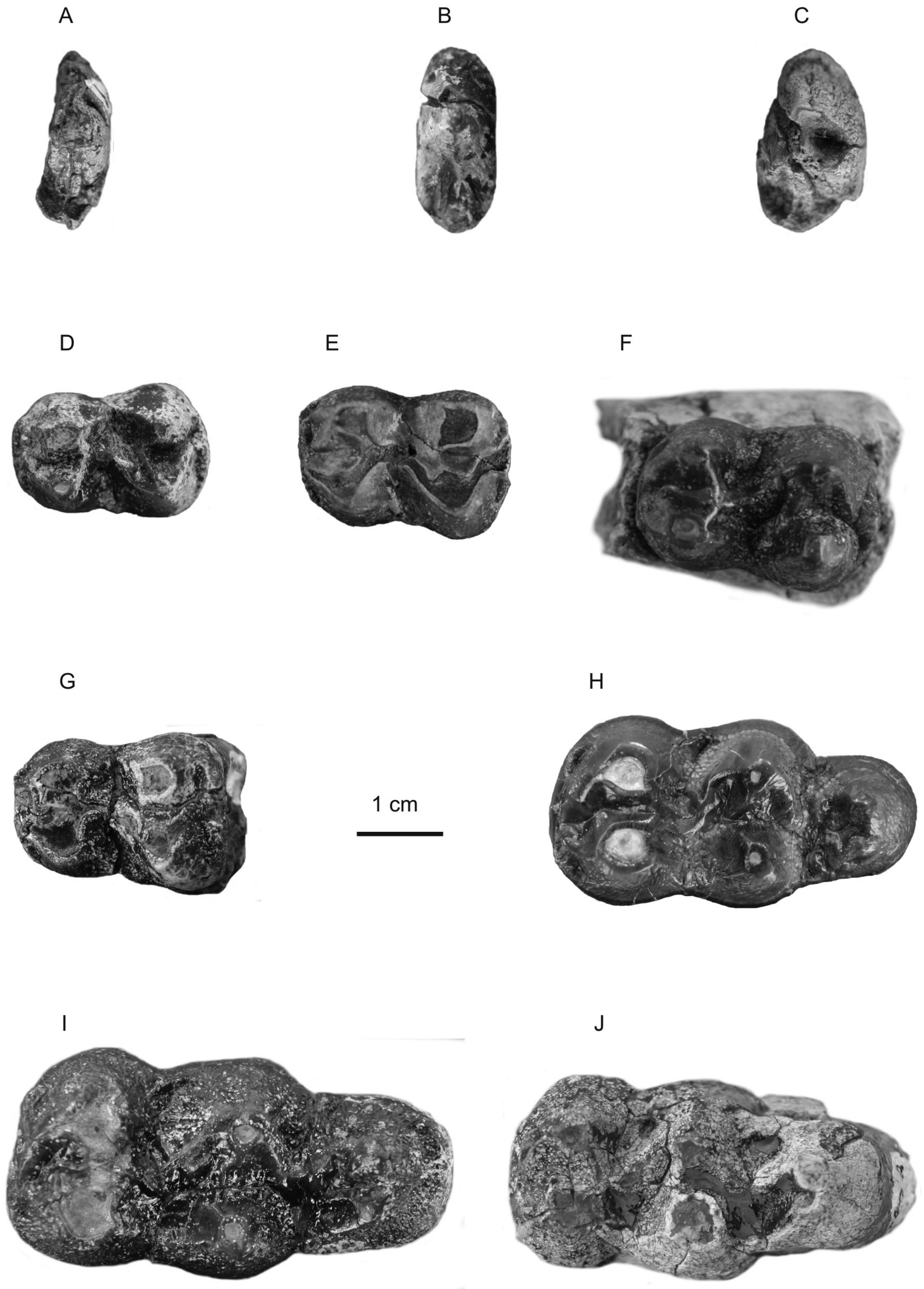


PLATE 9

Lower dentitions of *Anthracotherium crassum* in occlusal views.

A: right m2 (Tmk-5);
B: left m1 (Pgn-3);
C: left p4 (Tdg-19);
D: left p3 (Pgn-172);
E: right m2 (Tudw-278);
F: left m1 (Bhn-105);
G: right m2 (Bhn-44);
H: left p4 (Bhn-1516);
I: left m3 (Pkg-139);
J: right m2-3 (Kdw-140);
K: left m3 (Mta-17);
L: right m2-3 (Bhn-1057);
M: left m2-3 (Bhn-56).

PLATE 9

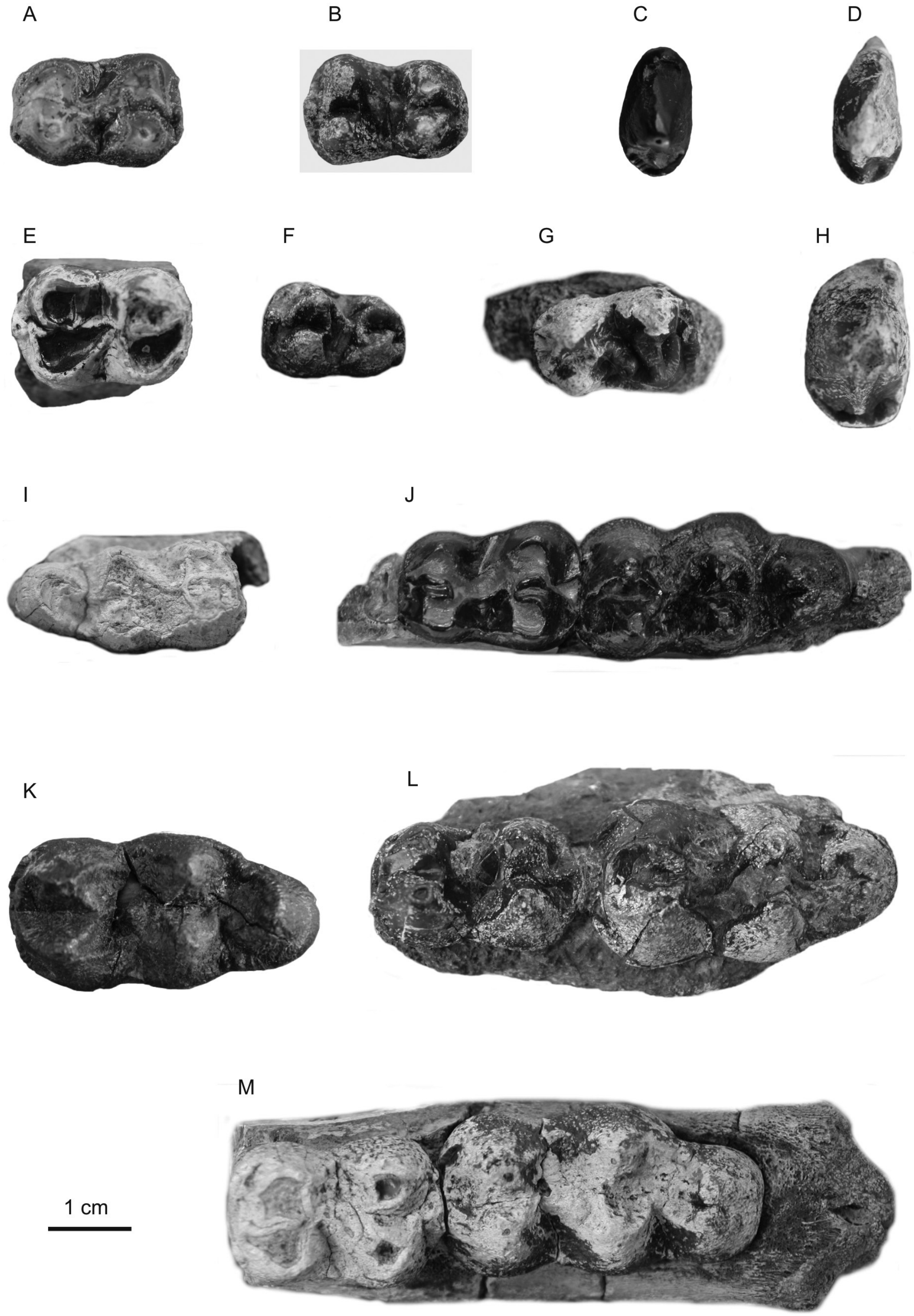


PLATE 10

Lower dentitions of *Anthracokeryx birmanicum*

A: left m1 in occlusal view (Bhn-34);

B: right m2 in occlusal view (Tudw-361);

C: right m2 in occlusal view (Bhn-25);

D: right m2 in occlusal view (Pkg-150);

E: right m1-2 in occlusal view (Mgg-13);

F: left fragmented mandible with m2 in occlusal view (Mgg-17);

G: right mandible with p4-m3 in lingual view (Pkg-28);

G1: occlusal view;

G2: buccal view.

PLATE 10

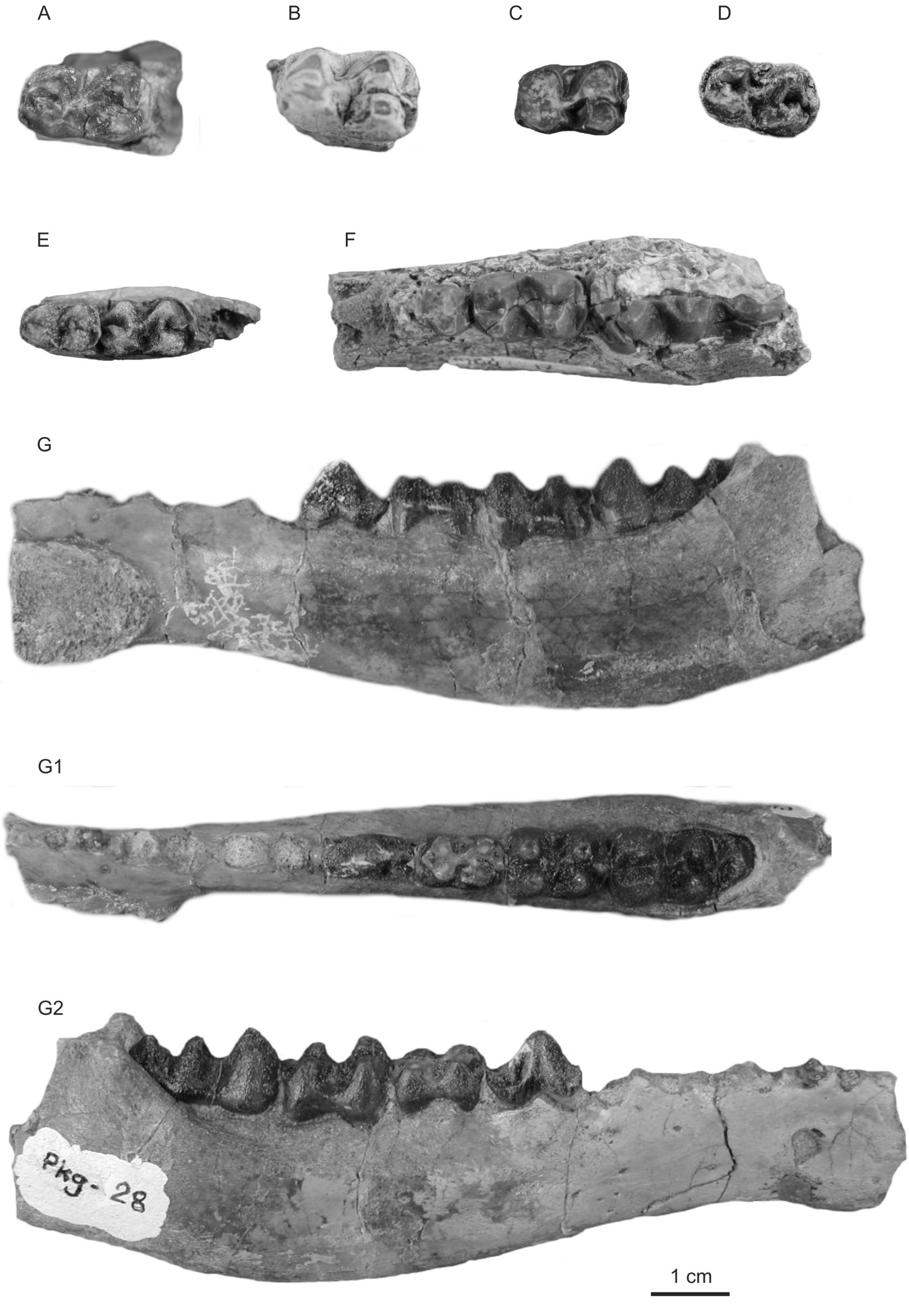


PLATE 11

Lower dentitions of *Anthracokeryx birmanicum*

A: right fragmented mandible with p4-m2-3 in occlusal view (Spg-34);

A1: buccal view;

B: right mandible with p4-m3 in occlusal view (Pkg-29);

B1: buccal view;

B2: lingual view.

PLATE 11

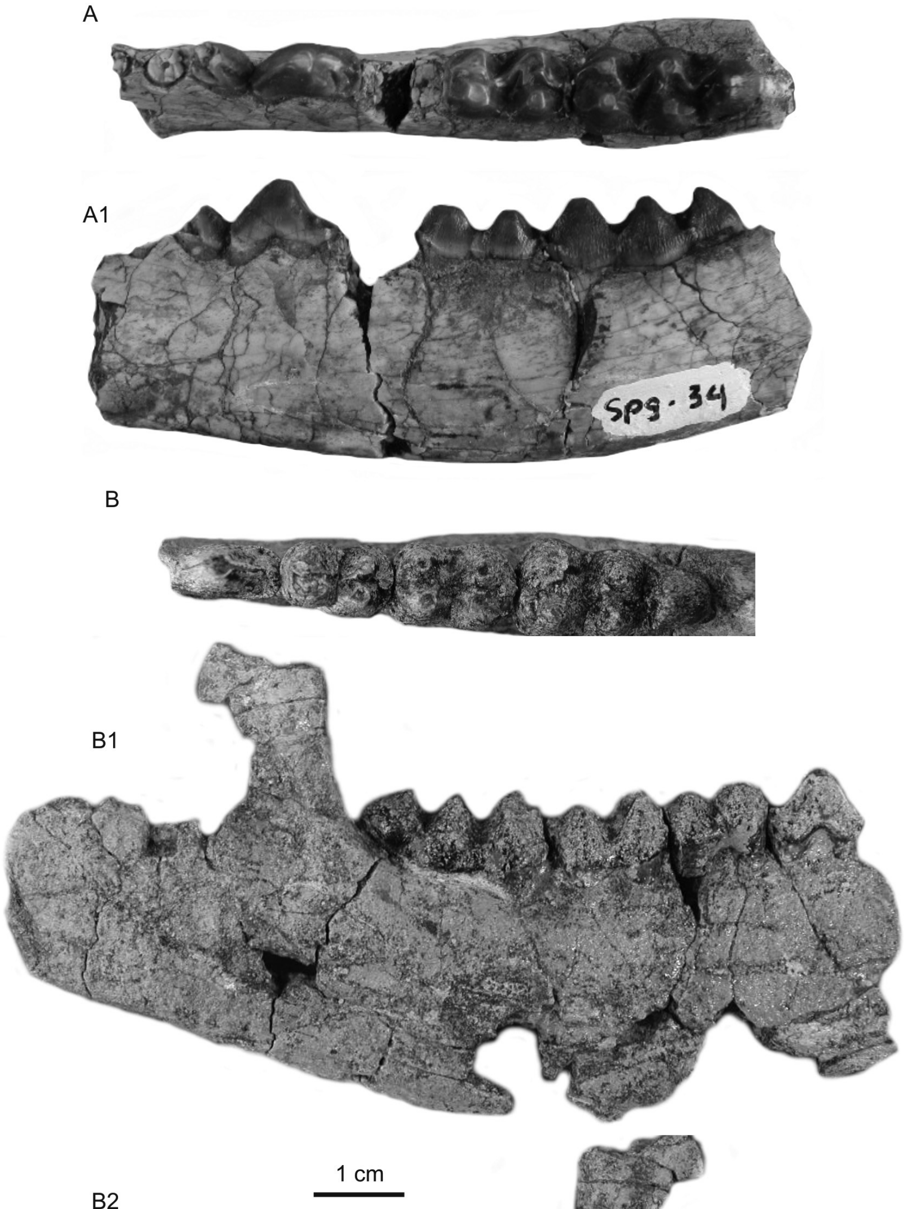


PLATE 12

Lower dentitions of *Anthracokeryx tenuis*

A: right m2 in occlusal view (Pkg-176);

B: left m1 in occlusal view (Tudw-281);

C: left p3 in occlusal view (Pkg-146);

D: right p4 in occlusal view (Lgn-6);

E: right fragmented mandible with m1-3 in occlusal view (Pkg-124);

E1: buccal view;

E2: lingual view;

F: right fragmented mandible with m2-3 in occlusal view (Bhn-1056);

F1: buccal view;

F2: lingual view;

G: left fragmented mandible with dp4-m1 in occlusal view (Pkg-9);

H: left fragmented mandible with m3 in occlusal view (Lma-42).

PLATE 12

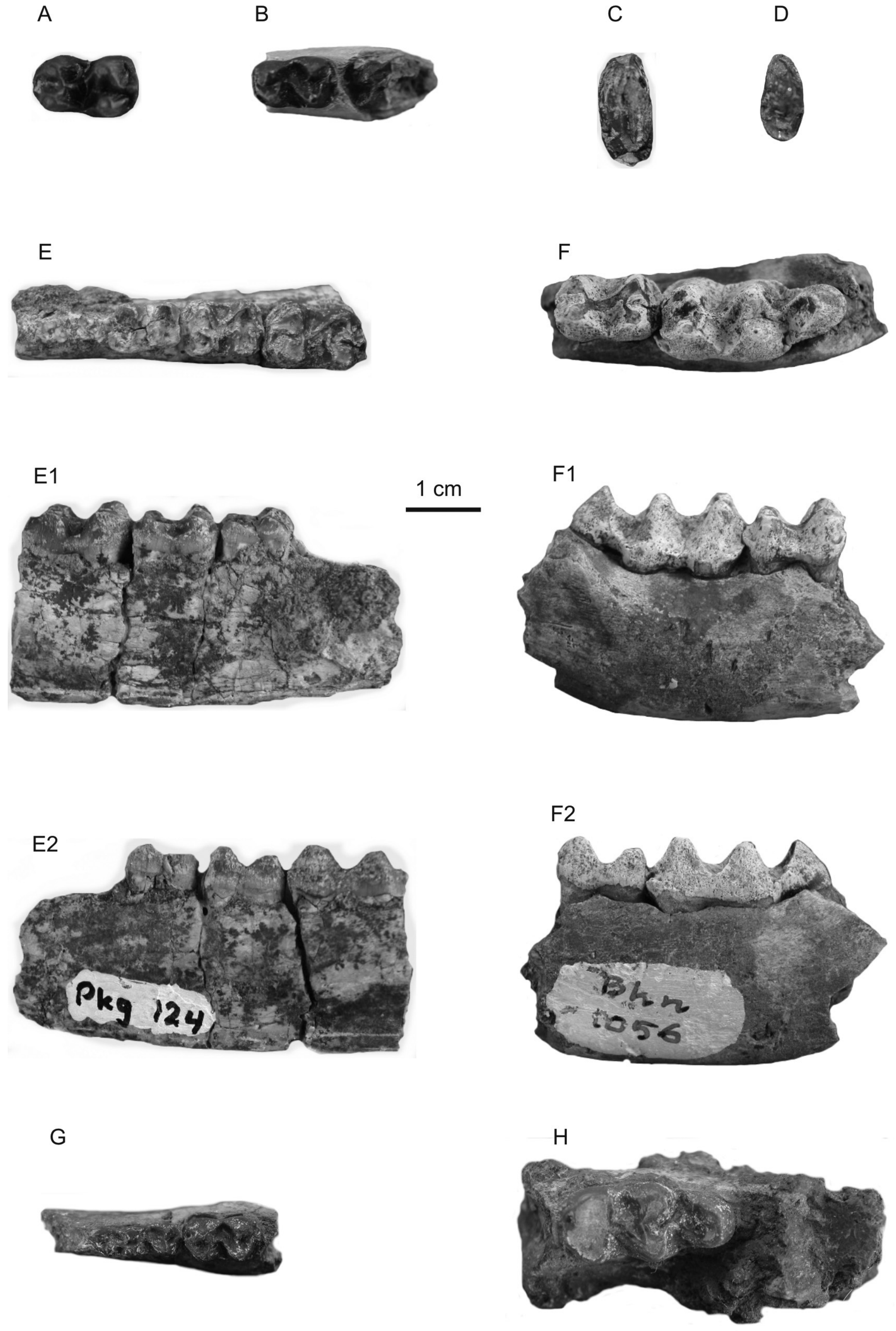


PLATE 13

Lower dentitions of *Anthracokeryx tenuis*

A: left mandible with p3-m3 in buccal view (Tudw-325);

A1: occlusal view;

A2: lingual view;

B: right mandible with p4-m3 in buccal view (Tudw-326);

B1: occlusal view;

B2: lingual view;

C: right fragmented mandible with m2 in occlusal view (Kdw-7);

D: left fragmented mandible with m2 in occlusal view (Tmk-78);

E: left fragmented mandible with m1-2 in occlusal view (Mta-30);

F: left fragmented mandible with m3 in occlusal view (Lgn-7).

PLATE 13

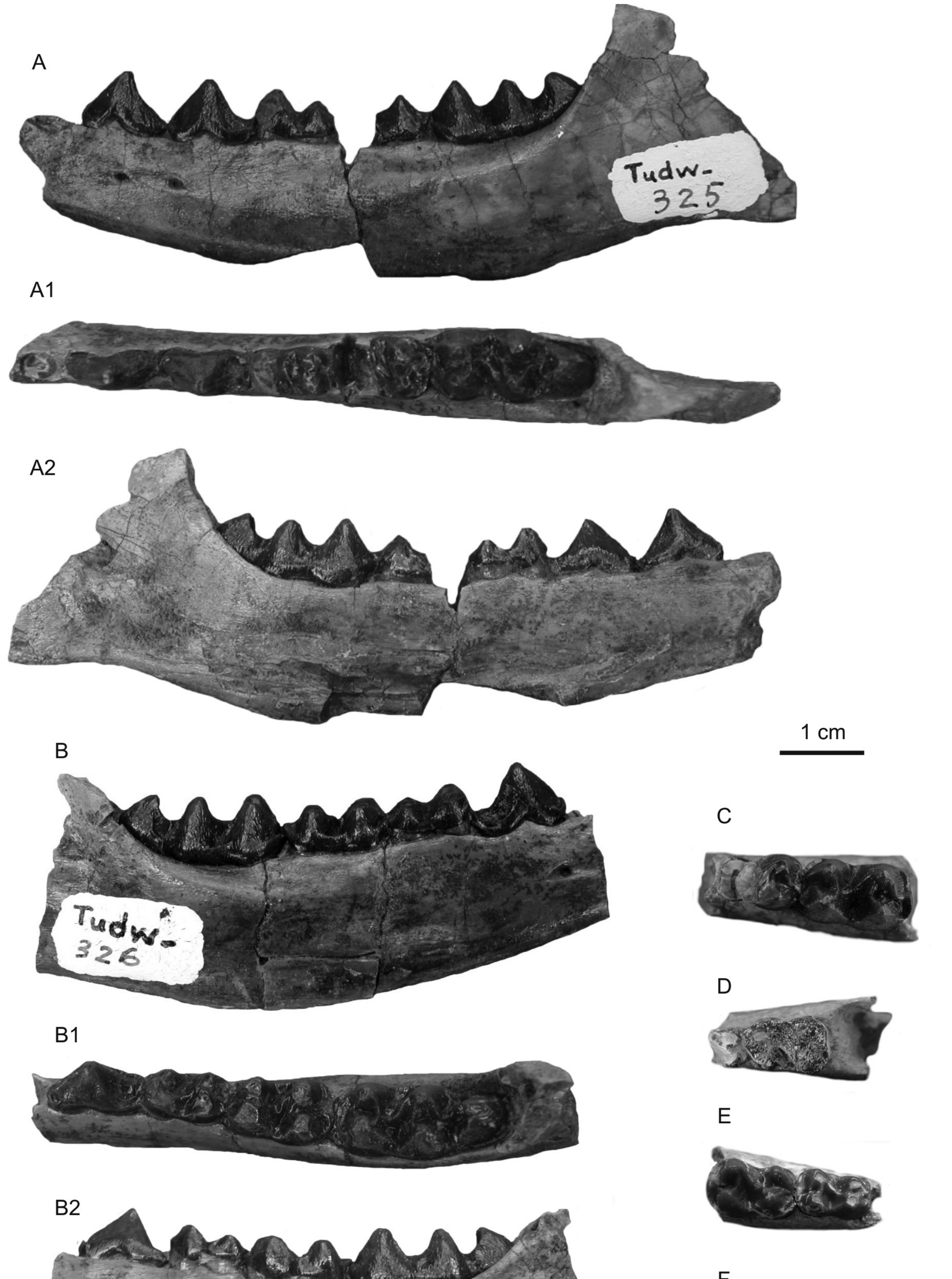


PLATE 14

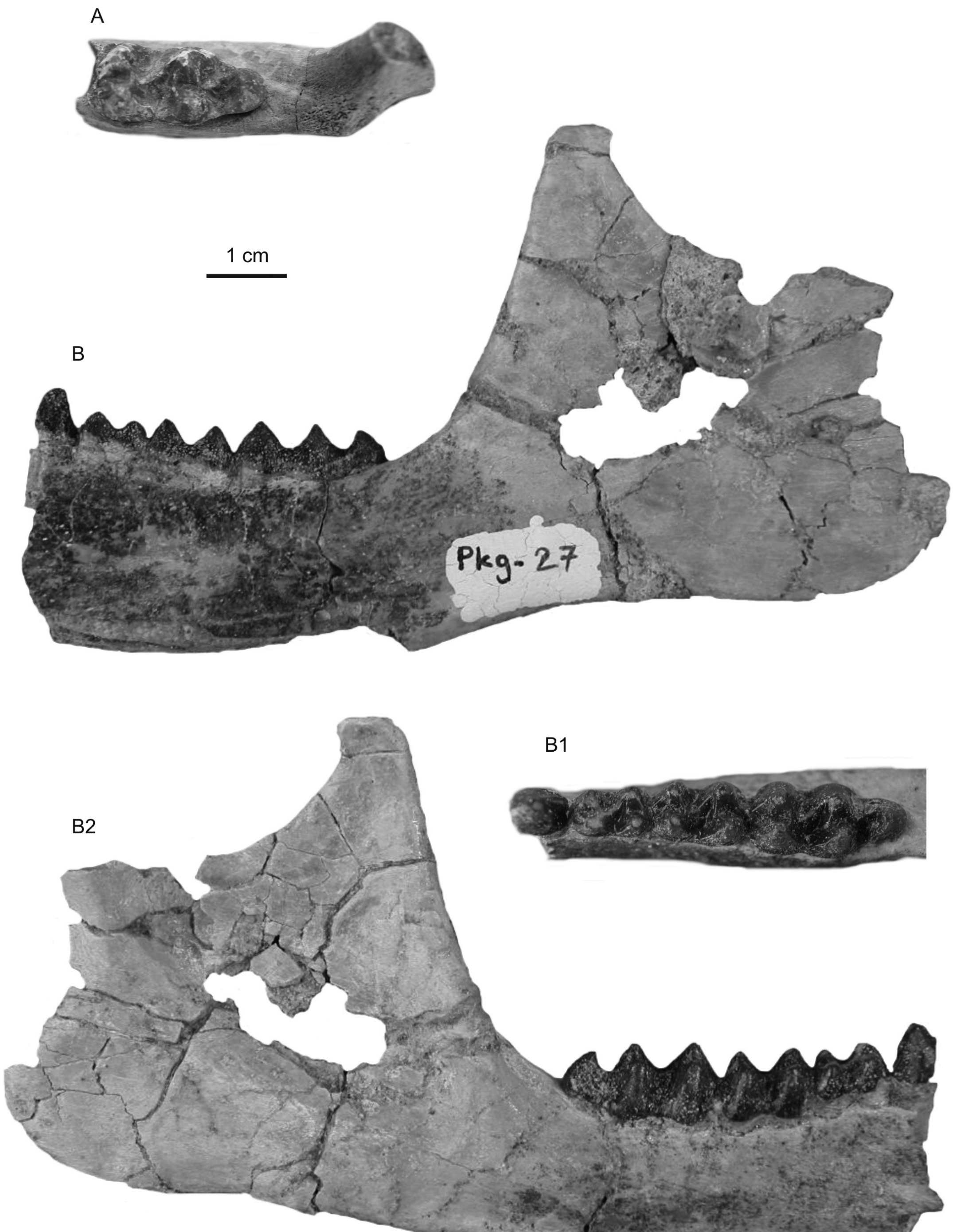
Lower dentitions of *Anthracokeryx tenuis*

A: right fragmented mandible with m3 in occlusal view (Pkg-7);

B: right mandible with distal part of p4 and m1-3 in lingual view (Pkg-27);

B1: occlusal view;

B2: buccal view.


A
1 cm
B
Pkg-27
B1
B2