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Postcranial materials of Pondaung mammals (middle Eocene, Myanmar)

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Abstract

Diversity of the Pondaung mammalian fauna (middle Eocene Myanmar) has been explored based on the dental materials. In this paper, we provided photos of skeletal materials of a rodent, carnivores, artiodactyls, and perissodactyls. Postcranial morphology of the endemic Pondaung mammals are compared with those of related fossil species from North America and Europe, revealing additional postcranial diversity in Eocene carnivorans, dichobunid artiodactyls, ruminants, and chalicotherioid perissodactyls. The postcranial materials indicated a presence of an additional taxon, a very small artiodactyl, that has not been known from the dental materials of the Pondaung mammals. The differences in postcranial morphologies suggested a divers locomotory behavior among the mammals of the Pondaung fauna, such that scansors, generalized terrestrialists with cursorial tendency, and generalized terrestrialists with digging adaptations were present among the carnivorous mammals, and that small-sized and medium-sized ungulates distributed on various stages of cursorial adaptations.

Introduction

The middle Eocene Pondaung Formation in central Myanmar has yielded numerous terrestrial vertebrate fossils since early 20th century (Pilgrim, 1925, 1927, 1928; Matthew, 1929; Colbert, 1937, 1938). An extensive paleontological expedition was conducted by the Myanmar government in 1997 (Pondaung Fossil Expedition Team, 1997). Since then, expeditions in the Pondaung area were carried out almost every year by Myanmar researchers and foreign research teams, such as Americans, French, and Japanese (Tsubamoto *et al.*, 2006, and cited therein). As a result of many new discoveries of new taxa, including several forms endemic to the fauna, the Pondaung fauna currently includes mammals from seven orders (25 families 37 genera 53 species) (Tsubamoto *et al.*, 2006). The number of known mammalian taxa from the Pondaung fauna tripled up during this past decade.

The Pondaung mammals have been studied mainly based on dentognathic materials, which are usually better preserved than bones and are useful for determining a generic or species-level taxonomy. This does not mean that skeletal materials were not collected during the expeditions but most of the skeletal materials have been neglected in descriptive works. As exceptions among tens of descriptive works on the Pondaung mammals, several papers have dealt with skeletal materials: the cranial fragments of primates (Takai *et al.*, 2003; Shigehara and Takai, 2004), the limb bones of primates (Ciochon *et al.*, 2001; Gebo *et al.*, 2002; Marivaux *et al.*, 2003; Kay *et al.*, 2004; Egi *et al.*, 2006), and the postcrania of creodonts (Egi *et al.*, 2005, in press).

In this paper, we introduce several postcranial materials of the Pondaung mammals that have not been described in anywhere previously. As proved by the above mentioned studies, skeletal materials are possible to provide new information on systematics and sensory and locomotory adaptations that can not be obtained from dentognathic materials. The materials presented here include limb bones of perissodactyls, artiodactyls, rodents, and carnivores.

Materials

The specimens presented in this paper were collected by the Pondaung Expedition Team in 1997 (Pondaung Fossil Expedition Team, 1997) and by the Myanmar-Japan Pondaung Paleontological Expedition Team since 1998 (Tsubamoto *et al.*, 2006). The former specimens are stored in National Museum of Myanmar in Yangon, and the latter are stored in Department of Geology, University of Yangon. These specimens have been catalogued under the serial NMMP-KU (National Museum - Myanmar - Paleontology - Kyoto University) specimen numbers by the Kyoto University field party (Tsubamoto *et al.*, 2000, 2006).

The Eocene Pondaung Formation is one of several Tertiary Formations widely distributed in central Myanmar (Bender, 1983). The vertebrate fossils were obtained from the lower part of the "Upper Member" of the Pondaung Formation (Aye Ko Aung, 1999, 2004). The age of this particular stratigraphic level has been calibrated as 37.2 +/- 1.3 Ma, the latest middle Eocene, based on the fission-track method applied on zircon grains from tuffaceous sediments (Tsubamoto *et al.*, 2002). The vertebrate fossil localities scatter in the east side of the Pondaung range (for a map, a locality list, and a detailed geological information, see Tsubamoto *et al.*, 2006). Locality of each specimen introduced in this study are listed in Tsubamoto *et al.* (2006: table 3).

Occurrence and taxonomic identifications of skeletal materials

It is usually difficult to make a taxonomic identification for a skeletal material when it is not associated with any dental parts. In the Pondaung localities, most of the specimens

Table 1. The mammals from the Pondaung fauna and their body size. Body size estimates were from Tsubamoto *et al.* (2005) for herbivores, Egi *et al.* (2005) for creodonts, and Egi (pers. data) for carnivorans. Approximate body mass range in kilograms are indicated in the parentheses.

size	primates	rodents	creodonts	artiodactyls	perissodactyls
			carnivorans	[ungulate indet.]	
very large					*Sivatitanops*
(>800)					*Paramynodon*
					Bunobrontops
					cf. *Metatelmatherium*
large					*Bunobrontops*
(100-500)					*Paramynodon*
				Anthracotherium	Amynodaontidae
			"*Pterodon*"		Cf. *Teletaceras*
medium			*Nimravus*	*Anthracotherium*	*Bahinolophus*
(8-60)			*Kyawdawia*		*Indolophus*
			Proviverrinae gen. nov.		"Eomoropidae"
			cf. *Chailicyon*	Artiodactyla indet.	*Eomoropus*
	Pondaungia		Amphicyonidae	*Pakkokuhyus*	
small	*Amphipithecus*		*Yarshea*	*Asiohomacodon*	
(2-8)	*Pondaungia*		Proviverrinae indet.		
	?Sivaladapidae		Nimravidae indet.	*Indomeryx*	
	Myanmarpithecus		*Vulpavus*	[*Hsanotherium*]	
very small	*Bahinia*				
(<1)	*Eosimias*	*Pondaungimys*			
	Primates indet.	Anomaluridae			

have been collected during surface perspectives after rainy seasons. The specimens are not moved very far from the original sediments, but the parts are hardly articulated. Among the nearly 2000 specimens collected (Tsubamoto *et al.*, 2006: table 3), only five skeletal materials are associated with dental materials that help taxonomic identification of the animal. Three of them were already published in previous papers (a frontal bone of *Amphipithecus*, Takai *et al.*, 2003; a humeral head of *Myanmarpithecus,* Egi *et al.*, 2006; postcrania and a skull of a creodont, Egi *et al.*, 2005). The other two specimens, limb bones of a small artiodactyl (*Indomeryx*) and those of a brontotheriid perissodactyl, are introduced in the below.

Because the taxonomy of a specimen is usually identified based on its dental morphology, taxonomic identification of isolated skeletal materials are limited. For certain skeletal parts such as ends of limb bones, we could identify their order level taxonomy based on the morphology. Then, assignments of skeletal materials to any of the known Pondaung mammals were attempted based on the size of animal for the materials. Body sizes of the Pondaung mammals have been estimated based on the occlusal surface area of molars (Egi *et al.*, 2004, 2005; Tsubamoto *et al.*, 2005; Table1). In a few occasions, there are no dentally known species in the body size range of the skeletal material of interest. In such case, the skeletal material suggests an existence of an additional indeterminate taxon that has not been known from any dental specimens.

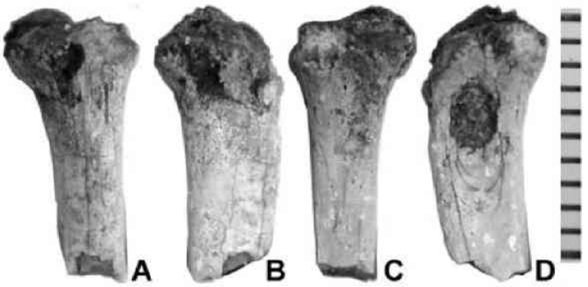

Figure 1. A left proximal tibia of a rodent, NMMP-KU 0827. **A,** anterior view. **B,** lateral view. **C,** posterior view. **D,** medial view. One division of scale equals 1 mm.

Rodent postcrania

(Figure 1)

NMMP-KU 0827 (Figure 1) is a left proximal tibia of a rodent, and its size is comparable to that of *Tupaia glis* (160 g; Macdonald, 2001). This body size corresponds to the anomalurid rodents from the Pondaung fauna (Tsubamoto *et al.*, 2005). The tibial tuberosity and the intercondylar eminence are weakly developed. The medial condyle is round. The anteroposterior length of the medial condyle is 4.9 mm. It is slightly higher than the medial one. An oval articulation for the fibula is located postrolaterally under the condyle. Overall, the morphology is similar to extant sciurids, suggesting scansorial to arboreal locomotion.

Carnivore postcrania

(Figures 2, 3)

Miacids (Figure 2)

NMMP-KU 1886 and 1379 are femoral fragments of carnivorans. These elements are comparable in size to those of a *Marten* with an associated body mass of 1.4 kg. A lower second molar of a miacid carnivoran, *Vulpavus*, has been reported from the Pondaung fauna (Takai and Shigehara, 2004). This tooth is about the size of *Miacis petilus* from North America (= 1.3 kg; Heinrich and Rose, 1995). It seems reasonable to consider that the postcranial materials belonged to the small species of *Vulpavus*.

In the proximal femur (NMMP-KU 1886; Figure 2A), the femoral head is spherical, and the fovea capitis is located slightly posteriorly from the most medial point. The femoral neck is short. The greater tuberosity is lower than the femoral head, and the anterior rugose surface extends inferiorly. In the distal femur (NMMP-KU 1379; Figure 2B), the medial and lateral condyles are about the same in width. The condyles are not elongated superoinferiorly or anteroposteriorly. The patellar groove is shallow. It is not as wide as that of arboreal carnivorans such as *Nandinia*, and it is broader and flatter than that of *Felis* and *Vulpes*. Overall, these morphologies agree with those of miacid carnivorans such as *Miacis* and *Vulpavus*, which have been estimated as arboreal to scansorial animals (Heinrich and Rose,

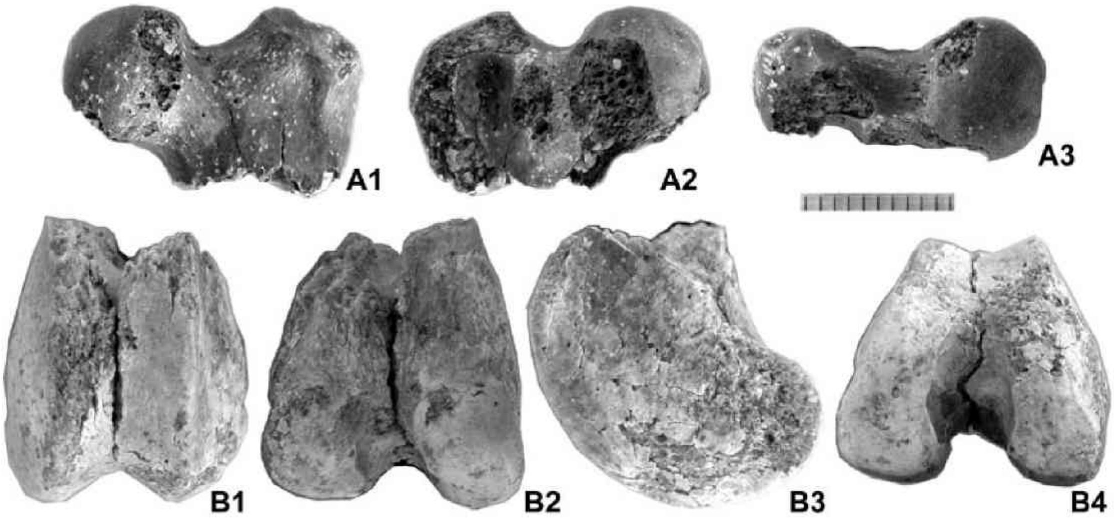

Figure 2. Femoral fragments of miacid carnivorans. **A**, a left proximal femur, NMMP-KU 1886; **A1,** anterior view; **A2,** posterior view. **A3,** superior view. **B,** a left distal femur, NMMP-KU 1379; **B1,** anterior view; **B2,** posterior view; **B3,** lateral view; **B4,** distal view. One division of scale equals 1 mm.

1995, 1997).

Medium-sized carnivoran (Figure 3A-C)

NMMP-KU 0689 consists of a medial part of the distal humerus, a humeral shaft, a radial head, and a cranial fragment. It belonged likely to a wolverine-size animal (10-15 kg; MacDonald, 2001). Creodonts and carnivorans of similar body size have been known from the Pondaung fauna. The deltopectoral and supinator crests are poorly developed on the humeral shaft of NMMP-KU 0689 (Figure 3A). This moderately developed deltopectoral crest suggests that NMMP-0689 is not closely related to an advanced Old World proviverrine creodont (Egi *et al.*, 2005) or an amphicyonid such as *Guangxicyon* (Zhai *et al.*, 2003); thus, the best candidate for NMMP-KU 0689 is cf. *Chailicyon* at present.

At the distal end of the humerus (Figure 3B), the medial epicondyle is unreduced and superoinferiorly thick. A large entepicondylar foramen is present. The medial edge of the trochlea is sharp, and the trochlea is conical. The olecranon fossa is not perforated, but deep. Length and width of the radial head (Figure 3C) are 14.47 and 9.18 mm, respectively. The capitular eminence is clear. The medial lobe is ovoid, and the smaller lateral lobe is semi-rectangular. The radial tuberosity is strong. The radial neck is narrow relative to the head. The morphology of these forelimb fragments suggests absence of powerful shoulder muscles (lack of fossorial adaptations), a limited pronation ability (not specialized for arboreal adaptations), and a slight specialization to fore-aft movements (tendency to cursoriality). This animal was likely to be a generalized terrestrialist that is exampled by an extant civet.

Medium-sized carnivorous mammals (Figure 3D, E)

Two proximal radii, NMMP-KU 1391 (Figure 3D) and NMMP-KU 1313 (Figure 3E), belong to carnivores larger than NMMP-KU 0689 (Figure 3C). The sizes of the radial heads

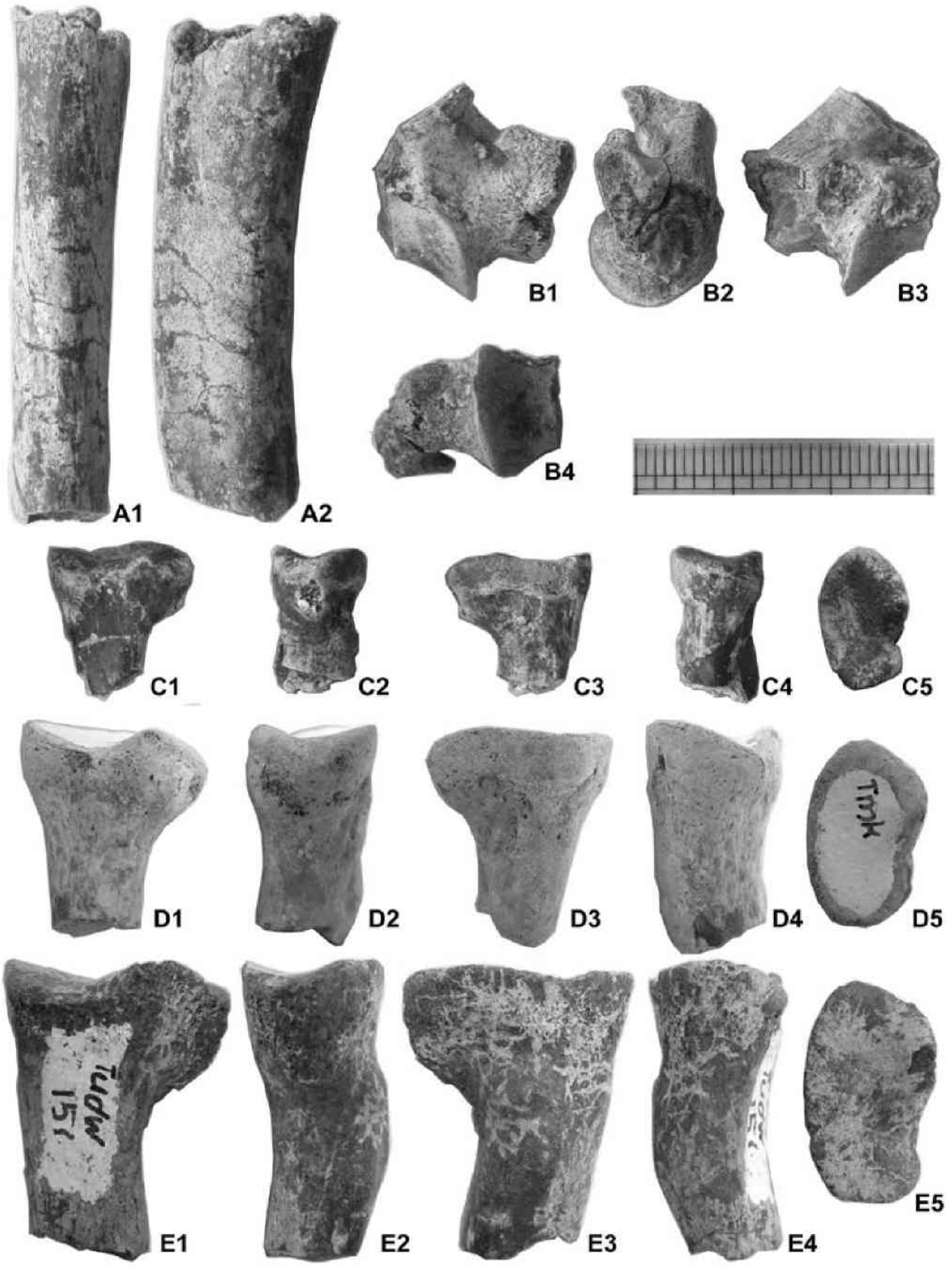

Figure 3. Forelimb fragments of carnivorans. **A,** humeral shaft: **A1,** anterior view; **A2,** lateral view. **B,** distal humeral fragment: **B1,** anterior view; **B2,** medial view; **B3,** posterior view; **B4,** distal view. **C, D, E,** proximal radii: **C1, D1, E1,** lateral view; **C2, D2, E2,** posterior view; **C3, D3, E3,** medial view; **C4, D4, E4,** anterior view. **A, B, C,** NMMP-KU 0689 (an associated carnivoran). **D,** NMMP-KU 1391 (cf. proviverrine creodont). **E,** NMMP-KU 1313 (carnivoran). One division of scale equals 1 mm.

are 18.21 x 11.96 mm in NMMP-KU 1391 and 21.98 x 12.77 mm in NMMP-KU 1313. Sizes of these materials fall in the range of proviverrine creodonts (*Kyawdawia* and proviverrinae gen. nov.) and a nimravid carnivoran (*Nimravus* sp. cf. *N. intermedius*). Locomotion of *Kyawdawia* has been estimated as a generalized terrestrialist with a powerful forelimb movements (Egi *et al.*, 2005), and that of nimravids has been suggested as scansorial (Van

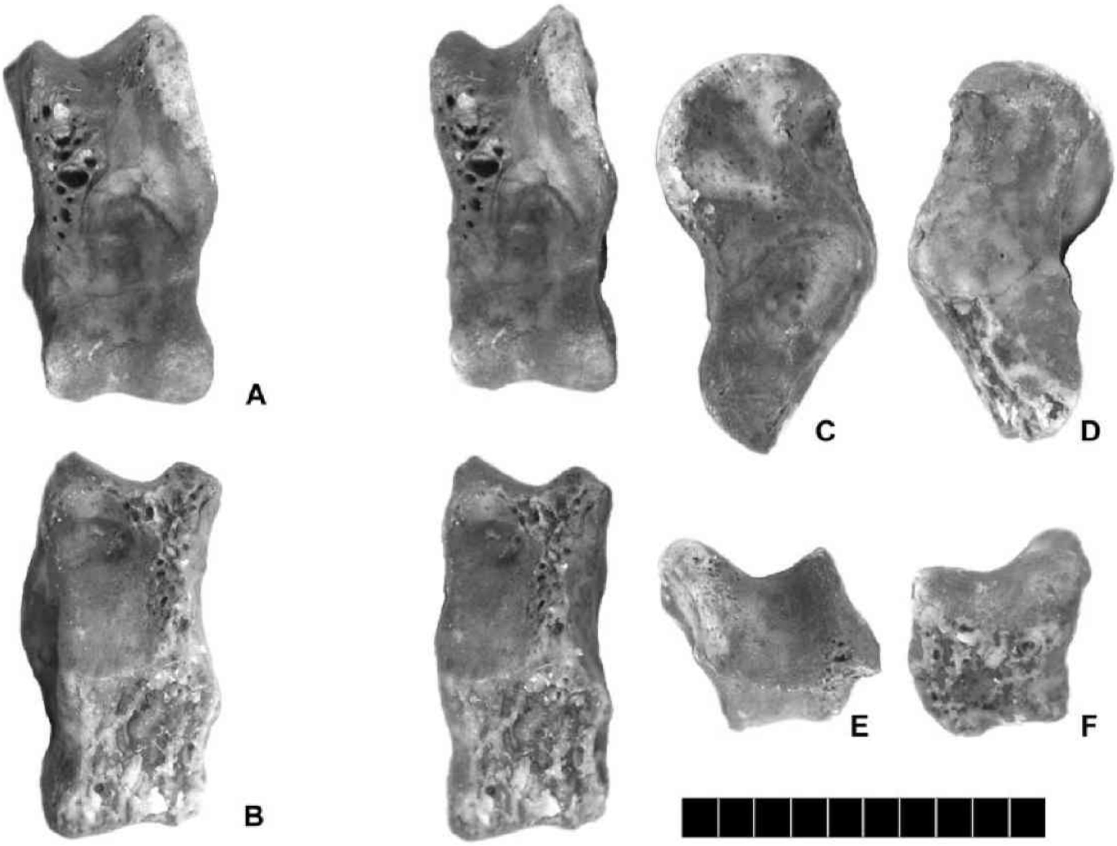

Figure 4. A left astragulus of a very small artiodactyl (Artiodactyla indet.), NMMP-KU 0826. **A,** dorsal view (a stereo pair). **B,** plantar view (a stereo pair). **C,** lateral view. **D,** medial view. **E,** proximal view; **F,** distal view. One division of scale equals 1 mm.

Valkenburgh, 1985). Both of the proximal radii (Figure 3D, E) have a clear capitular eminance, a clear separation between the medial and lateral lobes, and a strong radial tuberosity. NMMP-KU 1391 differs from the others in relatively wider radial neck. Because the powerful forelimb movements of the Pondaung proviverrine creodonts likely required a robust radius, this specimen seems to have belonged to a proviverrine creodont rather than to a carnivoran. The radial head of NMMP-KU 1313 is rectangular compared with the ovoid radial heads of NMMP-KU 0689 and 1391, suggesting that NMMP-KU 1313 has some cursorial adaptations (MacLeod and Rose, 1993).

Artiodactyl postcrania

(Figures 4-10)

Very small artiodactyl (Figure 4)

NMMP-KU 0826 (Figure 4) is a left astragalus of a very small artiodactyl. The estimated body mass of this very small artiodactyl (NMMP-KU 0826) using the regression equation by Martinez and Sudre (1995) is about 1181 g. This body mass is much smaller than the estimated body masses of the previously reported small Pondaung artiodactyls (*Indomeryx* and *Asiohomacodon*: the range is 2.3 – 6.3 kg) (Tsubamoto *et al.*, 2005; Table 1).

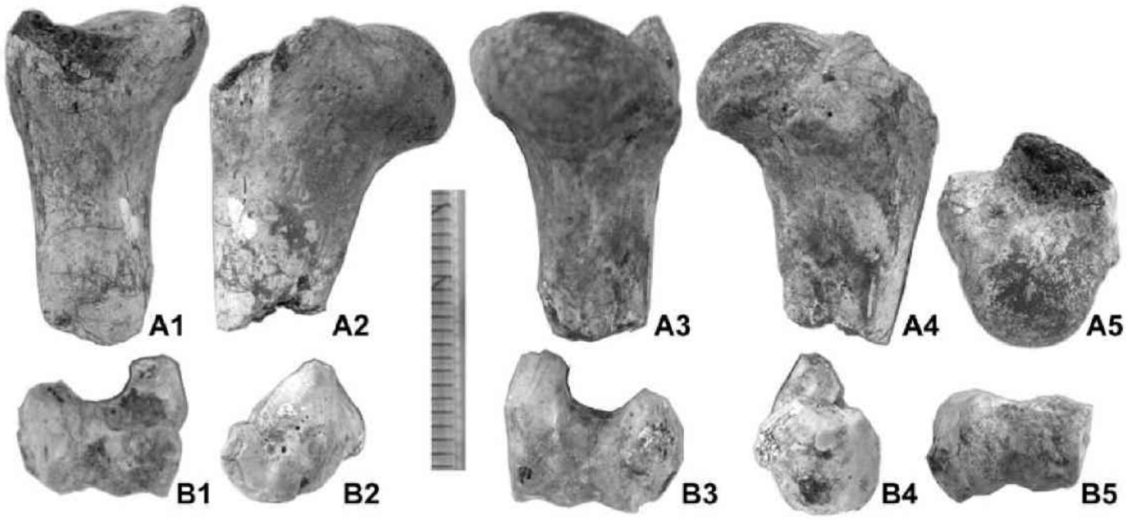

Figure 5. Right humeral fragments of *Indomeryx*, NMMP-KU 0712 (associated with a molar). **A,** proximal humerus; **A1,** anterior view; **A2,** medial view; **A3,** posterior view; **A4,** lateral view; **A5,** proximal view. **B,** distal humerus; **B1,** anterior view; **B2,** medial view; **B3,** posterior view; **B4,** lateral view; **B5,** distal view. One division of scale equals 1 mm.

The size of this animal is comparable to small Eocene dichobunids such as *Diacodexis* and *Messelobunodon* (Rose, 1982, 1985; Martinez and Sudre, 1995), and this astragalus suggests an occurrence of a very small (*Diacodexis*-size) artiodactyl species in the Pondaung fauna.

The distoplantar portion of the astragalus is broken. This astragalus is slender: the length is 11.13 mm, the width is 4.89 mm, and the dorso-plantar height (Martinez and Sudre, 1995) is 4.70 mm. NMMP-KU 0826 is slender than astraguli of *Cainotherium* (Cainotheriidae; Hülzeler, 1936), *Messelobunodon* (Franzen, 1981), and *Diacodexis* (Rose, 1982, 1985). The length/width ratio of NMMP-KU 0826 is 2.28, which is close to that of the astragalus of *Doliochoerus* (the ratio = 2.3) (Martinez and Sudre, 1995). The distal trochlea is slightly diagonal to the tibial trochlea, but not so diagonal as in an extant *Sus*. The distal surface bears a weakly developed keel that separate the IVth tarsal (the cuboid) articulation from the central tarsal (the navicular) articulation.

Indomeryx (Figures 5, 6)

NMMP-KU 0712 (Figure 5) is associated with a molar talonid, and is identified as *Indomeryx* (Ruminantia). The size of these elements are approximately comparable to that of a *Lepus* with an associated body mass of 2.15 kg. Thus, this specimen is a right size for the smaller species of *Indomeryx*, *I. arenae* (2.3 kg; Tsubamoto *et al.*, 2005). Several other limb bone fragments (NMMP-KU 0115, 1050, 1359, and 1083; Figure 6) of small artiodactyls seem to have belonged to *Indomeryx* (2.3 – 4.1 kg; Tsubamoto *et al.*, 2005) based on the size.

The humeral head (Figure 5A) is hemispherical in the lateral aspect and flat in the posterior aspect. The greater tuberosity is large and thick. Its height is unknown because of the damage on the specimen. The bicipital groove is shallow, and the deltopectoral crest is poorly developed. The proximal shaft surface is smooth, showing more similarity

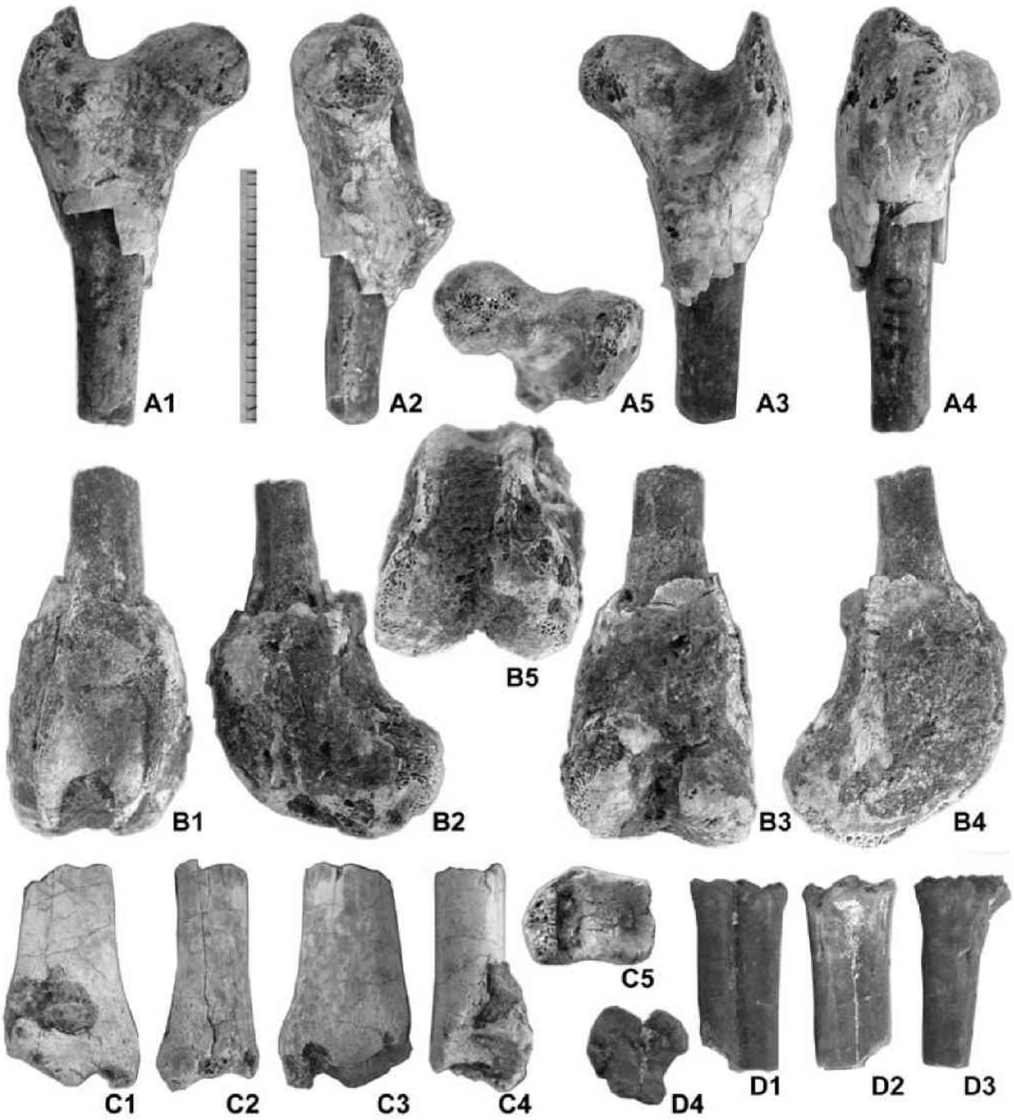

Figure 6. Hindlimb fragments of ?*Indomeryx*. **A,** proximal femur, NMMP-KU 0115; **A1,** anterior view; **A2,** medial view; **A3,** posterior view; **A4,** lateral view; **A5,** proximal view. **B,** distal femur, NMMP-KU 1050; **B1,** anterior view; **B2,** medial view; **B3,** posterior view; **B4,** lateral view; **B5,** distal view. **C,** distal tibia, NMMP-KU 1359; **C1,** anterior view; **C2,** medial view; **C3,** posterior view; **C4,** lateral view; **C5,** distal view. **D,** proximal metatarsals III, IV, and a vestigial V, NMMP-KU 1083; **D1,** dorsal view; **D2,** plantar view; **D3,** lateral view; **D4,** proximal view. One division of scale equals 1 mm.

to *Diacodexis* (Rose, 1985) than to *Cainotherium* (Hülzeler, 1936). The distal humerus (Figure 5B) is narrow. *Indomeryx* is more advanced than *Diacodexis* (Rose, 1985, 1990) and *Cainotherium* (Hülzeler, 1936) in lacking the lateral condyle, but more primitive than recent ruminants such as *Cervus* and *Capra* in retaining a small medial condyle. The olecranon fossa is perforated as a foramen. The articulation is cylindrical. The capitulum is modified into a narrow intercondylar ridge as in dichobunids and other ruminants.

The femoral head (Figure 6A) is superoinferiorly compressed, so that it is in an intermediate condition between those of dichobunids and *Cainotherium* (Hülzeler, 1936; Rose, 1985) and those of ruminants. The neck is short. Similar to dichobunids and *Cainotherium*, the greater trochanter protrudes slightly above the head. The lesser trochanter projects posteromedially, similar to tragulids and *Cainotherium* but dissimilar to dichobunids (Rose, 1985). The distal femur (Figure 6B) is mediolaterally narrow. The patellar groove is narrow and deep. The medial ridge of the patellar groove is more elevated and thicker than the lateral one. These features are shared with dichobunids and tragulids (Rose, 1985). The distal tibia (Figure 6C) has two deep parallel grooves for the astragulus. The lateral surface of the distal part of the shaft is flat, providing an articular surface for the fibular malleolus. The proximal parts of the metatarsal III and IV (Figure 6D) indicate that the metatarsals are attached to one another but have not been fused. The metatarsals seem to be more gracile than those of *Cainotherium* and extant tragulids (Hülzeler, 1936; Rose, 1985). The size of the metatarsal IV is relatively reduced compared with that of *Cainotherium* and *Diacodexis* (Hülzeler, 1936; Rose, 1985) and becomes similar to the size of the metatarsal III. The metatarsal IV bears a small fragment of a vestigial metatarsal V, suggesting that the reduction of this digit is more progressed in *Indomeryx* than in *Cainotherium* and *Diacodexis* (Hülzeler, 1936; Rose, 1985). A small metatarsal II was probably present and articulated at the convex of the medial surface of the proximal metatrasal III.

Asiohomacodon (Figures 7, 8)

Asiohomacodon (Dichobunidae) is another small artiodactyl that is known from the Pondaung fauna, and it is slightly larger (6.3 kg) than *Indomeryx* (Tsubamoto *et al.*, 2005). The distal humeri of NMMP-KU 1803 and 1013 (Figure 7A, B) are elements of a small artiodactyl, and are larger than the *Indomeryx* humerus. These distal humeri differ from that of *Indomeryx* and are similar to that of dichobunid such as *Diacodexis* (Rose, 1985) in having a better developed medial condyle and a swelling of the lateral condyle. Thus, the size and the morphology agree with the assignment of this material to the dichobunid *Asiohomacodon*. The olecranon fossa is perforated, and the capitulum is cylindrical as in other small artiodactyls. The capitulum is relatively wider than that of *Diacodexis* and *Indomeryx*, and the medial trochlear edge protrudes slightly distally.

The proximal radius of *Asiohomacodon* (Figure 7C) is similar to that of *Diacodexis* (Rose, 1985, 1990). The morphology of the medial surface of the shaft indicates that the radius is appressed to the ulna. The radial head surface is indented by a shallow groove for the intercondylar ridge of the capitulum, indicating that the radial head articulates with the whole distal humeral articulation. The medial lobe is more distally deflected in *Asiohomacodon* than in *Diacodexis*, that seems to be related with the distal protrusion of the medial edge of the humeral trochlea. Distally, the radius (Figure 7D) has two articular facets for carpals, presumably for the radial carpal (the scaphoid) and for the intermediate carpal (the lunate). The rugose surface at the posteromedial side of the distal shaft indicates that the reduction of the ulna was not as great as that of extant ruminants. The distal part of the ulna was bound to the radius by connective tissue fibers.

The distal tibia (Figure 8A) is associated with a distal humerus (NMMP-KU 1803). The

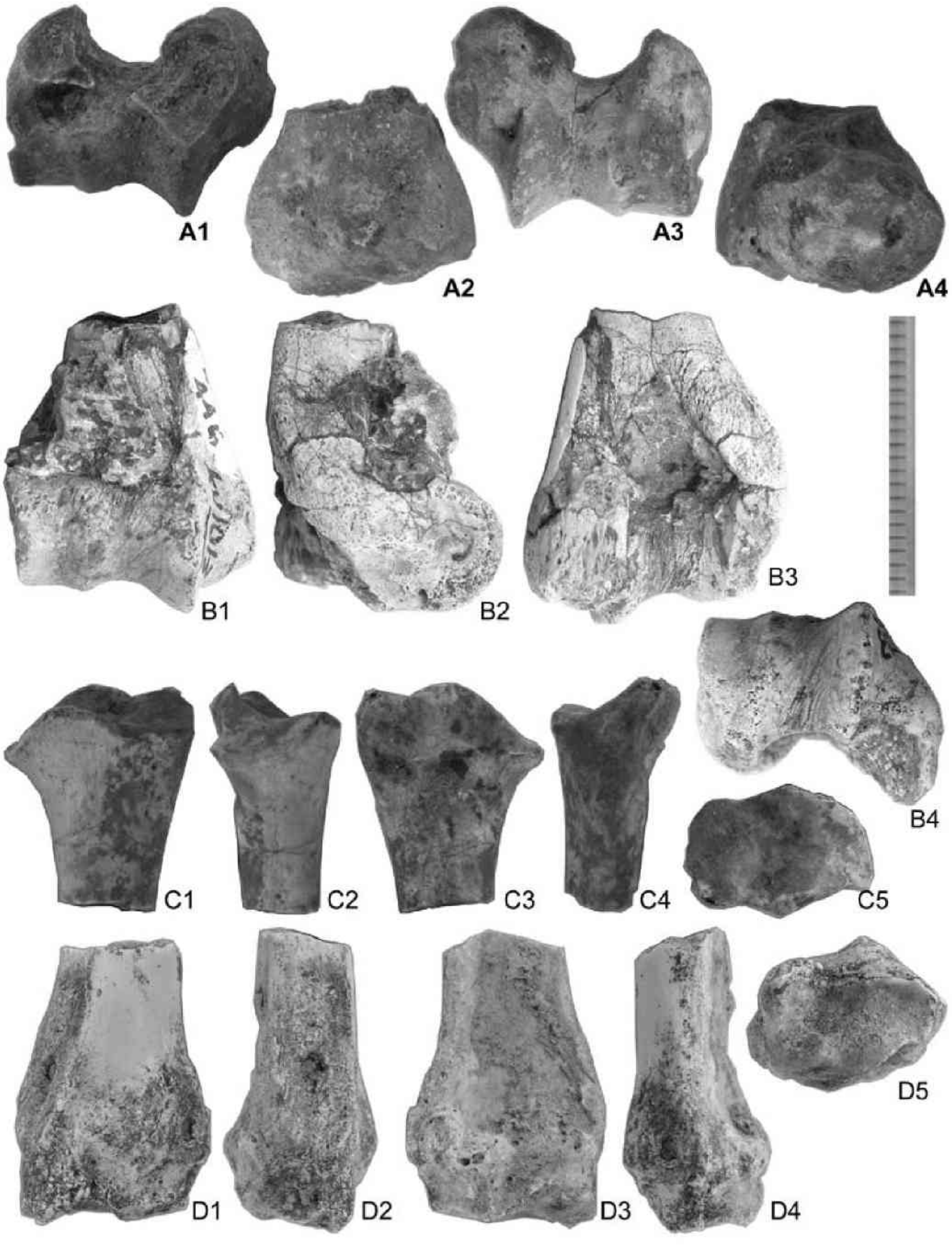

Figure 7. Forelimb fragments of small artiodactyls (?*Asiohomacodon*). **A, B,** distal humerus; **A1, B1,** anterior view; **A2, B2,** medial view; **A3, B3,** posterior view; **A4,** lateral view; **B4,** distal view. **A,** NMMP-KU 1803 (associated with the distal tibia in Figure 8A). **B,** NMMP-KU 1013. **C,** proximal radius, NMMP-KU 1372: **C1,** anterior view; **C2,** medial view; **C3,** posterior view; **C4,** lateral view; **C5,** proximal view. **D,** distal radius, NMMP-KU 1882: **D1,** anterior view; **D2,** medial view; **D3,** posterior view; **D4,** lateral view; **D5,** distal view. One division of scale equals 1 mm.

distal tibia is mediolaterally narrow. There is an articular surface for the fibular malleolus on the lateral side of the distal shaft, similar to that of *Indomeryx*. The two grooves for the astragular trochlea are deep, and the medial one is longer. The astragulus (Figure 8B) is relatively slender as in *Cainotherium* (Hülzeler, 1936), *Messelobunodon* (Franzen, 1981),

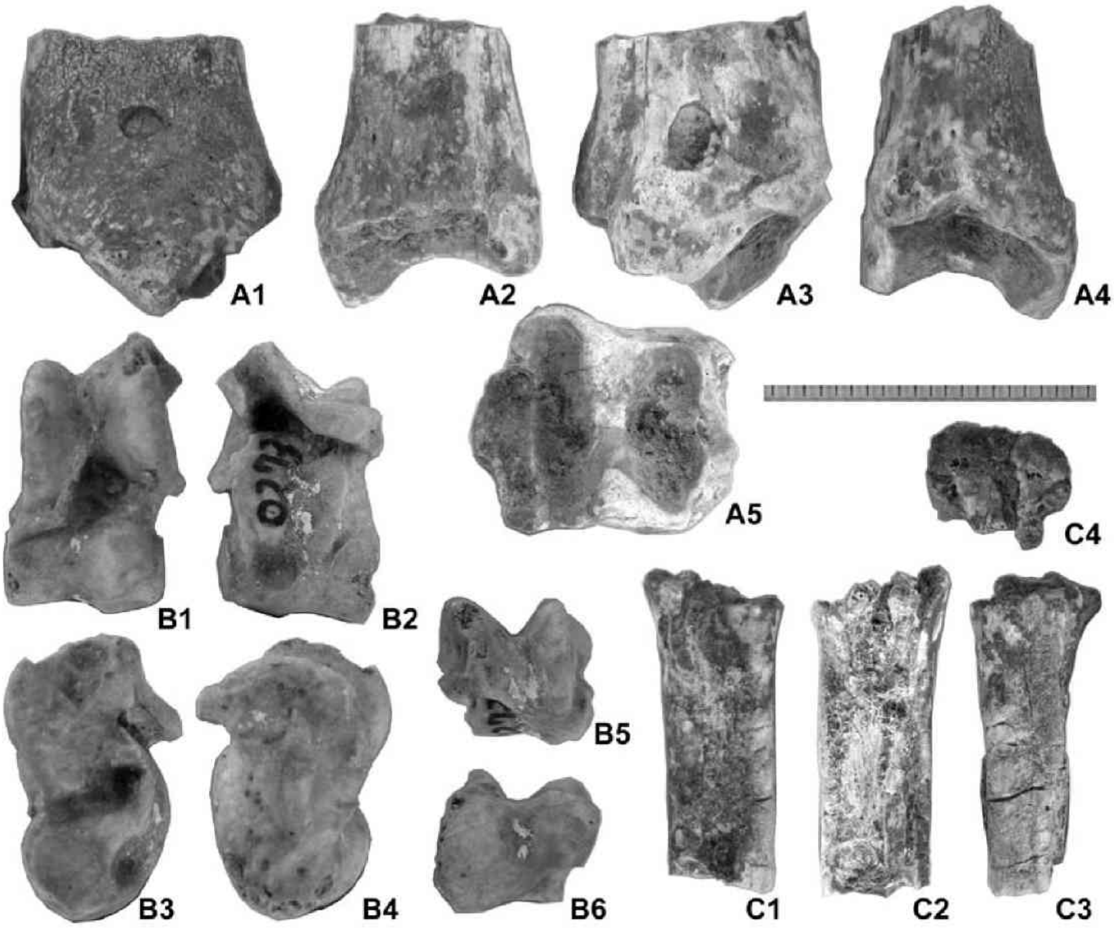

Figure 8. Hindlimb fragments of small artiodactyls (?*Asiohomacodon*). **A,** distal tibia, NMMP-KU 1803 (associated with the distal tibia in Figure 7A): **A1,** anterior view; **A2,** medial view; **A3,** posterior view; **A4,** lateral view; **A5,** distal view. **B,** astragulus, NMMP-KU 0273: **B1,** dorsal view; **B2,** plantar view; **B3,** lateral view; **B4,** medial view; **B5,** proximal view; **B6,** distal view. **C,** proximal metatarsals III, IV, and a vestigial V, NMMP-KU 1077; **C1,** dorsal view; **C2,** plantar view; **C3,** lateral view; **C4,** proximal view. One division of scale equals 1 mm.

and *Diacodexis* (Rose, 1982, 1985). The tibial trochlea is very deep and slightly diagonal to the distal trochlea. There is a distinct keel that separates the articulation for the central tarsal (the navicular) from that for the IVth tarsal (the cuboid). At the plantar side, the articulation with the calcaneum is limited to the two thirds of the bone width. NMMP-KU 1077, proximal metatarsals, are covered with matrices, but some morphologies are still identifiable. As in *Indomeryx*, these slender metatarsals are not fused. The metatarsal V is reduced and sits at posterolateral side of the metatarsal IV. The metatarsal IV is slightly wider than the metatarsal III in this specimen. This feature is similar to other dichobunids, such as *Diacodexis* and *Bunolophus* (Rose, 1985) rather than to *Indomeryx*.

Anthracotherium (Figures 9, 10)

Anthracotherium (Suiformes; Anthracotheriidae) is the most abundant mammal in the Pondaung fauna, consisting of 40 % of the identifiable dental materials (Tsubamoto *et al.*, 2005). Four species of *Anthracotherium* are presently known from the fauna, and their body

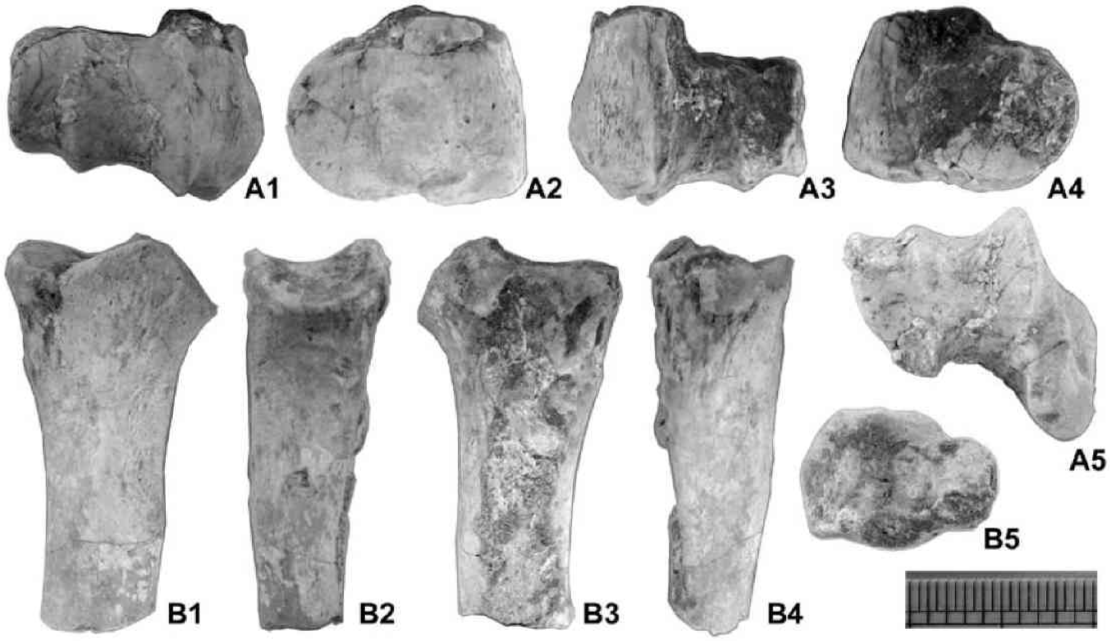

Figure 9. Forelimb fragments of *Anthracotherium*. **A,** distal humerus, NMMP-KU 1356; **A1,** anterior view; **A2,** medial view; **A3,** posterior view; **A4,** lateral view; **A5,** distal view. **B,** proximal radius, NMMP-KU 1590; **B1,** anterior view; **B2,** medial view; **B3,** posterior view; **B4,** lateral view; **B5,** proximal view. One division of scale equals 1 mm.

size ranges from 16 to 237 kg (Tsubamoto *et al.*, 2005). Several distal tibiae and astraguli of *Anthracotherium* have been collected from the fauna, reflecting the abundance of the genera. However, the number of specimens that were identified as *Anthracotherium* is not large for other postcranial elements. This may be due to collection biases towards to neglecting skeletal materials of these medium to large sized mammals or due to taphonomic biases to eliminating this size of specimens.

The medial condyle of the distal humerus in *Anthracotherium* (Figure 9A) is better developed than that of an extant *Sus*. The lateral side is incomplete, but the remaining morphology indicates absence of a lateral condyle. A large olecranon foramen opens on the distal articular surface. The capitulum forms an intercondylar ridge as in other artiodactyls, and has a smaller diameter than the trochlea. The capitulum is cylindrical, differing from the laterally flared capitulum in an extant *Sus*. The medial surface of the trochlea curves internally, in contrast to that of an extant *Sus*, which bulges out and forms a round surface. These morphology in the distal humerus is reflected to the radial head (Figure 9B). The medial lobe is larger and anteroposteriorly much thicker than the lateral lobe. There is a shallow groove for the intercondylar ridge, and a ridge from the capitular eminence fits with the trochlear groove. The medial edge of the articular surface is deflected distally. The radial shaft is anteroposteriorly compressed. Rugose impressions are widely distributed on the posterior surface of the shaft, indicating a wide ulnar shaft was bound to the radius by connective fibers.

The distal femur of *Anthracotherium* (Figure 10A) is similar to that of an extant *Sus*.

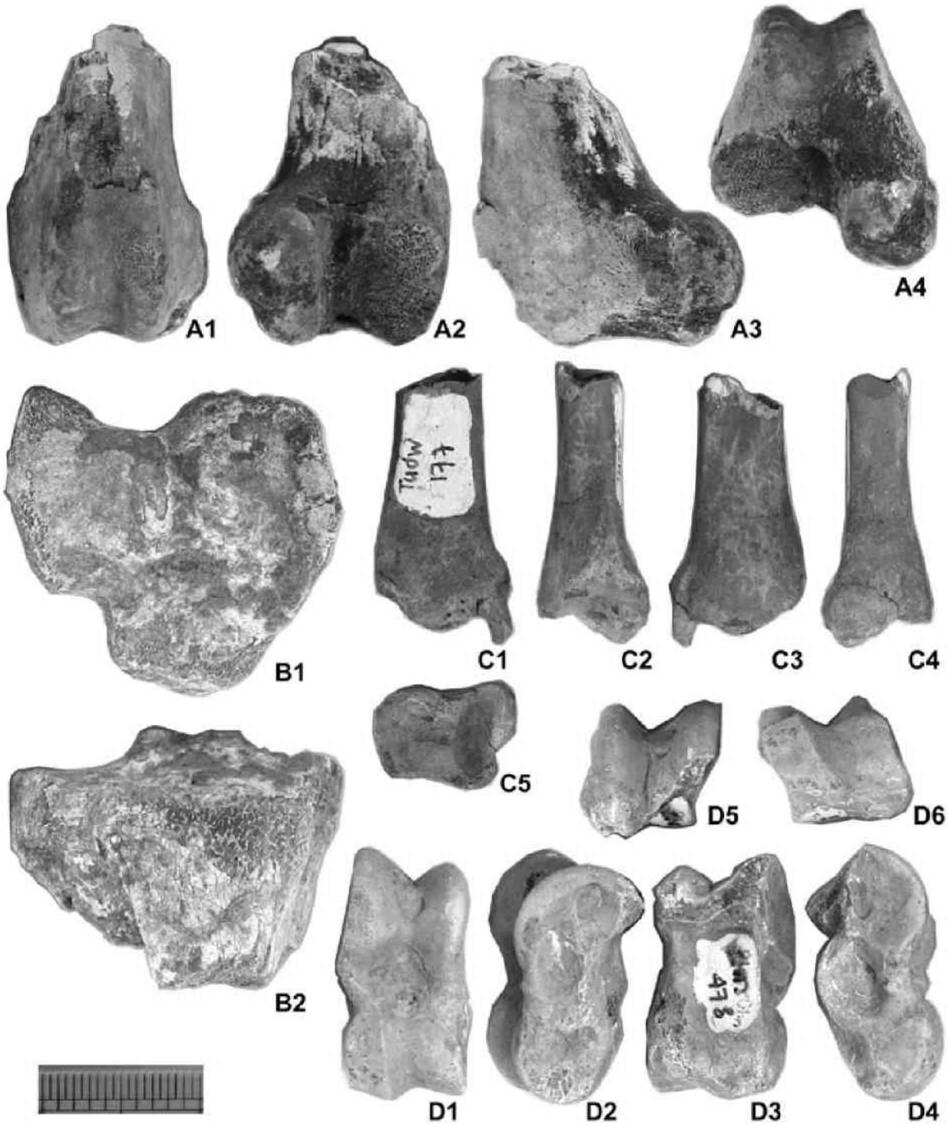

Figure 10. Hindlimb fragments of *Anthracotherium*. **A,** distal femur, NMMP-KU 0706; **A1,** anterior view; **A2,** posterior view; **A3,** lateral view; **A4,** distal view. **B,** proximal tibia, NMMP-KU 1606; **B1,** proximal view; **B2,** anterior view. **C,** distal tibia, NMMP-KU 0977 (a subadult individual): **C1,** anterior view; **C2,** lateral view; **C3,** posterior view; **C4,** medial view; **C5,** distal view. **D,** astragulus, NMMP-KU 0972: **D1,** dorsal view; **D2,** medial view; **D3,** plantar view; **D4,** lateral view; **D5,** proximal view; **D6,** distal view. One division of scale equals 1 mm.

The width of the distal part is narrow as in ungulates. The patellar groove is deep and curves slightly medially at the distal end. The medial ridge of the patellar groove is higher than the lateral one, but the difference is not as clear as in extant ruminants. The proximal tibia of *Anthracotherium* (Figure 10B) is similar to that of an extant *Sus* than to an extant ruminant, in having poor developments of intercondylar eminence, extensor groove, and tibial tuberosity. The medial condyle is longer and extends more anteriorly than the lateral one as in an extant *Sus*. The tibial tuberosity is relatively wide.

There are some differences in ankle morphology between *Anthracotherium* and an extant *Sus*. The distal tibia (Figure 10C) is mediolaterally wider in *Anthracotherium*. The medial malleolus is large, but the tibial cochlea, which is an articulation for the astragular trochlea

Figure 11. Forelimb fragments of medium perissodactyls (?chalicotherioids). **A,** a left distal humerus, NMMP-KU 0639; **A1,** anterior view; **A2,** lateral view; **A3,** posterior view; **A4,** medial view; **A5,** distal view. **B,** a right proximal radius, NMMP-KU 1591; **B1,** anterior view; **B2,** posterior view; **B3,** medial view; **B4,** proximal view. One division of scale equals 1 mm.

groove, is not as distinct as an extant *Sus* and ruminants. The difference between the medial and lateral grooves are not as great as an extant *Sus*. The overall proportion of the astragulus of *Anthracotherium* (Figure 10D) is similar to that of an extant *Sus* and longer than that of extant *Cervus* and *Capra*. The angle of the tibial trochlea relative to the distal trochlea is less diagonal in *Anthracotherium* than in an extant *Sus*. The lateral ridge of the tibial trochlea is sharp as in *Asiohomaodon*. The fossa at the distal end of the tibial trochlear groove is shallow, reflecting the small tibial cochlea of the distal tibia. The distal trochlear groove and the ridge between the central tarsal (the navicular) and the IVth tarsal (the cuboid) articulations are more clear in *Anthracotherium* than in *Asiohomacodon*, and the condition is rather similar to that in an extant *Sus*. In an extant *Sus*, the distal trochlea increases its width distally, so that the articular surface for the IVth tarsal (the cuboid) is large. In *Anthracotherium*, the medial and lateral walls of the distal trochlea is parallel. The articulation for the calcaneum is widely spread at the plantar surface.

Perissodactyl postcrania

(Figures 11-17)

Medium-sized perissodactyls (Figures 11, 12)

Besides *Anthracotherium*, the Pondaung fauna has yielded some medium-sized ungulates (Table 1). They are tapiromorph perissodactyls, and some postcranial materials likely belonged to these perisodactyls.

NMMP-KU 0639 (Figure 11A) is a distal humerus of a perissodactyl with a body size of *Gazella* (15 – 32 kg; Macdonald, 2001). NMMP-KU 1591 and 1311 are distal radii (Figures 11B, 12B). They also seem to have belonged to *Gazella*-sized animals but show very different morphologies. Two types of *Gazella*-sized perissodactyls are known from the Pondaung fauna: chalicotherioids (*Eomoropus* and "Eomoropidae" indet.) and an indolophid (*Indolophus*) (Tsubamoto *et al.*, 2005). Based on the morphology discussed the below, NMMP-KU 0639 and 1591 are here tentatively assigned to Chalicotherioidea, and NMMP-KU 1311 are assigned to the other taxon, *Indolophus*.

The distal humerus, NMMP-KU 0639 (Figure 11A), is similar to that of primitive perissodactyls such as *Heptodon* and *Hyracotherium* in having reudced medial and lateral condyles, a low and sharp supinator crest, and a perforated deep olecranon fossa (Rose, 1996). The capitulum is narrow, but the intercondylar ridge has not been formed yet. NMMP-KU 0639 differs from the distal humeri of *Heptodon* and *Hyracotherium*, in more reduced condyles, a loss of the capitular tail, and a more conically shaped capitulum. The capitulum and the trochlea form a spool-shaped articulation in NMMP-KU 0639. One very peculiar feature in this specimen is that the lateral edge of the distal humeral articulation protrudes more distally than the medial edge, so the plane defined by the trochlear groove is not parallel to the shaft. The proximal radius, NMMP-KU 1591 (Figure 11B), has morphologies that can articulate with such distal humeral articulation; thus, we can assume that NMMP-KU 1591 belonged to the animal same as NMMP-KU 0639. A ridge from the capitular eminence is formed at the middle of the radial fovea. This ridge articulates with the trochlear groove of the humerus, and it curves slightly laterally. The articular surfaces medial and lateral to the ridge are subequal in surface area size. The medial half is deflected distally. The groove for an intercondylar ridge is absent. The radial head and the shaft are mediolaterally wide. The posterior surface of the proximal shaft provides a wide attachment with the ulna.

The morphologies of the distal humeral articulation and the radial head suggest that the humerus is abducted when the forearm is set vertical to the ground, or that the hand is positioned medially compared with the elbow and the shoulder. The long bones angled to the parasaggital plane are not efficient during running activity, because it reduces the stride length relative to the limb bone length and increases the bending and torsional loadings on the limb bone shaft, suggesting the lineage of this animal had abandoned to enhance cursorial adaptations. Such a peculiar limb posture seems unlikely to be present in usual perissodactyls except in chalicotherioids, which are known for their elongated forelimbs and clawed fingers and toes, and even for the knuckle-walking posture in some species (Coombs, 1983, 1998). The Eocene member of Chalicotherioidea were not as specialized as the later species (Coombs, 1983), but it seems to be possible for a middle Eocene eomoropid to have some modifications in their forelimb. This medium-sized perissodactyl from the Pondaung fauna differs from the *Heptodon* and *Hyracotherium* (Rose, 1996) in its greatly reduced condyles and loss of the capitular tail in the distal humerus and more mediolaterally elongated radial head. These

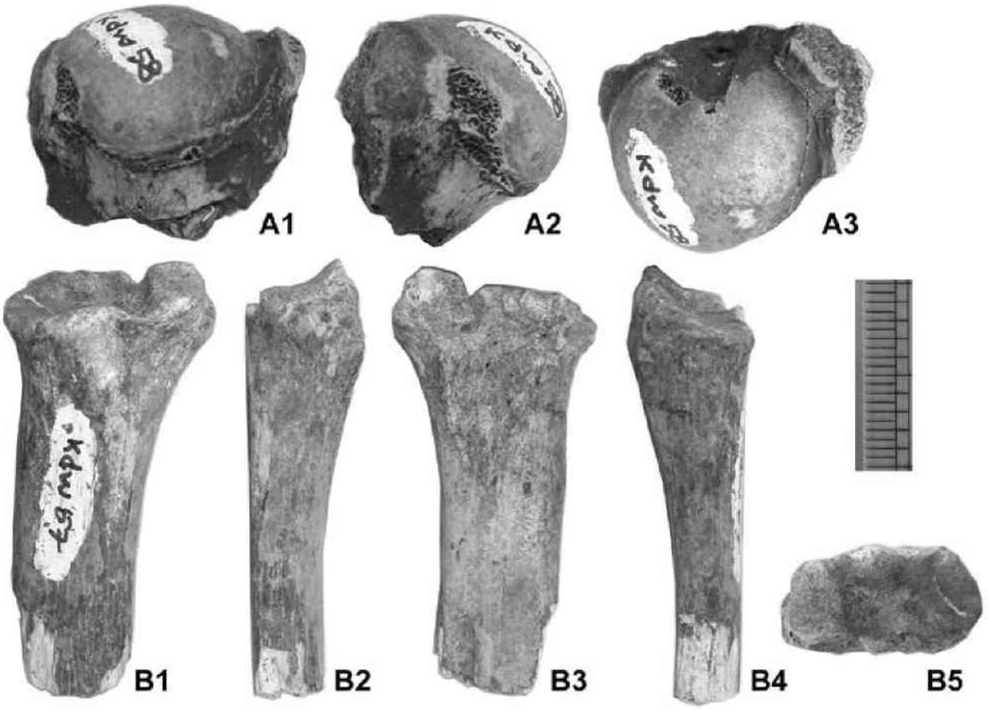

Figure 12. Forelimb fragments of a medium perissodactyl (?*Indolophus*), NMMP-KU 1311. **A,** humeral head; **A1,** posterior view; **A2,** medial view; **A3,** proximal view. **B,** proximal radius; **B1,** anterior view; **B2,** lateral view; **B3,** posterior view; **B4,** medial view; **B5,** proximal view. One division of scale equals 1 mm.

indicate that the lineage of this animal had once reached a more derived stage of cursorial adaptations of ungulates than the early Eocene *Heptodon* and *Hyracotherium*.

NMMP-KU 1311 consists of a humeral head and a proximal radius (Figure 12). Although the proximal radius of NMMP-KU 1311 (Figure 12B) is approximately same in size as the above mentioned NMMP-KU 1591 (Figure 11B), the overall morphology of the former is that of usual cursorial perissodactyls. At present, *Indolophus*, of which body mass has been estimated as 20.7 kg (Tsubamoto *et al.*, 2005), seems to be the best candidate for this kind of perissodactyls. The humeral head (Figure 12A) is spherical in the superior view, is hemispherical in the medial view, and is flat in the posterior view. The greater tuberosity is slightly wider than the lesser tuberosity. The greater tuberosity is not very thick. The radial head (Figure 12B) is mediolaterally elongated. The lateral one third of the articular surface is higher than the rest, indicating that the capitulum had the intercondylar ridge and that its height was smaller than that of the trochlea. The ridge for the trochlear groove runs at the lateral third of the radial head, and it is parallel to the groove for the intercondylar ridge. The anterior edge of the radial head parallel to the posterior edge and the horizontal articular surface for the trochlea indicates that the humeral trochlea was cylindrical and that the elbow joint movement is limited in the parasaggital plane. The articulation surface with the ulna is wide at the posterior surface of the radial head but it narrows rapidly at the radial neck, indicating that the radius is not mobile relative to the ulna and that the ulnar shaft was reduced. The posterior surface of the radial shaft curves anteriorly, similar to many extant

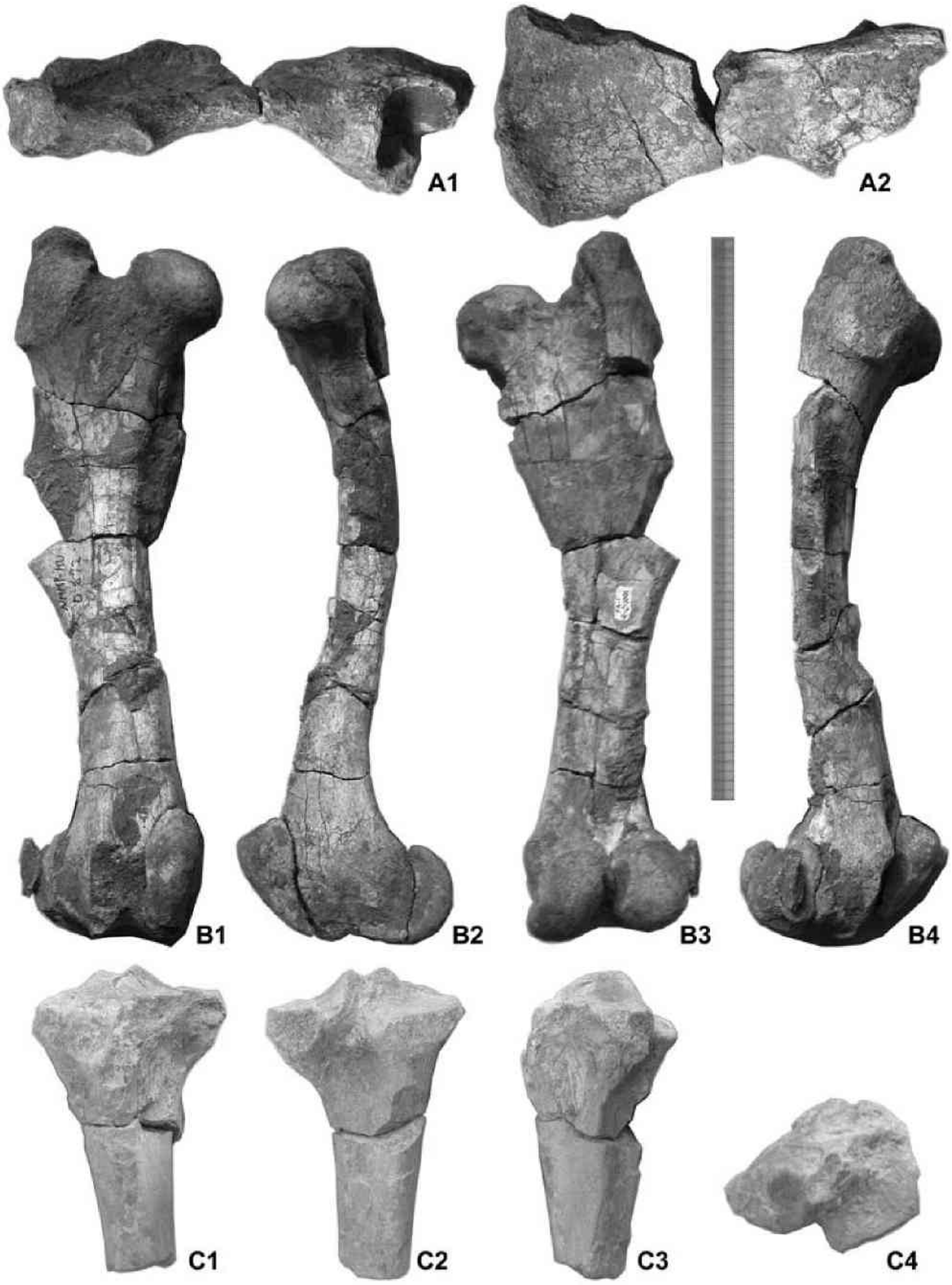

Figure 13. Hindlimb fragments of a brontotheriid (**A, B,** NMMP-KU 0672) and a cf. brontotheriid (**C,** NMMP-KU 0621). **A,** ilium to acetabulum part of the pelvis; **A1,** inferior view; **A2,** medial view. **B,** femur; **B1,** anterior view; **B2,** medial view; **B3,** posterior view; **B4,** lateral view. **C,** proximal tibia; **C1,** anterior view; **C2,** posterior view; **C3,** lateral view; **C4,** proximal view. One division of scale equals 5 mm.

ungulates. Overall, the morphologies of the proximal radius indicate that this animal is the most cursorial mammal in the Pondaung fauna.

Large perissodactyl (Figures13-17)

Most of large mammals are brontotheriid and rhinocerotoid perissodactyls in the Pondaung fauna. They are taxonomically divers in the fauna, and six genera and eleven

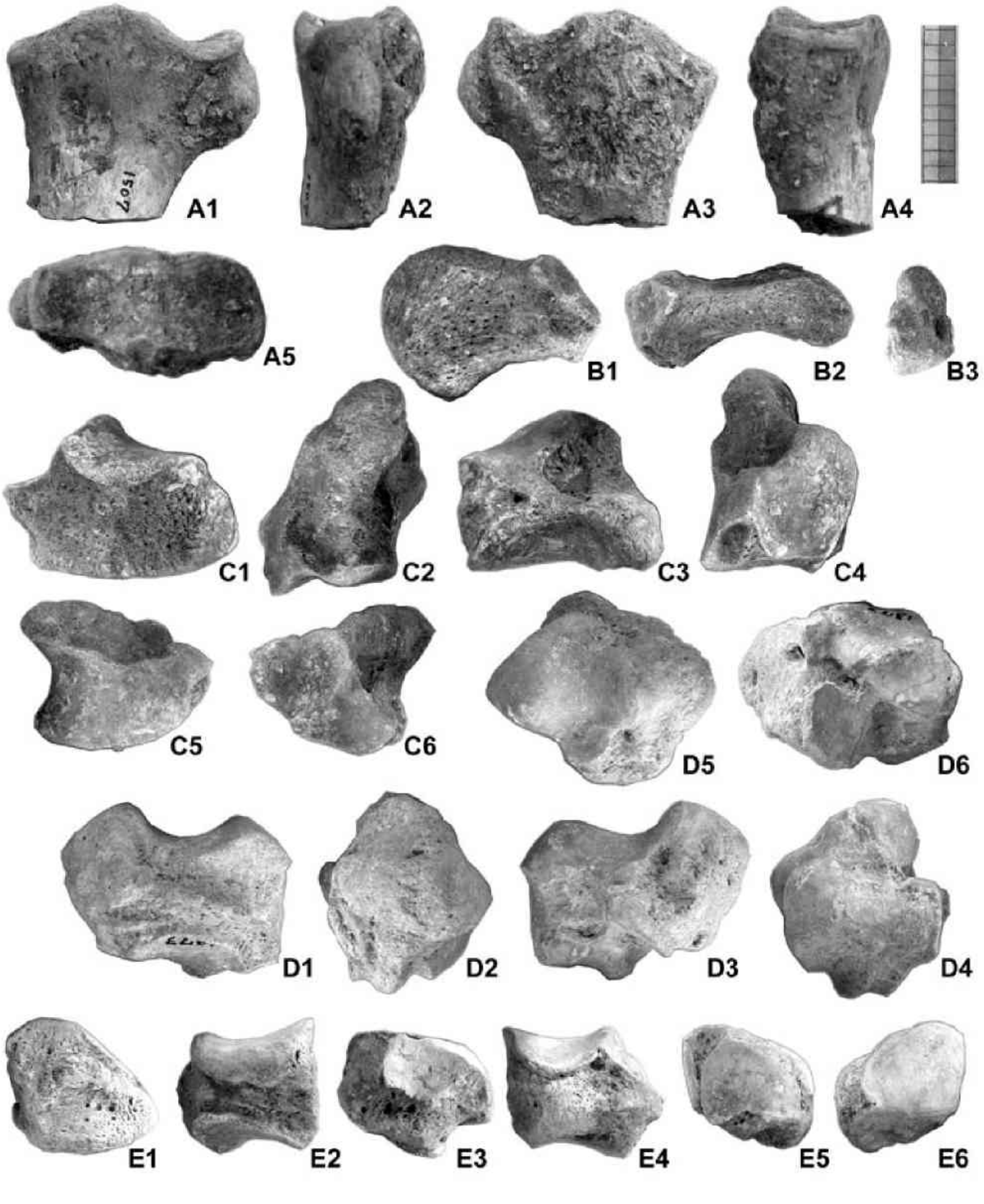

Figure 14. Proximal radius and carpals of large perissodactyls (cf. brontotheriids). **A,** proximal radius; **A1,** anterior view; **A2,** medial view; **A3,** posterior view; **A4,** lateral view; **A5,** proximal view. **B,** accessory carpal; **B1,** lateral view; **B2,** superior view; **B3,** proximal (dorsal) view. **C,** ulnar carpal; **C1,** dorsolateral view; **C2,** lateral view; **C3,** plantar view; **C4,** medial view; **C5,** proximal view; **C6,** distal view. **D,** radial carpal; **D1,** dorsomedial view; **D2,** medial view; **D3,** plantolateral view; **C4,** lateral view; **C5,** proximal view; **C6,** distal view. **E,** carpal IV; **E1,** dorsolateral view; **C2,** plantar view; **C3,** plantomedial view; **E4,** dorsal view; **E5,** proximal view; **E6,** distal view. **A,** NMMP-KU 1507; **B, C, E,** NMMP-KU 1245; **D,** NMMP-KU 1373. One division of scale equals 5 mm.

species have been known based on the dental materials (Tsubamoto *et al.*, 2006). The body size of amynodontid rhinocerotoid ranges from 154 kg of an indeterminate genus to 1 t of *Paramynodon cotteri* in the Pondaung fauna, while the body size of brontotheriid ranges from 512 kg of *Bunobrontops sp.* to 5 t of *Sivatitanops birmanicus* (Tsubamoto *et al.*, 2005). Large fragments of limb bones are likely to have belonged to these perissodactyls, but taxonomic identifications are not possible because of the incompleteness of the materials and the lack

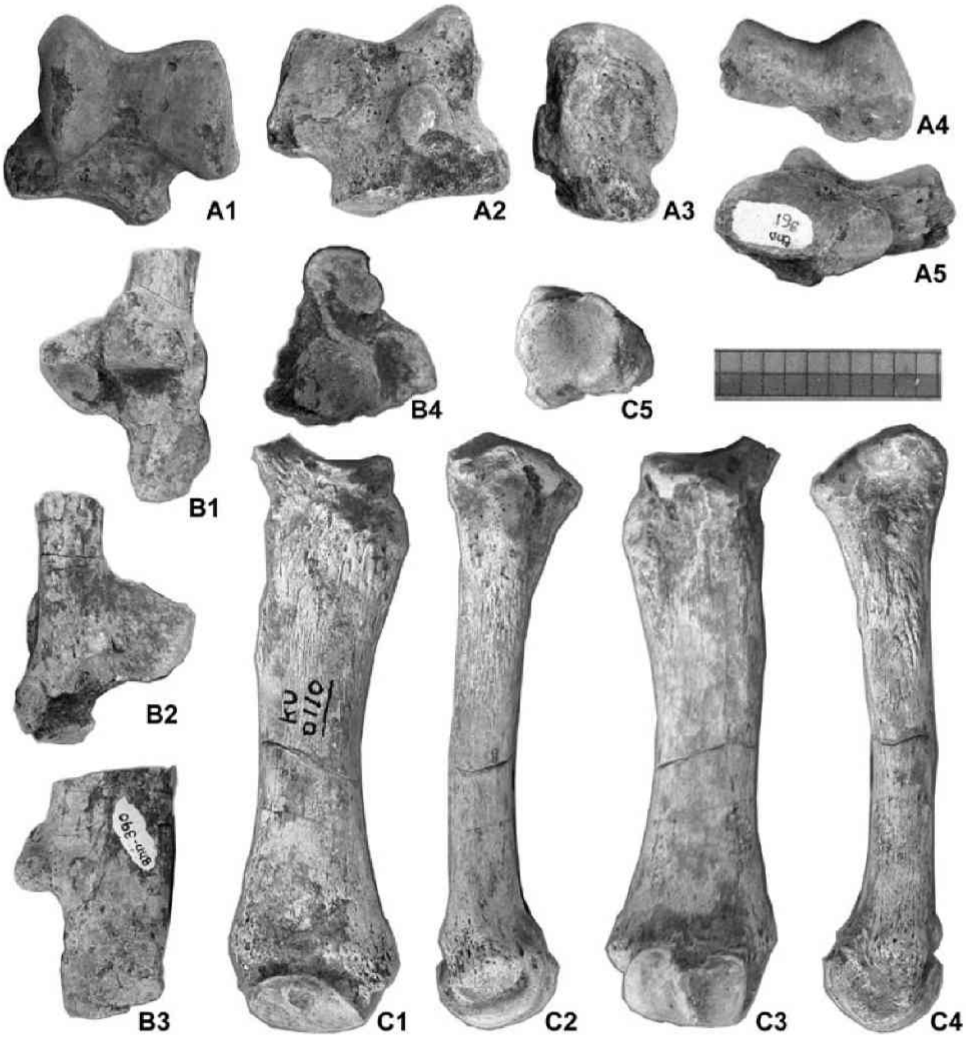

Figure 15. Foot elements and a metacarpal of large perissodactyls (cf. brontotheriids). **A,** astragulus, NMMP-KU 1012a; **A1,** dorsal view; **A2,** plantar view; **A3,** medial view; **A4,** proximal view; **A5,** distal view. **B,** calcaneum, NMMP-KU 1012b; **B1,** dorsal view; **B2,** plantar view; **B3,** lateral view. **C,** metacarpal II, NMMP-KU 0110; **C1,** dorsal view; **C2,** medial view; **C3,** plantar view; **C4,** lateral (median) view; **C5,** proximal view. One division of scale equals 5 mm.

of association with any dental materials. The skeletons of brontotheriids and rhinocerotoids have been reconstructed for better known species (Osborn and Wortman, 1895; Osborn, 1898, 1929). We do not attempt comparisons of the materials from the Pondaung fauna with brontotheriids and amynodontids from the other places, because the preservation of the Pondaung materials is too incomplete.

NMMP-KU 0672 is an associated skeleton of a brontotheriid (Figure 13). Most of the elements are fragmentary, but it included an upper molar and M_3, which helped taxonomic identification, and mostly complete femora. The total length of the femur (Figure 13B) is 37 cm, which is as same as an extant horse. The mediolateral and anteroposterior diameters of the mid-shaft are 41.7 and 36.8 mm, so the anteroposterior elongation of the shaft cross-section seen in extant horses is absent in this brontotheriid. The diameters of the femoral head are 48.3, 51.0, and 29.6mm in anteroposteriorly, superoinferiorly, and mediolateral

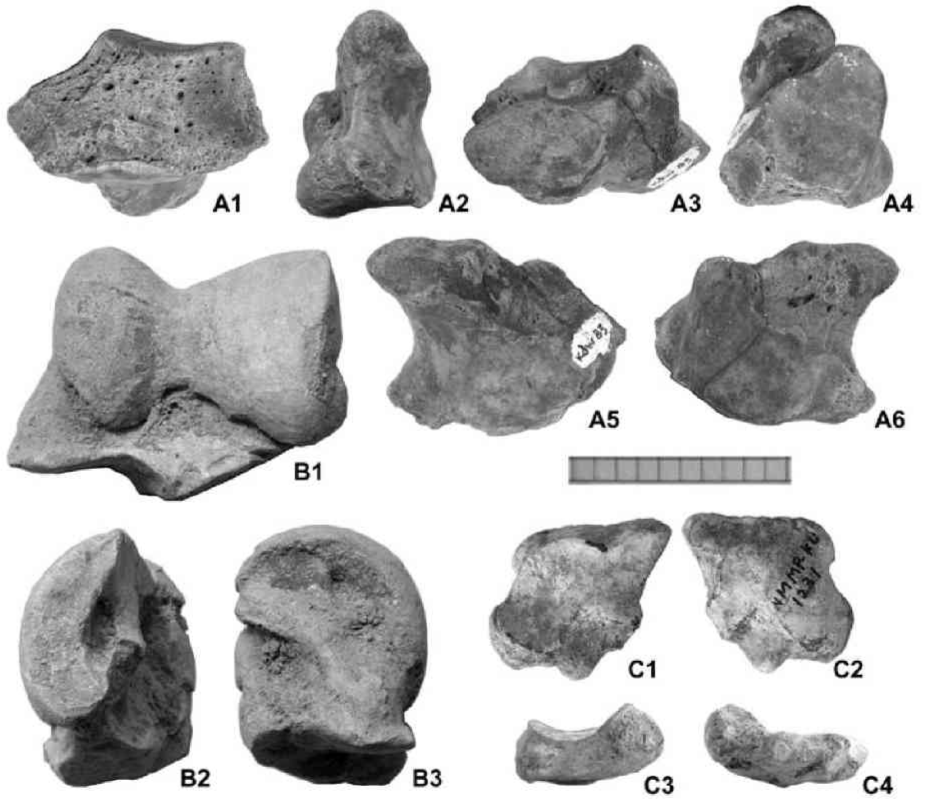

Figure 16. Carpal and tarsal elements of very large perissodactyls. **A,** ulnar carpal, NMMP-KU 1326; **A1,** dorsolateral view; **A2,** lateral view; **A3,** plantar view; **A4,** medial view; **A5,** proximal view; **A6,** distal view. **B,** astragulus, NMMP-KU 1355; **B1,** dorsal view; **B2,** lateral view; **B3,** medial view. **C,** central tarsal, NMMP-KU 1231; **C1,** proximal view; **C2,** distal view; **C3,** dorsomedial view; **C4,** plantolateral view. One division of scale equals 5 mm.

directions, respectively. The proximal half of the femoral head is spherical. The lesser and third trochanters are large and extend nearly to the 50 % of the shaft. The distal femur is anteroposteriorly deep. The total width of the distal end is 78.2 mm, and it is smaller relative to the proximal femur than that of an extant horse. The patellar groove is deep and is bordered by a thick medial ridge. The height, width, and depth of the medial condyle are 51.3, 31.2, and 30.5 mm, respectively, and those of the lateral condyle are 46.6, 31.5, and 28.0 mm, respectively. A fragmentary distal humerus associated with this individual indicates that the size of this part (total width, 83.55 mm; capitular height, 43.0 mm; trochlear height, 53.9 mm) is as large relative to the femoral length as that of an extant horse. The illium is not greatly expanded relative to the acetabular part of the pelvis (Figure 13A). Although later large brontotheriids are characterized as a widely sprayed illiac blade, the morphology seen in this Pondaung brontotheriid agrees with primitive and moderate-sized brontotheriids (Mader, 1998). Many other postcranial elements such as the proximal tibia, forelimb, and foot elements of this sized animal have been collected (Figures 13C, 14, 15). There are not many amynodontid species in this body size range in the Pondaung fauna, so a skeletal fragment of a horse-sized mammal likely belongs to a brontotheriid in the fauna. Tibial shaft is not as slender relative to the proximal articulation as that of *Titanotherium* and *Brontops*

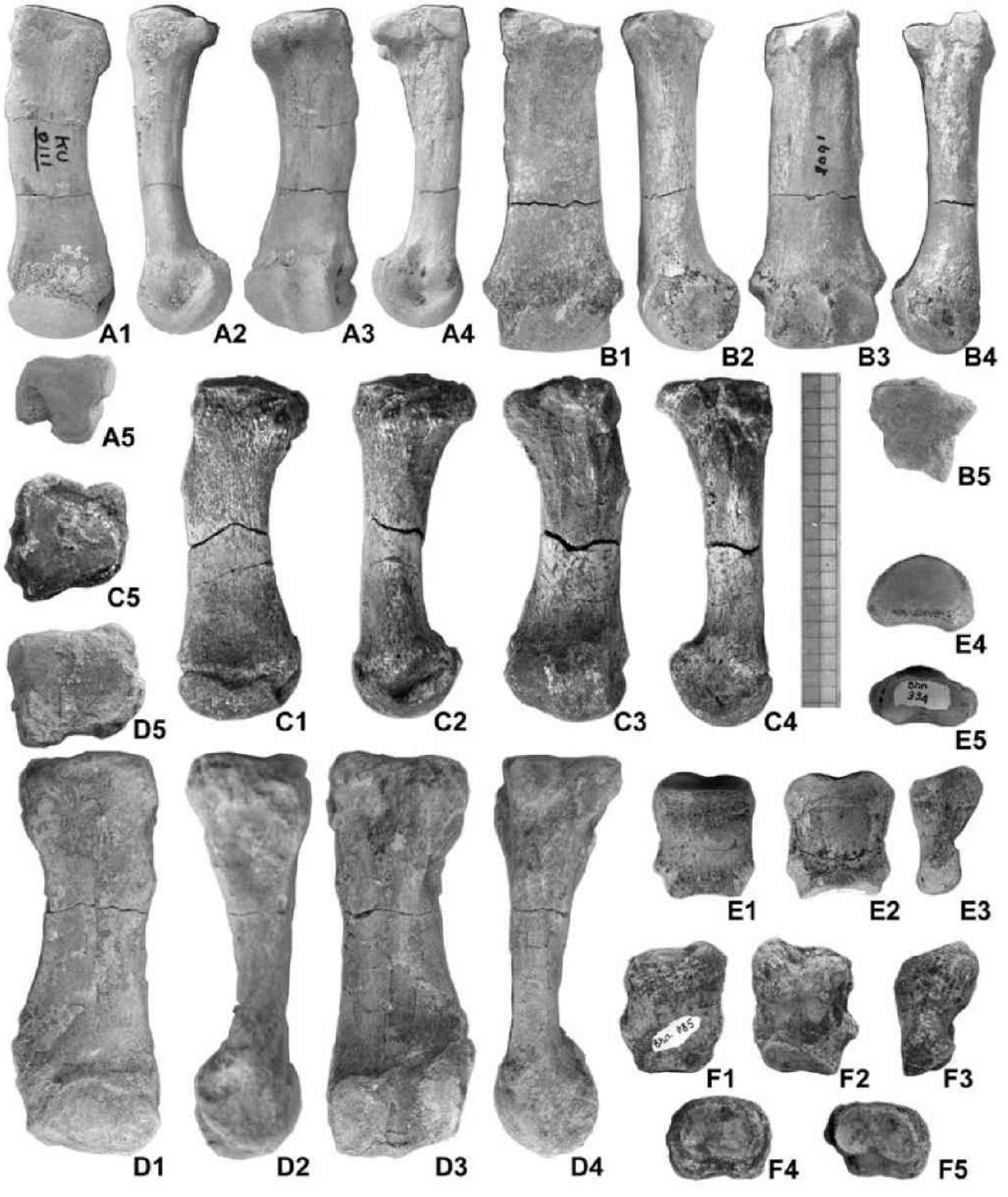

Figure 17. Phalages of very large perissodactyls. **A,** metacarpal IV, NMMP-KU 0111; **A1,** dorsal view; **A2,** lateral view; **A3,** plantar view; **A4,** medial (median) view; **A5,** proximal view. **B,** metacarpal III, NMMP-KU 1608; **B1,** dorsal view; **B2,** lateral view; **B3,** plantar view; **B4,** medial view; **B5,** proximal view. **C,** metacarpal IV, NMMP-KU 0642; **C1,** dorsal view; **C2,** lateral view; **C3,** plantar view; **C4,** medial (median) view; **C5,** proximal view. **D,** metatarsal II, NMMP-KU 1114; **D1,** dorsal view; **D2,** medial view; **D3,** plantar view; **D4,** lateral (median) view; **D5,** proximal view. **E,** proximal phalange, NMMP-KU 1021; **E1,** dorsal view; **E2,** plantar view; **E3,** medial or lateral view; **E4,** proximal view; **E5,** distal view. **F,** middle phalange, NMMP-KU 1020; **F1,** dorsal view; **F2,** plantar view; **F3,** medial or lateral view; **F4,** proximal view; **F5,** distal view. One division of scale equals 5 mm.

(Osborn and Wortman, 1895; Mader, 1998). The astragulus and the calcaneum indicate that the astragular neck is unreduced. The metacarpal is not shortened relative to the diameter. These morphologies of the postcranial materials indicate that these Pondaung brontotheriids (*Bunobrontops* and/or cf. *Metatelmatherium*) are primitive among the family in lacking graviportal specializations and seems to have retained cursorial adaptations considerably.

The postcranial specimens of gigantic sized mammals are represented by hand and foot elements in the Pondaung fauna (Figures 16, 17). Limb bone fragments have been hardly collected for mammals of this size, because they are usually broken to pieces before being discovered. The mammals that are at the upper end of the body size range of the Pondaung fauna are *Sivatitanops* (Brontotheriidae) and/or *Paramynodon* (Amynodontidae) . For brontotheriid, skeletal modifications for graviportal adaptations have been known forms appeared after the middle Eocene (Mader, 1998). Metamynodontines, the amynodontids include *Paramynodon*, have been reconstructed as heavy-limbed and barrel-chested animal, and they have been suggested to have had habitat analogous to extant *Hippotumus* (Wall, 1998). The astragulus of a very large perissodactyl (Figure 16B) bears a shorter neck and a wider articular surface for the central and IVth tarsals than that of the above mentioned brontotheriid specimen (Figure 15A). The mesopodials (Figure 17A-D) are robust, and the proximal and middle phalanges (Figure 17E, F) are short. It is not clear that these materials belonged to brontotheriids or amynodontids, but at least they indicate that the gigantic herbivorous mammals consisted of hippo- or rhino-like heavily built stout animals in the Pondaung fauna.

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