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FOSSIL REMAINS OF A NEW, DIMINUTIVE *BUBALUS* (ARTIODACTYLA: BOVIDAE: BOVINI) FROM CEBU ISLAND, PHILIPPINES

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We describe a partial skeleton of a new species of *Bubalus* (*Bubalus*) from soft karst near Balamban, Cebu Island, Philippines. The specimen is likely Pleistocene or Holocene in age and includes left and right humeri, a left metatarsal, 2 posterior thoracic vertebrae, 2 left lower molars, and a pair of ungual phalanges. *Bubalus* sp. nov. differs from all previously described *Bubalus* in both the size and proportions of the skeleton and in possessing a unique combination of discrete character states. Possible autapomorphies for *Bubalus* sp. nov. evident in the metatarsal include a very broad dorsal longitudinal sulcus; a broad, triangular anterior cubonavicular facet; and a sulcus that bisects a small tuberosity on the proximolateral surface. Limb elements of *Bubalus* sp. nov. are less than two-thirds the length of corresponding elements of the Asiatic water buffalo, *B.* (*Bubalus*) *bubalis*, and are about 80% the length of those of the tamaraw, *B.* (*Bubalus*) *mindorensis*; they are similar in length to limb bones of the lowland anoa, *B.* (*Anoa*) *depressicornis*, but are more robust. Mass estimates based on regression equations for modern bovids suggests a mass of 150–165 kg for *Bubalus* sp. nov.; this is approximately 25% smaller than *B. mindorensis* (180–220 kg) and at least 15% larger than *B. depressicornis* (approximately 135 kg). The small size of *Bubalus* sp. nov. relative to other *B.* (*Bubalus*) is likely attributable to island dwarfing; this is supported by a consistent relationship between body size and island size in *Bubalus* sp. nov., *B. mindorensis*, and *B. bubalis*, and by the relatively larger dentition of *B.* sp. nov. relative to body size. *Bubalus* sp. nov. is the 1st fossil mammal to be reported from Cebu Island and is the only nonproboscidean documented from the Negros–Panay Philippine Faunal Region. In conjunction with the presence of *Bubalus* on Mindoro Island (and potentially Luzon), this specimen suggests that *Bubalus* may once have ranged throughout the Philippines.

Key words: *Anoa*, body size, Bovini, *Bubalus*, dwarfism, fossil, island biogeography, Philippines, Pleistocene, tamaraw

The Philippines comprise more than 7,000 islands situated between Borneo and Taiwan in the northeastern corner of the Malay Archipelago. The vast majority of these islands are tiny (only 1–2 km^2) but the 2 largest (Luzon and Mindanao) are each approximately 100,000 km^2 in area (Fig. 1). Although a few of the islands (the Palawan group) are continental, most are oceanic in origin, and their current configuration is the result of complex tectonic interactions among the Eurasian continental plate, the Philippine oceanic plate, and various microcontinental blocks (e.g., Hall 1998, 2002; Yumul et al. 2000; Zamoras and Matsuoka 2004).

The fractured geography of the Philippine islands and their variable degrees and timing of connection and separation have given rise to a diverse fauna of terrestrial vertebrates. At least 172 species of native mammals have been recorded, of which 111 (64%) are endemic (Heaney et al. 1998). This degree of endemism is exceeded only by Madagascar, an island of nearly twice the total area; on a per-area basis, the Philippines may harbor the greatest number of endemic mammals in the world (Heaney 1993). Because of this endemism, the Philippines has been recognized both as one of the most ''megadiverse'' countries and as one of the ''hottest'' biological hotspots, making it a top priority for conservation efforts (Ricketts et al. 2005; Shi et al. 2005). Newly discovered mammals continue to

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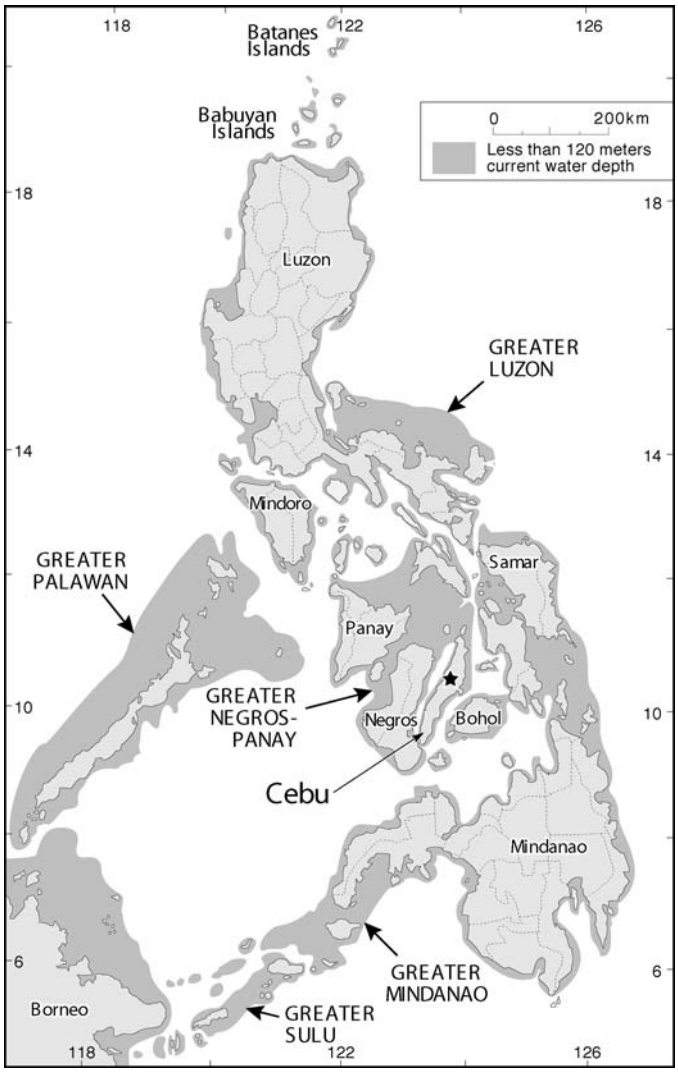


Fig. 1.—The Philippines. Areas that were exposed as dry land during the last glacial maximum are shown by gray shading; faunal regions are labeled in capital letters. Location where fossil specimen was found on Cebu Island is indicated by a star.

Table 1.—Extinct and extant Philippine ungulates listed by faunal region (Bautista 1991; Heaney et al. 1998). Animals obviously brought to the Philippines by the Spaniards (e.g., *Equus*) are not included.

Extinct species	Extant species
Luzon	
Artiodactyla	Artiodactyla
cf. *Antilope*	*Cervus mariannus*
Bubalus	*Sus philippensis*
Cervus	
Perissodactyla	
Rhinoceros philippinensis	
Proboscidea	
Elephas beveri	
Elephas cf. *namadicus*	
Paleoloxodon	
Stegodon luzonensis	
Stegodon cf. *sinensis*	
Stegodon cf. *trigonocephalus*	
Mindanao	
Proboscidea	Artiodactyla
Stegodon mindanensis	*Cervus mariannus*
	Sus philippensis
Mindoro	
(None)	Artiodactyla
	Bubalus mindorensis
	Sus philippensis
Negros–Panay	
Artiodactyla	Artiodactyla
Bubalus cebuensis sp. nov.	*Cervus alfredi*
Proboscidea	*Sus cebifrons*
Elephas	
Stegodon	
Palawan	
(None)	Artiodactyla
	Axis calamianensis
	Sus barbatus
	Tragulus napu
Sulu	
(None)	(None)

be described from the region (e.g., Rickart et al. 2002, 2003, 2005), indicating that the true species richness of the country is still unknown.

The large number of Philippine islands and their diverse mammal faunas make the archipelago particularly amenable to studies of island biogeography and the relative effects of colonization, extinction, and speciation (Heaney 1986, 2000). Such investigations have been aided by the recognition that the present configuration of islands is a geologically recent event. During the last glacial maximum of the late Pleistocene (approximately 20,000 years ago), the great quantity of water trapped in polar and continental ice sheets lowered sea levels worldwide, exposing areas of land that had previously been submerged (e.g., Bird et al. 2005; Meijaard 2003). In the Philippines, these exposed areas connected many previously isolated islands, resulting in 6 major Philippine faunal regions (Heaney 1991; Heaney et al. 1998; Fig. 1). Although these islands once again became isolated after the Pleistocene, disparities in faunal resemblance between intraregional and interregional island pairs are still dramatic (Heaney 1986; Heaney and Regalado 1998; Heaney et al. 1998) and may differ from those that existed before that event.

Unfortunately, the terrestrial fossil record of the Philippines is poor and has provided few insights into the development of the country's unique fauna. Thus far, only a few Pleistocene and Holocene ungulates have been reported (Bautista 1991; Beyer 1957; Koenigswald 1956; Table 1), although increased efforts to collect and study microvertebrate fossils could considerably expand knowledge of the recent biotic history of the islands (Reis and Garong 2001). The present report describes fossil remains of a new species of bovid that lived on Cebu Island, perhaps as recently as a few thousand years ago. The specimen was discovered in 1958 by Michael Armas, a mining engineer, during exploration for phosphate (Fig. 2). In 1995, it was brought to the attention of Dr. Hamilcar Intengan, who subsequently brought the bones to The Field Museum for

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initial identification by our late colleague, Steven McCarroll, and JJF. Armas and LRH visited the site in April 1999; it is an area of soft karst, formed from poorly consolidated coral reef. The fossil was found at the end of an approximately 10- to 11-m horizontal tunnel that had been dug into the side of a ridge for the purpose of phosphate mining. The sediments in which the fossil was found likely represent fissure-fill (i.e., sediments that had accumulated within a crack or crevice in the limestone). All elements of the specimen were found on a single day, in close proximity to each other, within loose matrix. No other fossils were found at this site or in other similar mining tunnels dug in the vicinity. This is the 1st fossil mammal reported from Cebu Island, and the only non-proboscidean fossil described from the entire Negros–Panay Faunal Region of the Philippines.

Materials and Methods

The descriptions below are based on direct observations of the original material (left humerus, vertebrae, teeth, and unguals) or casts of the original material (right humerus and left metatarsal) that are now housed at the National Museum of the Philippines (PNM). Morphological comparisons were made with osteological specimens from the Recent mammal collections of the Division of Mammalogy at The Field Museum of Natural History (FMNH) and the University of Michigan Museum of Zoology (UMMZ); a list of these specimens is provided in Appendix I.

All measurements were made to the nearest 0.5 mm, using a digital caliper. Estimated measurements (e.g., for articulated specimens) are indicated by parentheses. Statistical analyses were performed using SPSS (SPSS Inc., Chicago, Illinois) on an Apple G4 computer (Capertino, California). The dagger symbol (†) is used to designate extinct species.

Systematics

Mammalia Linnaeus, 1758
Artiodactyla Owen, 1848
Bovidae Gray, 1821
Bovinae Gray, 1821
Bovini Gray, 1821
Bubalina Pilgrim, 1939
Bubalus Hamilton-Smith, 1827

Type species.—*Bubalus* (*Bubalus*) *bubalis* (= *B. arnee*).

Included species.—*Bubalus* (*Bubalis*) *bubalis*, †*B. brevicornis*, *B.* (*Anoa*) *depressicornis*, †*B. guzhensis*, †*B. mephistopheles*, *B.* (*Bubalus*) *mindorensis*, †*B. murrensis*, †*B. palaeindicus*, †*B. palaeokerabau*, †*B. platyceros*, *B.* (*Anoa*) *quarlesi*, †*B. sivalensis*, †*B. teilhardi*, †*B. tingi*, †*B. triangulatus*, †*B. wansijocki*, †*B. youngi*.

Comments.—As is evident from the list above, in addition to the extant species, a large array of fossil species have been referred to *Bubalus*. The majority of these species are incompletely known, however, and are differentiated primarily by horn core characters (e.g., Geraads 1992; Xue and Li 2000; Young 1936). The new species described herein is represented by 2 teeth and various postcranial elements and therefore cannot be directly compared to most fossil taxa. Of necessity, therefore, the diagnosis below focuses on character states that distinguish the new Cebu Island species from extant species of *Bubalus*, the only taxa for which sufficient postcranial specimens are available for diagnostic differentiation. The new species can only be stated with certainty to differ from all fossil species of *Bubalus* by its dramatically smaller size.

Four extant species of *Bubalus* are currently recognized (Grubb 2005; Nowak 1999). The most widespread of these is *Bubalus bubalis*, the Asiatic water buffalo; domestic *B. bubalis* is found virtually throughout the world (Kierstein et al. 2004), but wild populations have declined and are considered endangered (Nowak 1999). Water buffaloes are the largest *Bubalus*, with wild males weighing more than 1,000 kg (Popenoe 1983). Some authorities distinguish between the wild and domestic forms, using the name *B. arnee* for the former and reserving *B. bubalis* for the latter (e.g., Geraads 1992; Groves 1969). We do not make this distinction in the present report because the 2 species cannot be readily distinguished from one another by anatomical differences. *Bubalus mindorensis*, the tamaraw or tamarau, is endemic to the Philippine island of Mindoro (Custodio et al. 1996). It is much smaller than *B. bubalis* (see below) and is highly endangered because of a variety of factors, including hunting and habitat destruction (Heaney and Utzurrum 1991; Oliver 1993). *B. bubalis* and *B. mindorensis* are generally grouped together in the subgenus *Bubalus* (Grubb 2005). The subgenus *Anoa* includes 2 very similar species of dwarf buffalo endemic to Sulawesi, Indonesia: *B. depressicornis*, the lowland anoa, and *B. quarlesi*, the mountain anoa (Burton et al. 2005; Dolan 1965; Groves 1969). They are the smallest Bovini, but the largest endemic mammals of Sulawesi, and are also endangered (Burton et al. 2005).

Bubalus cebuensis, sp. nov.
Figs. 3–8; Tables 2–5

Holotype.—PNM 2006-A, an associated partial skeleton including left and right humeri, left metatarsal, 2 thoracic vertebrae (?T9 and ?T11), 2 unguals, and left m1–2. More of the skeleton (including several ribs and additional teeth and vertebrae) was present when the specimen was discovered (M. Armas, pers. comm.), but these were given away or lost subsequently; the aforementioned elements were the only ones available to us for study. The individual elements are partially permineralized (i.e., ''fossilized'') but the degree of permineralization varies both within and between elements. The original specimen will be deposited at the National Museum of the Philippines; casts of the bones will be retained in the geology collections of The Field Museum (FMNH PM 61097) and a duplicate set of casts will retained in the Recent mammal collections.

Type locality.—The specimen was collected from the end of a horizontal tunnel in soft karst at approximately 50 m elevation in K-Hill near Balamban, Cebu Island, Philippines (approximately 10°51′N, 123°72′E; Fig. 2). No stratigraphic data were recorded when the specimen was collected.

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Diagnosis.—*Bubalus cebuensis* differs from all previously described *Bubalus* in the size and proportions of the humerus and metatarsal (and presumably the rest of the postcranial skeleton). Based on linear dimensions, *B. cebuensis* is less than two-thirds the size of modern *B. bubalis* and is about 80% the size of modern *B. mindorensis*. *B. cebuensis* is similar in size to members of the subgenus *Anoa* (within approx. 10% for limb element lengths), but its skeleton is much more robust. The humerus, metatarsal, and vertebrae differ noticeably from those of *B.* (*Anoa*) and display a mixture of characters shared with *B. bubalis*, *B. mindorensis*, or both (e.g., roughly spherical humeral head, large greater tuberosity on humerus, low and broad deltopectoral crest, elongate metatarsal relative to humerus, straight metatarsal in medial view, small posterior cubonavicular facet on articular surface of metatarsal, T9–11 spinous processes straight in lateral view, and mammillary processes absent on T9–11; Table 2). The relative width of the dorsal longitudinal sulcus on the metatarsal is greater than that exhibited by any modern *Bubalus* and may be an autapomorphy for the new species. The unusual configuration of the proximal end of the metatarsal (i.e., with a broad, triangular anterior cubonavicular facet on the articular surface and a sulcus that bisects a small tuberosity on the proximolateral surface) may also be autapomorphic for *B. cebuensis*.

Age and distribution.—The specimen is likely Pleistocene or Holocene in age, based on the geology of the region, but we were unable to obtain an absolute date because of a lack of preserved collagen (i.e., carbon dating was unsuccessful; University of Arizona, Tucson, Accelerator Mass Spectrometry Laboratory sample AA57785). The species is known only from the type locality.

Etymology.—After Cebu Island, the type locality and only known locality for the species. The specific epithet is analogous to that of the tamaraw, *B. mindorensis*, named in reference to Mindoro Island, Philippines, and reinforces the insular nature of this endemic species.

Humerus.—The humerus (Fig. 3) is very similar in length to that of *B. depressicornis* but is much more robust, as evidenced by all other humeral measurements (Table 3). The head of the humerus is roughly spherical in shape, similar to the condition in *B. mindorensis* and *B. bubalis*; in *B. depressicornis* the proximal surface of the humeral head is flattened, and the transition between the proximal and caudal surfaces is more abrupt, approximating a right angle. As in other *Bubalus*, the greater tubercle in *B. cebuensis* projects far above the humeral head and arches medially over the intertubercular groove, creating a tunnel. The greater tubercle is much larger and more developed in *B. cebuensis*, *B. mindorensis*, and *B. bubalis* compared to *B. depressicornis*. A well-defined pit is present in the tubercular fossa (i.e., the area anterior to the humeral head and medial to the base of the greater tubercle); this pit is absent in *B. depressicornis* and is present but less defined in *B. mindorensis* and *B. bubalis*. The greater tubercle extends inferiorly beyond the articular surface of the humeral head in *B. cebuensis* and *B. bubalis*; this contrasts with the condition in *B. mindorensis*, in which the greater tubercle ends at approximately the same level as the articular surface. A rugose deltopectoral crest is present in *B. cebuensis*, but the deltoid tuberosity is low and broad, strongly differing from the conditions observed in *B. depressicornis* (in which it is a thin, platelike process) and *B. mindorensis* (in which it is a high ridge). It resembles the condition in *B. bubalis*, but is less developed. The scar marking the insertion of the teres minor

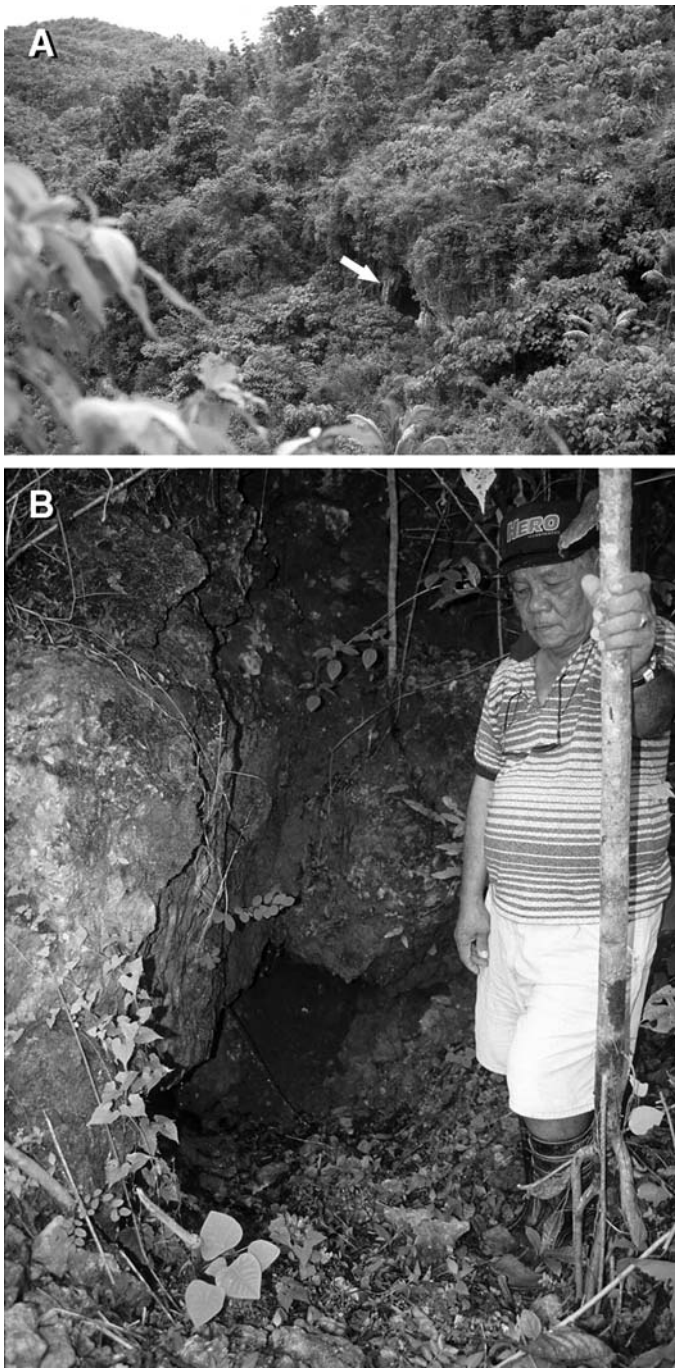


Fig. 2.—Locality where fossil was found near Balamban, Cebu Island, Philippines. A) Distant view of tunnel entrance (indicated by white arrow) amid dense vegetation. B) Close-up of tunnel entrance illustrating soft texture of soil and remains of poorly consolidated coral reef. The discoverer of the fossil specimen, Michael Armas, is pictured to the right of the entrance.

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Table 2.—Variation in selected morphological characters among species of *Bubalus*. Character states shared between *B. cebuensis* and other species are underlined; character states that are autapomorphic for *B. cebuensis* are italicized. T9–11 = 9th through 11th thoracic vertebrae.

Morphological character	*B. depressicornis*	*B. cebuensis*	*B. mindorensis*	*B. bubalis*
Shape of humeral head	With abrupt angle	Roughly spherical	Roughly spherical	Roughly spherical
Size of greater tuberosity	Small	Large	Large	Large
Pit in trochanteric fossa	Absent	*Well developed*	Slight	Slight
Deltopectoral crest	Thin and platelike	Low and broad	High ridge	Low ridge
Teres minor scar	Narrow	Broad	Narrow	Broad
Metatarsal length/humeral length	65%	70%	60%	65–75%
Metatarsal shape in medial view	Slightly bowed	Straight	Straight	Straight
Metatarsal posterior cubonavicular facet	Mediolaterally elongate	?Small	Small and circular	Mediolaterally elongate
Metatarsal anterior cubonavicular facet	Narrow	*Broad, triangular*	Broad, quadrangular	Broad, quadrangular
Proximolateral sulcus on metatarsal	Absent	*Bisects tuberosity*	Medial to tuberosity	Medial to tuberosity
T9–11 spinous processes	Curved	Straight	Straight	Straight
T9–11 mammillary processes	Well developed	Absent	Absent	Absent
Molar length/humeral length	<7.2%	>7.9%	<7.2%	>7.9%

muscle is large and broad in *B. cebuensis*, again more closely resembling the condition in *B. bubalis* than in either *B. depressicornis* or *B. mindorensis* (in which it is narrow). *B. cebuensis* differs from both *B. bubalis* and *B. mindorensis* in having a smaller lesser tubercle and in having a less-pronounced medial ridge on the lesser tubercle for insertion of the subscapularis muscle.

To investigate size and shape variation of the humerus in *Bubalus*, a principal components analysis was performed using the raw data for the 9 measurements presented in Table 3. The factor loadings for the first 2 principal components (PCs) are presented in Table 4 and the specimens are plotted against these 2 factors in Fig. 4. As expected, PC1 clearly represents size (all variables have high positive loadings), and *B. cebuensis* plots closer to *B. depressicornis* on this axis than to any other species. PC2 represents humeral robustness; mid-shaft and distal anteroposterior diameters have high positive loadings, and length has a high negative loading. This axis clearly distinguishes the robust humeri of *B. cebuensis* and *B. bubalis* from the more gracile humerus of *B. mindorensis*,

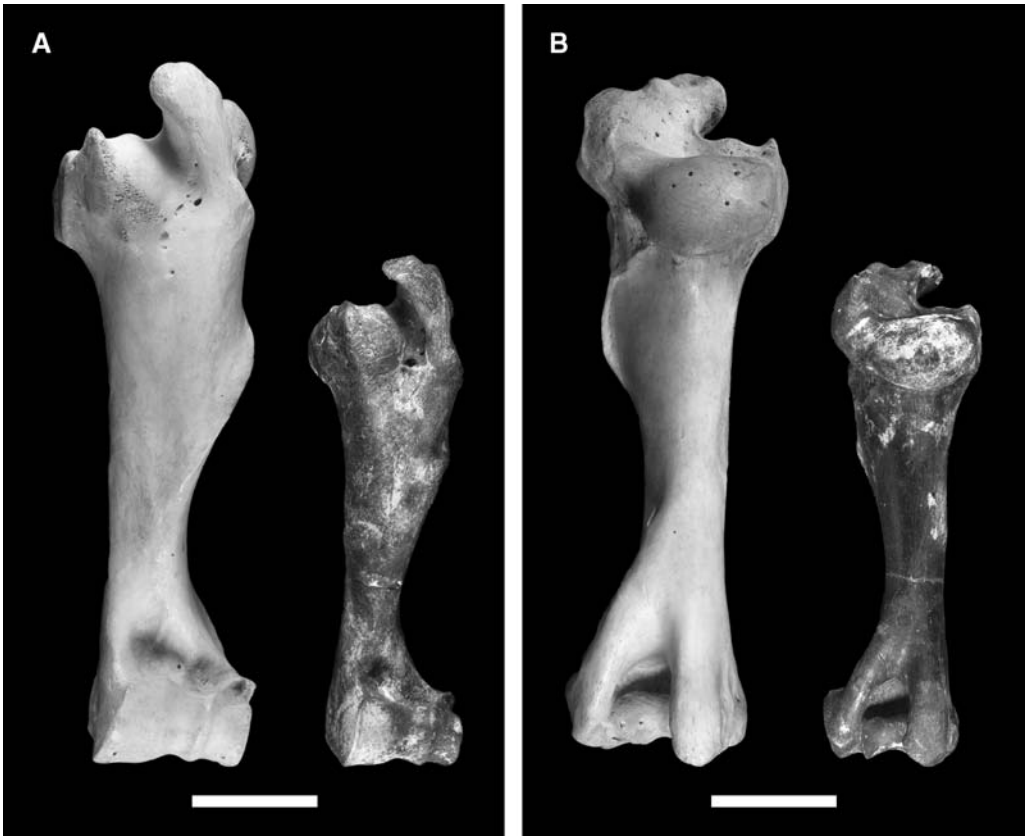


Fig. 3.—Left humeri of *Bubalus mindorensis* (FMNH 18817, left) and *Bubalus cebuensis* (PNM 2006-A, right) in A) anterior and B) posterior views. Scale bars = 5 cm.

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TABLE 3.—Humeral and metatarsal measurements (mm) for selected specimens of *Bubalus*. Measurements at proximal and distal ends are greatest diameters. Humeral trochlear diameter was measured in a proximodistal orientation. FMNH = The Field Museum of Natural History; PNM = National Museum of the Philippines; UMMZ = University of Michigan Museum of Zoology; AP = anteroposterior; ML = mediolateral.

Measurement	*B. depressicornis* FMNH 98791	*B. cebuensis* PNM 2006-A	*B. mindorensis* FMNH 18817	*B. mindorensis* UMMZ 84106	*B. bubalis* FMNH 92912	*B. bubalis* UMMZ 157862
Humerus						
Length	210.5	207.0	279.5	280.0	320.0	289.0
Proximal ML diameter	61.0	62.5	88.0	90.0	99.5	99.5
Proximal AP diameter	60.0	68.0	94.0	93.5	120.0	108.0
Teres minor ML diameter	35.5	44.5	54.0	52.0	74.0	72.0
Midshaft ML diameter	22.5	25.0	33.0	32.5	42.0	36.5
Midshaft AP diameter	27.5	30.5	41.5	41.0	48.0	45.0
Distal ML diameter	46.0	52.5	65.0	62.5	90.0	87.0
Distal AP diameter	47.0	53.5	67.0	65.0	87.5	77.5
Trochlear diameter	26.0	30.5	39.0	39.5	52.0	45.5
Metatarsal						
Length	137.5	148.0	(165)	167.0	232.0	196.0
Proximal ML diameter	30.5	37.0	44.0	43.5	59.5	52.5
Proximal AP diameter	26.0	33.5	38.5	38.0	55.1	42.0
Midshaft ML diameter	20.0	23.5	31.0	28.0	32.5	31.5
Midshaft AP diameter	17.5	22.0	23.5	24.0	33.0	27.0
Distal ML diameter	32.5	42.0	49.5	49.5	69.0	61.0
Distal AP diameter	19.5	24.5	28.0	26.5	39.0	34.0
Dorsal longitudinal groove breadth	7.5	11.0	8.5	9.0	11.0	10.5

whereas the humeral morphology of *B. depressicornis* is intermediate between these 2 groups.

Metatarsal.—In contrast to the humerus, the metatarsal of *B. cebuensis* is more similar in length to that of *B. mindorensis* than *B. depressicornis* (Fig. 5; Table 3). As in both *B. mindorensis* and *B. bubalis*, it is straight in medial view; in *B. depressicornis*, this bone is slightly bowed (concave dorsally) and is much more gracile. The most conspicuous feature of the metatarsal in dorsal view, the dorsal longitudinal sulcus (i.e., the sulcus for the extensor digitorum longus tendon), is quite broad in *B. cebuensis*. It is absolutely wider than that of the larger *B. mindorensis* and *B. depressicornis*, and is equal in width to that of the much larger *B. bubalis* (and thus proportionally is much wider). The sulcus also differs from that of *B. mindorensis* and *B. depressicornis* in lacking overarching sides, although this may be an artifact of preservation.

A triangular process projects cranially from the posterior edge of the tarsal articular surface of the metatarsal in *B. cebuensis*. Although it is incompletely preserved, it is longer than that of *B. depressicornis* and is more similar in form to that of *B. mindorensis* and *B. bubalis*. In extant *Bubalus*, this process supports various facets for articulation with the posterior portions of the cubonavicular (= centroquartal) and fused tarsals II and III. In *B. depressicornis* and *B. bubalis*, the posterior cubonavicular facet is mediolaterally elongate; in *B. mindorensis*, it is small and circular. The size and position of this facet cannot be discerned precisely in the fossil cast, but it appears it would have more closely resembled the condition in *B. mindorensis* than in *B. bubalis* or *B. depressicornis*. The remaining tarsal facets are much broader in *B. bubalis*, *B. mindorensis*, and *B. cebuensis* than in *B. depressicornis*. In *B. cebuensis*, the anterior cubonavicular facet tapers slightly anteriorly; in both *B. mindorensis* and *B. bubalis* it is more constant in breadth. The facet for tarsals II and III is relatively larger in *B. bubalis* than in *B. mindorensis*; the condition in *B. cebuensis* more closely resembles that in *B. mindorensis*.

The tuberosity on the proximomedial end of the planter surface of the metatarsal is proportionately broader in *B. cebuensis* than in *B. depressicornis*, *B. mindorensis*, and *B. bubalis*. This tuberosity is proximodistally elongate in both *B. mindorensis* and *B. bubalis*, but extends further proximally in the former. In *B. cebuensis*, the tuberosity is broad proximally, resembling a triangle with its apex pointed distally. In both *B. mindorensis* and *B. bubalis*, a sulcus delimits the medial edge of the tuberosity from the plantar surface; no sulcus is present in *B. depressicornis*. In *B. cebuensis*, the feature that appears to be the homologous sulcus is positioned more laterally, essentially bisecting the tuberosity; this condition strongly contrasts with that present in all extant species of *Bubalus*.

In *B. cebuensis*, a slight crest extends distally from the proximomedial tuberosity of the metatarsal along its plantar surface; it is similarly developed in *B. mindorensis*. This crest is more strongly developed in *B. bubalis*, and is essentially absent in *B. depressicornis*. The heads of the metatarsal of *B. cebuensis* are reminiscent of those of modern *Bubalus*.

A principal component analysis was performed to explore size and shape variation in the metatarsal among different *Bubalus*. Seven of the measurements presented in Table 3 were used in this analysis; breadth of the dorsal longitudinal groove was excluded because the condition in *B. cebuensis* differs so dramatically from that of other *Bubalus*. The factor loadings for PC1 and PC2 are presented in Table 4 and the specimens are plotted against these 2 factors in Fig. 4. Again, PC1 clearly represents size (all variables have high positive loadings), but

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TABLE 4.—Factor loadings and proportion of variation for first 2 principal components (PCs) from principal component analyses of *Bubalus* humeral (H) and metatarsal (MT) measurements. PC1 accounts for 96.8% of the variation in the data; PC2 accounts for 2.3%. AP = anteroposterior; ML = mediolateral; NA = not available.

Measurement	PC1 (H)	PC2 (H)	PC1 (MT)	PC2 (MT)
Length	0.971	−0.226	0.981	−0.162
Proximal ML diameter	0.971	−0.173	0.998	0.0215
Proximal AP diameter	0.999	−0.029	0.984	−0.0959
Teres minor ML diameter	0.995	−0.021	NA	NA
Midshaft ML diameter	0.989	−0.128	0.914	0.403
Midshaft AP diameter	0.970	0.228	0.988	−0.123
Distal ML diameter	0.992	0.089	0.997	0.0214
Distal AP diameter	0.972	0.225	0.994	−0.0371
Trochlear diameter	0.995	0.035	NA	NA
Variation explained (%)	96.8	2.3	96.0	3.1

in contrast to the humeral results, *B. cebuensis* is positioned between *B. depressicornis* and *B. mindorensis* on this axis, reflecting the relatively larger size of the metatarsal in the new species compared to the humerus. PC2 represents metatarsal robustness to some degree—midshaft mediolateral diameter has a high positive loading and length has a high negative loading—but proximal and midshaft anteroposterior diameters also exhibit somewhat higher negative loadings. There is less discrimination along this axis than in the same axis in the principal component analysis of humeral measurements, reflecting a greater amount of individual or ontogenetic shape variation, or both, in the *Bubalus* metatarsal than in the humerus. Both *B. mindorensis* and *B. bubalis* vary greatly in their scores on PC2, but show surprisingly little overlap; *B. cebuensis* and *B. depressicornis* are within the range of variation of *B. bubalis*, distinct from *B. mindorensis*.

Vertebrae.—Two thoracic vertebrae of *B. cebuensis* are preserved but they differ in several respects from thoracic vertebrae of modern *Bubalus* (Fig. 6); because of this, their precise positions within the thoracic series are uncertain. Both preserved vertebrae exhibit relatively small costal articular facets (both on the vertebral body and transverse process), which suggests they pertain to the caudal half of the thoracic region (i.e., T7–13). They differ from vertebrae in this region of *B. depressicornis* in being larger, more robust, and lacking well-developed mammillary processes on the dorsal surfaces of the transverse processes. Both vertebrae exhibit lateral vertebral foramina, a feature present in most *Bubalus* vertebra.

The more complete of the 2 vertebrae (Fig. 6A) is likely the more anterior; its spinous process is less vertical (positioned at an angle of just under 45° to the horizontal), its transverse costal facets are slightly larger and directed more cranially, and its vertebral body is longer and narrower. It compares reasonably well with T9 of *B. mindorensis* in having a spinous process that is long and straight and mediolaterally expanded at its distal end (although the epiphysis is not preserved in the fossil vertebra). The caudal articular facets are positioned at approximately the same angle as the spinous process (45°) and are elliptical. The vertebra differs from the T9 of *B. mindorensis,* however, in

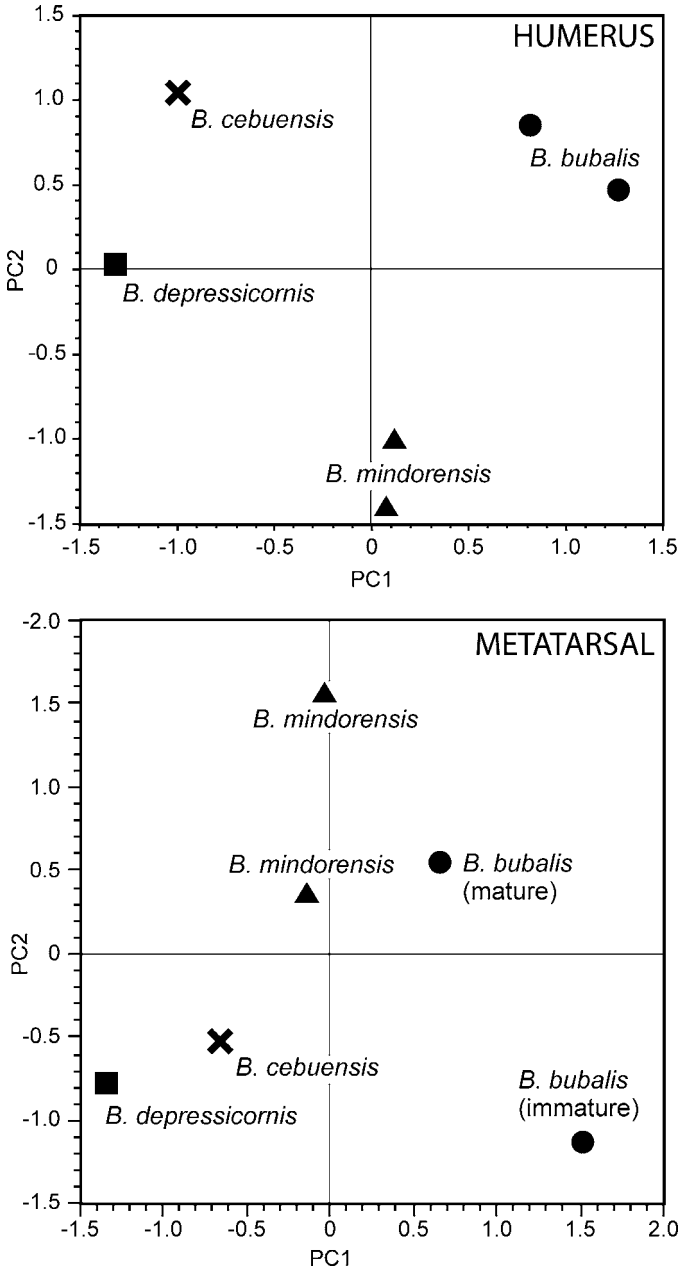


FIG. 4.—Bivariate plot of the first 2 factor scores from principal components analyses of 9 humeral measurements (above) and 7 metatarsal measurements (below) for selected specimens of *Bubalus*. Factor loadings for each principal component (PC) axis are listed in Table 4.

having the transverse costal facets oriented more laterally (as opposed to cranially). In this respect, it is more similar to T10 of *B. mindorensis*. The vertebra differs dramatically from both T9 and T10 of *B. depressicornis*; in those vertebrae, the spinous processes arch caudally (i.e., they are concave caudally) and the caudal costal facet is positioned more dorsally on the vertebral body than the cranial costal facet (they are at the same level in *B. cebuensis*). In anterior view, the neural arch more closely resembles that of *B. bubalis* than *B. mindorensis*; the transverse processes do not extend as far

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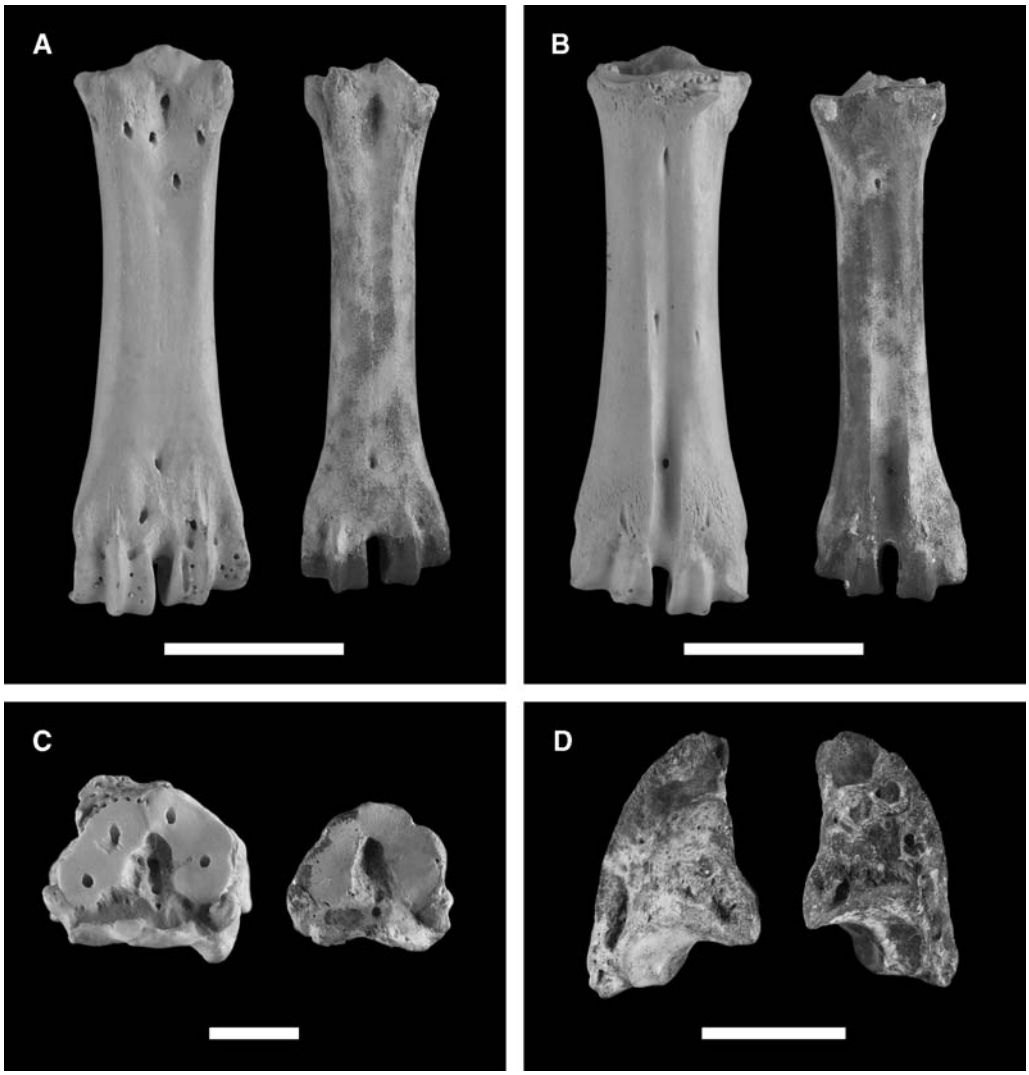


Fig. 5.—Left metatarsals of *Bubalus mindorensis* (FMNH 18817, left) and *Bubalus cebuensis* (cast of PNM 2006-A, right) in A) plantar (posterior), B) dorsal (anterior), and C) proximal (with dorsal toward the top) views. D) Paired unguals of *Bubalus cebuensis* in dorsal view. Scale bars = 5 cm in A and B, 2 cm in C and D. The extra foramina in FMNH 18817 are the result of its previously having been articulated with wires and screws.

superiorly as in *B. mindorensis*. The vertebra is intermediate in length between that of *B. depressicornis* and *B. mindorensis* and the vertebral body is wider than tall, more closely resembling the condition in *B. mindorensis* than in either *B. depressicornis* or *B. bubalis* (Table 5).

The less-complete vertebra (Fig. 6B) appears to represent T11. It possesses caudal articular facets that are directed inferiorly from the base of the spinous process, precluding the possibility of its referral to T12 or T13 (both of which have facets that are oriented more vertically and laterally, as in the lumbar vertebrae). The vertebra also exhibits a more vertical spinous process than typical T12 and T13 of modern *Bubalus*. It cannot represent T10, however, if the identification of the more complete vertebra described above is correct; when placed in approximate articulation, the 2 vertebrae do not appear to represent consecutive positions. The vertebra is more similar to T11 of *B. mindorensis* than of *B. depressicornis*, although the transverse processes are less well developed than in *B. mindorensis*. The vertebral body is very robust; it is intermediate in length between that of *B. depressicornis* and *B. mindorensis*, but is similar in breadth to the latter, making it relatively broader than in any modern material of *Bubalus* examined (Table 5). The within-species variability in this character is not known. The relative height of the vertebral body approximates that of *B. bubalis*.

Unguals.—The morphology of the unguals of *B. cebuensis* is similar to that of other *Bubalus* (Fig. 5D). The most conspicuous feature is a large, anteroposteriorly elongate depression on the posterolateral surface, an area that normally exhibits 1 or more large nutrient foramina in extant taxa. In *B. cebuensis*, it appears that several of these nutrient foramina might have coalesced. Whether this is a constant, discriminating feature of the taxon is unknown. This more closely resembles the condition seen in some individuals of *B. bubalis* than of *B. mindorensis* (no comparative specimens of *B. depressicornis* were available).

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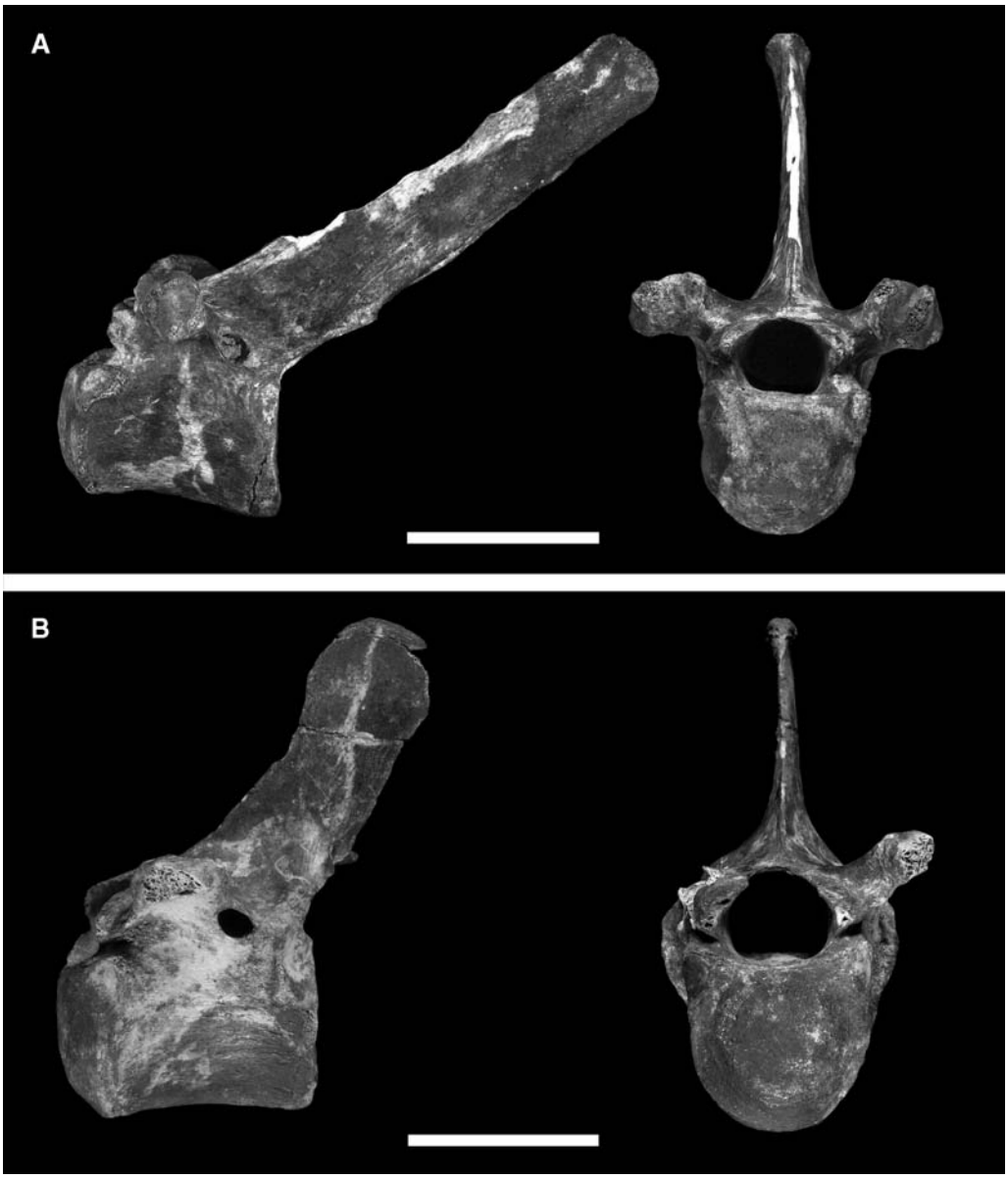


Fig. 6.—Vertebrae of *Bubalus cebuensis* (PNM 2006-A) in left lateral (left) and cranial (right) views. A) ?T9. B) ?T11. Scale bars = 5 cm.

It is unclear whether these elements represent manual or pedal unguals. In *B. mindorensis*, the manual unguals appear to circumscribe a larger arc than the pedal ones. Additionally, the medial sides of the plantar surfaces are flatter in manual unguals; they are slightly upturned in the pedal unguals. The *B. cebuensis* unguals display an intermediate morphology between the anterior and posterior, precluding a confident identification of homology and suggesting a slightly different relationship between the ungual and pedal phalanges in this extinct taxon. The left ungual measures 50 mm (anteroposterior) × 25 mm (mediolateral); the right measures 49.5 mm (anteroposterior) × 23 mm (mediolateral).

Dentition.—The only dental elements preserved are 2 isolated lower molars, left m1–2 (Fig. 7; Table 6). In overall form, they closely resemble the corresponding teeth of modern *Bubalus*. In size, they are most similar to *B. mindorensis*; they are slightly smaller mesiodistally but are comparable buccolingually (Fig. 8). Both teeth exhibit moderate wear, suggestive of a mature individual; only the talonid fossette is present in m1, whereas in both trigonid and talonid fossettes are present in m2. They closely resemble the state of wear exhibited by UMMZ 157862 (*B. bubalis*).

The enamel is thick relative to tooth size in both m1 and m2, but this may be a function of wear stage. In m1, the crown height is 14.8 mm labially and 17.2 mm lingually. The corresponding values for m2 are 12.0 mm and 12.8 mm. A well-developed labial projection is present between the trigonid and talonid in both teeth. The presence or absence of this feature appears to vary individually and with wear in extant *Bubalus*. The enamel islands approximate a figure eight in *B. cebuensis*; enamel island shape also appears to vary with wear state in extant *Bubalus*, and a larger sample size of both *B.*

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TABLE 5.—Measurements of 9th (T9) and 11th (T11) thoracic vertebrae for selected specimens of *Bubalus*. FMNH = The Field Museum of Natural History; PNM = National Museum of the Philippines; UMMZ = University of Michigan Museum of Zoology; AP = anteroposterior.

Measurement	*B. depressicornis* FMNH 98791	*B. cebuensis* PNM 2006-A	*B. mindorensis* FMNH 18817	*B. mindorensis* UMMZ 84106	*B. bubalis* UMMZ 157862
T9					
Length of body	33.0	42.0	47.0	51.0	58.0
Anterior width of body	20.0	27.5	34.0	31.5	36.5
Anterior height of body	20.5	25.0	27.0	28.0	38.5
Spinous process length	58.5	89.5	84.0	98.0	107.5
Spinous process AP width	18.0	20.0	24.5	24.5	35.5
T11					
Length of body	33.5	39.0	46.0	49.0	57.5
Anterior width of body	20.5	30.0	30.0	31.5	38.0
Anterior height of body	20.0	26.0	26.5	28.0	38.5
Spinous process length	30.5		49.0	47.0	66.0
Spinous process AP width	16.0	18.5	25.5	28.5	30.5

cebuensis and other *Bubalus* would be required to test the taxonomic significance of this character.

?Radius.—One other long bone (lacking epiphyses) originally was found with the holotype, but we were unable to examine it firsthand. Based on study of a plaster cast preserving little detail, it most likely represents a ?right radius, potentially referable to *B. cebuensis*. It certainly represents an individual distinct from that of the holotype, however, in which all appendicular epiphyses are solidly fused (i.e., any sutures have been obliterated). The element measures 136 mm in length; the proximal end measures 47.5 × 24.5 mm and the distal end measures 34.5 × 28 mm.

PHYLOGENETIC AFFINITIES

Only a single cladistic analysis has examined relationships within Bovini. Geraads (1992) performed a phylogenetic analysis of 32 fossil and extant taxa based on 57 morphological characters. The monophyly of Asiatic buffaloes (the traditionally recognized Bubalina clade) was not supported in the consensus tree, but Geraads (1992) favored a slightly longer tree that included a monophyletic Bubalina (including *Bubalus*, †*Hemibos*, *Anoa*, and †*Proamphibos*). All but one of the characters used in this analysis were craniodental, however, precluding testing of the phylogenetic position of *B. cebuensis* using this data set. Xue and Li (2000) examined relationships among Chinese fossil *Bubalus*, but that analysis also was based exclusively on craniodental (especially horn core) characters. Rautian et al. (2000) examined morphological and molecular differentiation within the Bovini (including a few fossil species), but did not perform a phylogenetic analysis nor include any extinct genera. Among extant taxa, Rautian et al. (2000) advocated a common ancestry of *Bubalus* and *Anoa* exclusive of other taxa. The same association was favored by Geraads (1992) among extant Bovini.

In sum, the few studies that have examined relationships among fossil Bovini have relied almost exclusively on craniodental characters and thus cannot be used to directly test the phylogenetic affinities of *B. cebuensis*. The lack of postcranial data in those analyses is due to the paucity of associated postcrania for fossil taxa. Although a comprehensive revision of fossil bovine postcrania would likely help identify postcranial characters useful for phylogenetic analysis, such an undertaking is well beyond the scope of the present report of this single new endemic island taxon.

Among extant *Bubalus* for which postcranial data are available, *B. cebuensis* much more closely resembles *B.* (*Bubalus*) than *B.* (*Anoa*); *B. cebuensis* shares a variety of discrete morphological character states with both *B. bubalis* and *B. mindorensis*, but shares none with *B. depressicornis*

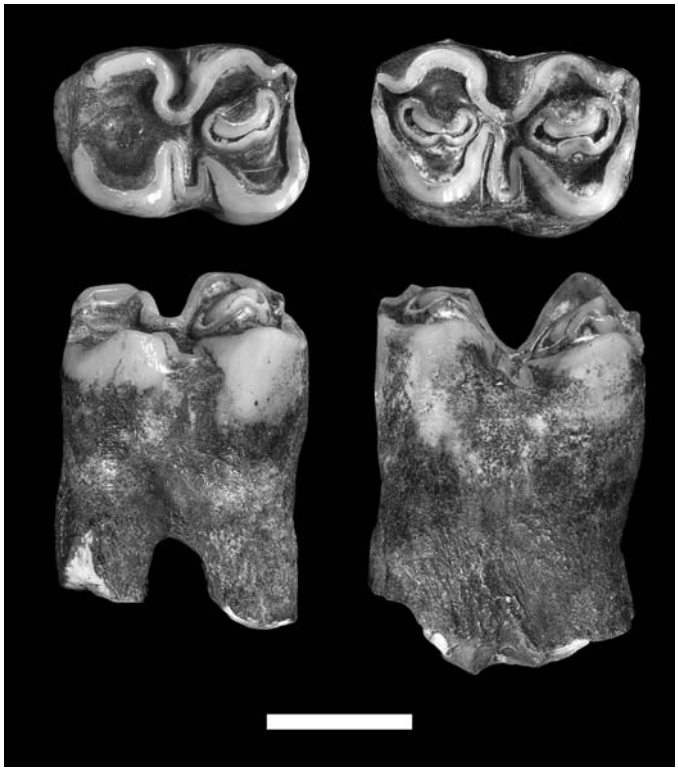


FIG. 7.—First (left) and 2nd (right) lower molars of *Bubalus cebuensis* (PNM 2006-A) in occlusal (above) and lingual (below) views. Scale bar = 1 cm.

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Table 6.—First (m1) and 2nd (m2) lower molar measurements for selected specimens of *Bubalus*. FMNH = The Field Museum of Natural History; PNM = National Museum of the Philippines; UMMZ = University of Michigan Museum of Zoology; L = length (measured mesiodistally); W = width (measured buccolingually).

Measurement	*B. depressicornis* FMNH 98791	*B. cebuensis* PNM 2006-A	*B. mindorensis* FMNH 18817	*B. mindorensis* FMNH 43300	*B. mindorensis* FMNH 43301	*B. bubalis* FMNH 92912	*B. bubalis* FMNH 31711?	*B. bubalis* FMNH 31711?	*B. bubalis* UMMZ 157862
Wear	Heavy	Medium	Medium	Medium	Light	Medium	Light	Medium	Medium
Side	Right	Left	Right	Right	Right	Right	Right	Right	Right
m1 L	12.3	16.5	18	17.4	22.4	28.1	33.1	29.5	24.2
m1 W	9.8	12.7	12.7	12.3	11.5	15.5	17.8	18.4	16.1
m2 L	15.1	18.3	19.8	20.9	25.1	30.1	37.6	32.8	29.5
m2 W	10.9	12	12.3	12.3	11.2	16.4	16.9	19.3	18

(Table 2). Given the greater similarity in size between *B. cebuensis* and *B.* (*Anoa*) than between the former and *B.* (*Bubalus*), the character states common to *B. cebuensis* and *B.* (*Bubalus*) cannot be attributed to allometry and are more likely indicative of phylogenetic relationship. Based on these resemblances, *B. cebuensis* can reasonably be referred to *B.* (*Bubalus*). Within *B.* (*Bubalus*), *B. cebuensis* shares more character states with *B. bubalis* than with *B. mindorensis*. The latter 2 species share several traits not observed in *B. cebuensis*, however, which may indicate a closer relationship between them than between either and *B. cebuensis*. The relationships among these 3 species are probably best considered unresolved until additional material of *B. cebuensis* is discovered and a thorough cladistic analysis (incorporating postcranial features, as well as living and fossil taxa) can be performed.

Body Mass

Long-bone lengths for *B. cebuensis* suggest an animal roughly similar in stature (i.e., limb length) to *B. depressicornis*; in contrast, the breadths of these bones suggest a more massive animal. To test this assertion, we estimated the body mass of *B. cebuensis* using postcranial regression equations for modern bovids published by Scott (1983). Eleven humeral and metatarsal measurements examined by Scott (1983) were preserved in the available material of *B. cebuensis* and 10 of these were used to estimate body mass; metatarsal length was excluded because it is poorly correlated with body mass in modern bovids (Scott 1983). The remaining 10 variables produced mass estimates of approximately 115–215 kg with $\bar{X}$ = 157.2 kg and *SD* = 36.6 kg (Table 7). Humeral mass estimates exhibited a much greater range than metatarsal mass estimates, but the average values were quite similar (154.0 kg and 162.0 kg, respectively). A reasonable mass estimate for this particular specimen of *B. cebuensis* is roughly 150–165 kg. Given the variability in estimates derived from individual measurements in living taxa, this estimate is probably within 15% of the true mass of this fossil animal (Scott 1983).

As discussed by Scott (1983), accurate individual or species body masses are difficult to obtain for extant large herbivores; this type of information is rarely recorded in the field, and body masses listed for these mammals frequently include only trophy or zoo animals (which are not representative of the species in general). In the case of rare ungulates such as *B. mindorensis* and *B.* (*Anoa*), even poor mass estimates are comparably scarce. Only 2 independent body masses have been published for *B. mindorensis*: Talbot and Talbot (1966) estimated the mass of a female zoo animal at 600 lb (= 275 kg) and Roth and Montemayor-Taca (1971) estimated the mass of a female zoo animal at 180–220 kg. Although sexual dimorphism is evident in the skull of *B. mindorensis*, body mass and limb proportions do not vary with sex (Custodio et al. 1996), and so these estimates also should apply to male *B. mindorensis*. Using the regression equations of Scott (1983), an average body mass of approximately 210 kg was obtained for the 2 male specimens examined in the present study; this accords well with the

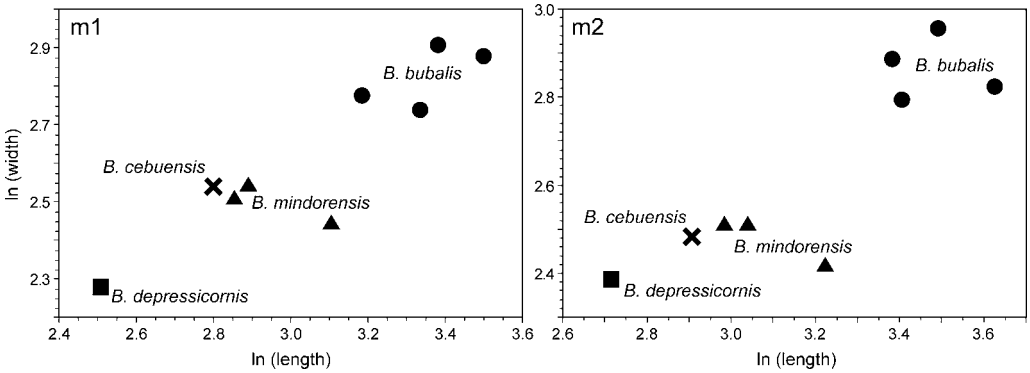


Fig. 8.—Bivariate plots of log-transformed measurements for m1 (left) and m2 (right) for selected specimens of *Bubalus*. Length is measured mesiodistally; width is measured buccolingually.

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estimate of Roth and Montemayor-Taca (1971) and highlights the lack of sexual dimorphism in this species.

Groves (1969) reported a body mass of 56 kg for an adult *B. quarlesi* and indicated it was the only body mass for *B.* (*Anoa*) that he was aware of; this same mass was used by Scott (1983) for *B. depressicornis*, presumably because no better data were available. Burton et al. (2005) estimated the body mass of *B. quarlesi* as <150 kg, but provided no data for individual specimens; they estimated the body mass of *B. depressicornis* as <300 kg, but noted that no specimen has ever been recorded at more than 150 kg. Based on skull length (Groves 1969), there does not appear to be dramatic sexual size dimorphism in *B.* (*Anoa*). Using the regression equations of Scott (1983), a body mass of approximately 135 kg was obtained for the single female specimen of *B.* (*A.*) *depressicornis* examined in the present study. Therefore, this suggests that a mass estimate of <150 kg for *B. depressicornis* may be more accurate than an estimate of <300 kg.

The data considered above indicate that *B. cebuensis* was intermediate in body mass between *B. depressicornis* and *B. mindorensis*, being about 15% larger than the former and 25% smaller than the latter. This contrasts with long-bone lengths, which suggest a stature more similar to that of *B. depressicornis* than *B. mindorensis*. The prominent muscle scars on the humerus and the breadth of the dorsal longitudinal sulcus of the metatarsal support the interpretation of relatively large appendicular muscles in *B. cebuensis*, indicative of its larger body mass (relative to *B. depressicornis*). Together, these observations paint a picture of a short, heavy-bodied *Bubalus*, perhaps similar in stature to an anoa, but certainly of greater mass; the structure of the skull is unknown, but the animal may have resembled a small tamaraw.

Table 7.—Humeral (H) and metatarsal (MT) variables used to predict body mass of *Bubalus cebuensis* using measurements from the holotype and predictive equations from Scott (1983). Predictive equations are in the form: log(body mass) = b × log(variable) + a. The mean of the predicted body masses for *B. cebuensis* is 151.4 kg and *SD* = 40.0. For more detailed explanations of variables, see Scott (1983). AP = anteroposterior; ML = mediolateral.

Variable	Value (mm)	b	a	Mass (kg)
Humerus				
H1 (head−trochlea length)	180.5	3.4556	−2.4150	217.6
H2 (tubercle−trochlea length)	205.0	3.3696	−2.4709	204.1
H3 (head breadth)	46.5	2.7311	0.2334	120.0
H4 (anterior distal articular width)	51.0	2.5499	0.4078	117.0
H5 (maximum distal width)	53.5	2.6246	0.2756	123.0
H6 (posterior trochlear width)	20.0	2.7630	1.3617	142.1
Metatarsal				
MT2 (proximal ML diameter)	37.0	2.9220	0.6162	181.0
MT3 (proximal AP diameter)	33.5	3.0306	0.5755	180.8
MT4 (distal ML diameter)	42.0	2.7421	0.5614	150.3
MT5 (distal AP diameter)	18.5	2.9763	1.1416	136.1

Insular Dwarfing

The phenomenon of insular "dwarfing" has been observed in many groups of large mammals, including proboscideans (Hooijer 1970; Roth 1990; Vartanyan et al. 1993), hippopotamids (Burney et al. 2004; Simmons 1988), cervids (Lister 1989), and possibly hominids (Brown et al. 2004; Morwood et al. 2005). Together with its converse—insular gigantism—insular dwarfing has been the subject of many studies over the past 40 years (e.g., Anderson and Handley 2002; Case 1978; Foster 1964; Heaney 1978; Lawlor 1982; Lomolino 1985, 2005; Meiri et al. 2004; Melton 1982; Michaux et al. 2002; Sondaar 1977; Van Valen 1973). Although the causes (and patterns) of insular body-size change are still being debated, certain cases continue to be exemplars of how a major life-history trait can evolve rapidly, over a geologically brief period of time, after isolation (e.g., Lister 1989).

Given the much larger size (in terms of both stature and mass) of the closest relatives of *B. cebuensis*, both fossil and extant, it is clear that this Cebu Island form represents another case of insular dwarfing. In fact, the long fossil record of *Bubalus* in Asia suggests that both *B. mindorensis* and *B. cebuensis* may be dwarf forms of *B. bubalis* that arose by dispersal to and within the Philippines. Given the rarity of fossils in the Philippines and the lack of a secure phylogeny for the species of *B.* (*Bubalus*), details of such a scenario must remain provisional. However, certain independent aspects of the distribution and morphology of these taxa do support this general interpretation.

Heaney (1978) examined body-size variation in the tri-colored squirrel, *Callosciurus prevostii*, and found a significant correlation between body size and island size. Based on this correlation and patterns of variation in other mammals, he constructed a model predicting that the effects of food limitation, predation, and interspecific competition on body size would vary depending on the body size of the species in question and the area of the island. In some cases, these factors would be expected to produce insular dwarfs; in others, giants would result. For large mammals, food limitation was proposed as the most significant factor affecting insular body size, and a direct correlation between body size and island size was the expected result. In support of this model, Heaney (1978) noted such a correlation in Pleistocene populations of *Elephas falconeri*, where increasingly smaller-bodied taxa are found on progressively smaller Mediterranean islands (Maglio 1973). Although this pattern may not apply to carnivorans (Heaney 1978; Meiri et al. 2004) or tree sloths (Anderson and Handley 2002) it does seem to be generally applicable to large ungulates, including *Bubalus*.

Based on body mass, *B. cebuensis* is some 25% smaller than *B. mindorensis*; *B. mindorensis* is itself less than half the size of wild (mainland) *B. bubalis*. Such a pattern in body size would be predicted based simply on the relative sizes of Cebu Island (5,088 km^2), Mindoro Island (10,243 km^2), and mainland Asia, if island size were a major factor in body-size evolution. This pattern does not hold if one substitutes the entire area of the late Pleistocene Negros–Panay Faunal Region for that of Cebu Island—a region probably 10 times larger—but this is a moot

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point if *B. cebuensis* evolved during the Holocene; given the numerous other examples of post-Pleistocene dwarfing in large mammals, *B. cebuensis* certainly could have undergone the observed changes in body size subsequent to Cebu's isolation. No well-preserved *Bubalus* have been discovered on other islands that might permit testing of this scenario; although isolated teeth from Luzon have been referred to *B. mindorensis* (Beyer 1957), they have not been critically examined (Custodio et al. 1996), and probably are not useful for estimating body size in bovids except in very general terms (Scott 1983; see also below).

Size reduction in insular dwarfs is not generally isometric across all parts of the body; allometric relationships have been noted both for the dentition (Fortelius 1985; Lister 1989) and distal limb elements (Köhler and Moyà-Solà 2001; Sondaar 1977), among other structures. In dentition, island dwarfs tend to have relatively larger teeth, an attribute apparently exhibited by *B. cebuensis*; although much less massive than *B. mindorensis*, the teeth of these 2 species are similar in size (Fig. 8). Based on this pattern of positive dental allometry, it has been suggested that paedomorphosis is the mechanism of insular dwarfing in some lineages (Fortelius 1985).

In contrast to the dentition, the metatarsal of *B. cebuensis* does not exhibit the pattern of size reduction typical of island dwarfs; it is 71.5% the length of the humerus in *B. cebuensis*, a value comparable to that of *B. bubalis* examined (68–72.5%). However, the metatarsal does appear to be reduced in *B. mindorensis*, being only 59–60% the length of the humerus. Whether such reductions in distal limb elements are attributable to paedomorphosis or simply are locomotor adaptations (e.g., Sondaar 1977) may depend on the mosaic pattern of insular evolution in the particular species in question; the metatarsal of *B. mindorensis* more closely resembles an osteologically mature *B. bubalis* than a slightly less mature one (Fig. 4), but testing for such an ontogenetically driven trend would certainly require examining much younger individuals of *B. bubalis*.

Conclusions

The new taxon described above is the 1st fossil mammal of any age to be reported from Cebu Island and the only nonproboscidean to be documented from the Negros–Panay Faunal Region. In conjunction with the presence of *Bubalus* on Mindoro Island (and potentially Luzon), discovery of this specimen suggests that *Bubalus* may once have ranged throughout the Philippines—a hypothesis that hopefully will be tested by future paleontological sampling across the islands. Similarly, this discovery, combined with the exceptionally high endemism and diversity of the extant mammal fauna of the Philippines, suggest that many more new late Cenozoic to Holocene fossil species remain to be recovered from this region. *B. cebuensis* is clearly referable to the subgenus *Bubalus*, and is diagnostically differentiated from *B. mindorensis* and *B. bubalis* by metric and morphological characteristics. In life, *B. cebuensis* was probably similar in stature to the lowland anoa, *B. depressicornis*, but regression equations from modern bovids suggest that it was approximately 15% more massive. The overall small size of *B. cebuensis* relative to other *B.* (*Bubalus*) appears to be attributable to island dwarfing, an explanation that is supported by the consistent relationship between body size and island size in *B. cebuensis*, *B. mindorensis*, and *B. bubalis*. Although the relatively large dentition of *B. cebuensis* suggests paedomorphosis as a possible mechanism of body-size reduction in this lineage, this is not supported by the relatively large (i.e., normal for this clade) size of the metatarsal relative to the humerus. Additional material of *B. cebuensis* would facilitate testing of paedomorphosis as a mechanism for dwarfing in these bovids, as would a detailed study of the postcranial osteology of *B. mindorensis*. Although the exact age of *B. cebuensis* is unknown, the condition of the material and its small size suggest it is no older than Pleistocene, and possibly Holocene. Further study of *B. cebuensis* and other island dwarfs may provide insights into the evolution of small-bodied hominins such as *Homo floresiensis*, yet another reason to be interested in dwarf mammals on oceanic islands in Indo-Australia.

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APPENDIX I

List of specimens examined from the Recent mammal collections of the Division of Mammalogy at The Field Museum of Natural History (FMNH) and the University of Michigan Museum of Zoology (UMMZ).

Bubalus (Anoa) depressicornis.—FMNH 98791, mature female, skull and skeleton, from Lincoln Park Zoo, Chicago, Illinois.

Bubalus (Bubalus) mindorensis.—FMNH 18817, mature male, skull and skeleton, from Mindoro Island, Philippines; FMNH 43300, mature male, skull only, Mindoro Island, Philipines; FMNH 43301, young male, skull only; UMMZ 84106 (holotype of *Anoa mindorensis* Steere), mature male, skeleton only, from Catuiran River, Mindoro Island, Philippines.

Bubalus (Bubalus) bubalis.—FMNH 92912, immature male, skull and skeleton, from Khuzistan, Iran; FMNH ?31711, 2 young female specimens, skulls only, differing in stage of wear, exact provenance unknown; UMMZ 157862, mature female, skull and skeleton, from Tanjay, Negros Oriental, Philippines.

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