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Palaeozoology of Palawan Island, Philippines

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ARTICLE INFO

Article history:

Available online 16 August 2010

Keywords:

Palawan Island
Palaeozoology
Terminal Pleistocene
Holocene
Mammal biodiversity
Extinctions

ABSTRACT

Excavations at the Ille site in north Palawan have produced a large Terminal Pleistocene to Late Holocene faunal assemblage. Derived both from the natural deaths of small mammals and the human hunting of large and intermediate game, the bone assemblage provides important new information about changes in the composition and structure of the mammal community of Palawan over the last ca. 14 000 years. The Ille zooarchaeological record chronicles the terrestrial vertebrate fauna of the island, and the disappearance of several large taxa since the end of the last glacial period due to environmental change and human impacts.

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1. Introduction

The study of archaeologically-derived animal bone assemblages provides invaluable information on the origin, dispersal and evolutionary history of different vertebrate communities. The data offer long-term perspectives on climatic and environmental change, the timing of the introduction of invasive species, extinction in native taxa and the impacts of people on ecological communities (Lyman, 2006). Current knowledge of the natural history of Island Southeast Asia and Wallacea is still limited, but studies of past animal communities in Borneo (Cranbrook, 2000, 2009; Cranbrook and Piper, 2007), Java (Morwood et al., 2008), Flores (van den Bergh et al., 2009; Hocknull et al., 2009) and East Timor (O'Connor and Aplin, 2007) suggest that substantial ecological changes occurred in past millennia as a result of environmental change and human activities (Heinsohn, 2003).

This study focuses on the Terminal Pleistocene and Holocene mammal faunas of the Philippine island of Palawan (Fig. 1). Palawan is 425 km in length with a maximum breadth of just 40 km, and covers approximately 11 785 km². It divides the South China Sea to the north from the Sulu Sea to the south. It is located on the north-eastern margins of the shallow ocean platform surrounding

Peninsular Malaysia, Java, Sumatra, Bali and Borneo, known as the Sunda Shelf (Mollengraaff, 1921).

The present-day environment of Palawan is broadly similar to that of north Borneo, comprising lowland tropical rainforest to approximately 1200 m, grading into submontane and eventually montane forest above 1600 m (Heaney, 2001). The contemporary mammal community comprises 58 native and four non-native species (Esselstyn et al., 2004). Thirteen species (22% of the total and 54% of the native non-flying species) are endemic to Palawan. Of these, 12 are non-bat and, along with almost all the native mammals, have their closest relatives on the Sunda Shelf. The only exceptions are the endemic fruit bat *Acerodon leucotis* whose nearest relatives inhabit the oceanic Philippines, and four other species that are widespread throughout the Sundaic region and the rest of the Philippine archipelago: the long-tailed macaque (*Macaca fascicularis* subsp.), common palm civet (*Paradoxurus hermaphroditus*), Malay civet (*Viverra zibellina*) and leopard cat (*Prionailurus bengalensis*). As a result of these affinities, Palawan is considered to represent the north-eastern boundary between the Sundaic biogeographic region and the isolated oceanic islands of Wallacea. This is an impoverished fauna compared with the 285 species of mammals (including 103 bat species) on the neighbouring land-mass of Borneo. Borneo does, however, demonstrate fairly high endemism, with 19% of all mammal species (or 28% excluding bats) only found on that island (Cranbrook, personal communication, 2010).

During Pleistocene glacial maxima when sea levels were lowered by as much as –116 to –139 m (Rohling et al., 1998; Hanebuth

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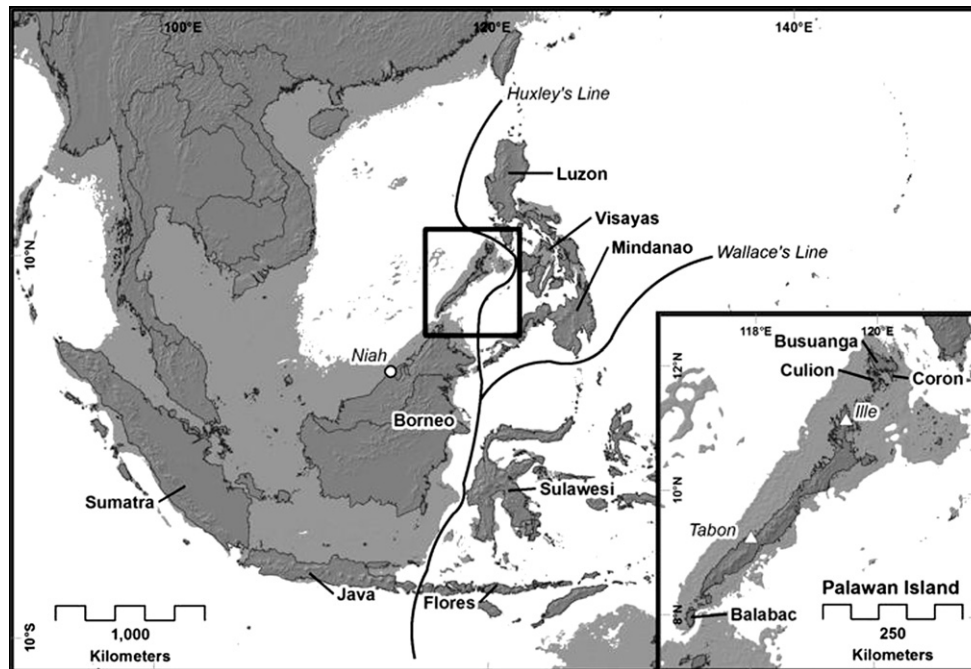


Fig. 1. Present-day (dark grey) and LGM (light grey) land distribution of Southeast Asia and the location of Palawan and Ille Cave (inset) along with key archaeological sites and islands mentioned in the text. Drawn by Emil Robles.

et al., 2000), Palawan was much larger than at present and joined to many smaller adjacent islands such as Culion, Coron and Busuanga to the north and Balabac to the south, forming what is known as the Greater Palawan region (Heaney, 1985). The Balabac Strait between Palawan and Borneo was considerably narrower and at times of sea-level low stands the two islands might have joined through a land bridge, facilitating the migration of Sundaic species to and from Palawan (Cranbrook, 2000; Tougaard, 2001).

In their study of the sub-fossil faunas from cave sites in central Palawan, Reis and Garong (2001) identified six orders, 11 families and 14 species of mammals dating back almost 12 000 years. The taxonomic composition of the assemblages studied, which consist almost exclusively of small mammals, reptiles and birds, is more likely to represent natural accumulations rather than the results of human intervention. In that study there was no conclusive evidence for a land bridge between Palawan and Borneo during the Last Glacial Maximum (LGM) around 18–20 ka, with Palawan demonstrating many characteristics of an isolated island with low taxonomic diversity and relatively high endemism in comparison to the rest of the Sundaic region. More extensive research was called for by Reis and Garong (2001) to develop a better understanding of the palaeozoological history of the island.

The animal bone assemblage from Ille Cave provides one such opportunity. Excavations have produced more than 50 000 bone fragments from well-stratified archaeological sequences dating from ca. 14 000 cal. BP to less than 4000 cal. BP (Lewis et al., 2008). The assemblage accumulated through two major mechanisms. Numerous small mammal and reptile inhabitants of the cave and its immediate surroundings accumulated as part of natural death assemblages. However, the majority of animal bones derive from intermediate and large-sized taxa, and represent human food debris. Hunter-gatherer populations often target preferred resources (Cranbrook and Piper, 2007; Rabett and Barker, 2007; Piper et al., 2008b; Piper and Rabett, 2009), but humans are generally opportunists and will, over time, collect a relative sample of the wild fauna available, providing a good indication of the range

of taxa present in the local and regional environment at different phases in the history of the site.

All radiocarbon (^{14}C) dates are reproduced as calibrated years before present.

2. Archaeological background

Ille Cave is located in the Dewil River valley in north Palawan, close to the village of New Ibajay at $11^{\circ}11'46''\text{N}$; $119^{\circ}30'19''\text{E}$. The cave is on the base of the south side of a ca. 75 m high limestone karst tower, with two main openings (east and west) and an adjoining short passageway no more than 5 m in length. Both entrances open onto a relatively flat platform 3–15 m wide, covering a total area of approximately 450 m² and ending in a sharp, short downward gradient onto lightly wooded ground and a small stream (Pawlik, 2004; Szabó et al., 2004). The platform lies 3–4 m above the surrounding landscape.

The local area is dominated by the floodplain of the Dewil River and its tributaries, covered by rice paddies, tree and vegetable crops, swiddened fields and secondary rainforest. The sea is visible in Sibaltan Bay from the top of the tower, lying 4 km to the east (Paz and Ronquillo, 2004).

The first exploratory archaeological investigations of Ille started in 1998 (De la Torre, 1999; Solheim, 2000; Hara and Cayron, 2001); since 2004 excavations at Ille have continued every year and have uncovered archaeological deposits in the East Mouth (EM) trench in excess of 4 m, and in the West Mouth (WM) trench to more than 2 m deep (Kress, 2004; Szabó et al., 2004; Lewis et al., 2008). More than 30 radiocarbon dates anchor the stratigraphy in the EM trench to a numerical chronology, making Ille currently the best-dated cave site in the Philippines (Szabó et al., 2004; Lewis et al., 2008). The WM trench sequence awaits comprehensive dating, but the layers can be associated with the EM through stratigraphic correlation. To differentiate layers and features encountered during excavation, each is given a unique identifying context number, permitting the archaeologist to interpret discrete sedimentary

units and associate recovered remains with the sediments from which they were excavated. These context numbers are used here to refer to the various sedimentary and archaeological deposits discussed (Fig. 2a and b).

The upper and chronologically youngest layers in both mouths comprise a series of late prehistoric and protohistoric burials (Szabó et al., 2004) and pits, truncating other late sedimentary layers. These are underlain by layers of shell midden (EM: 332; WM: B912) dated

to ca. 5000–7000 cal. BP, overlying an early cremation cemetery (Lewis et al., 2008). Beneath this lies a sequence of silty clay deposits (e.g. EM: 334, 336 and 769; WM: 1626A, B and C) dating to between 9400–11 000 cal. BP, and containing evidence of human activity, including hearths, charcoal, shell, unburnt and burnt animal bones and stone tools. The deepest deposits comprise steeply sloping layers of orange and brown clay, some containing evidence of human activity, whilst others are devoid of material culture, suggesting

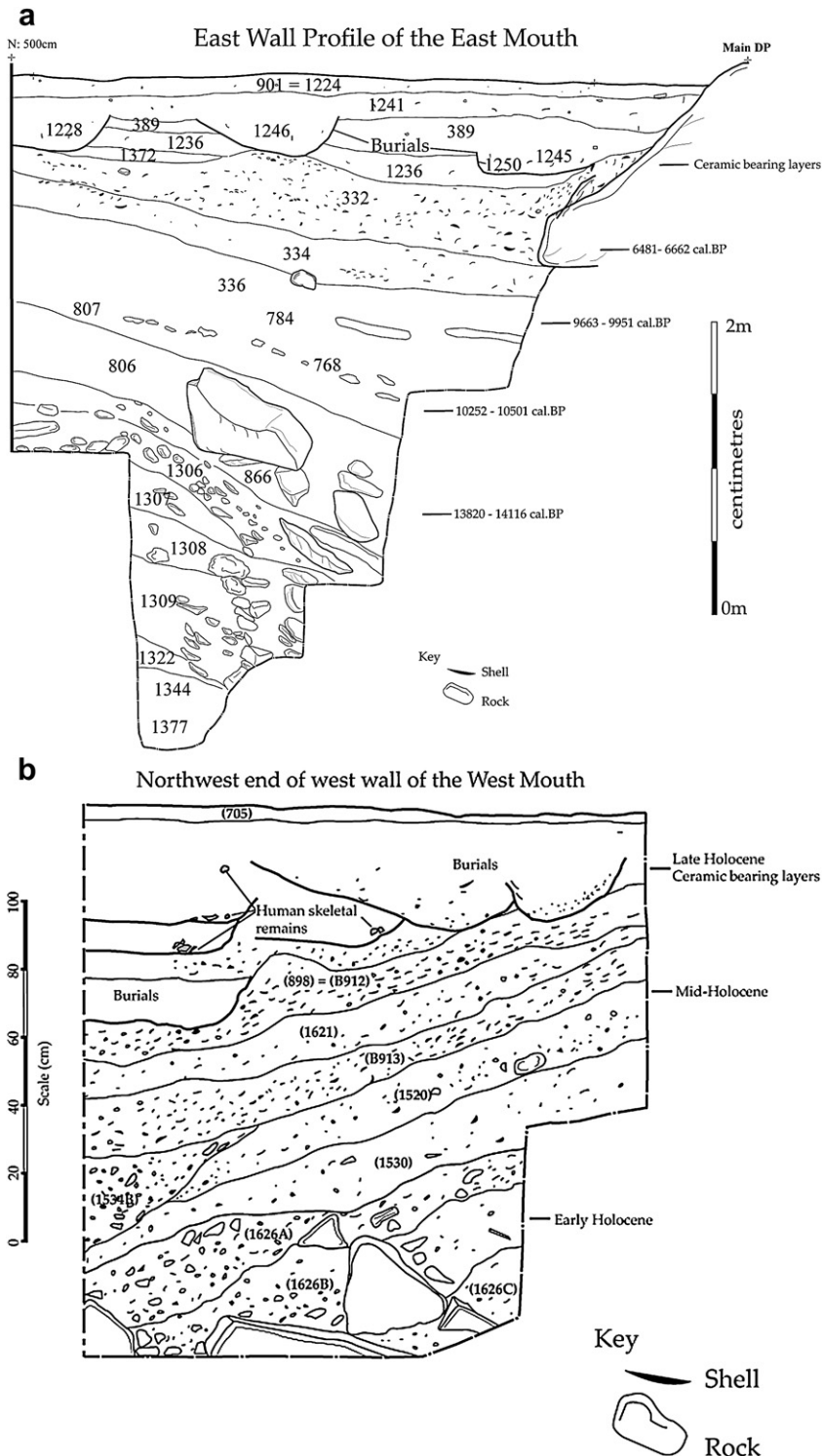


Fig. 2. a: A partial sedimentary profile of the east wall of the East Mouth of Ille Cave. b: A partial sedimentary profile of the west wall of the West Mouth of Ille Cave.

intermittent phases of cave occupation. The oldest deposit at Ille containing stone tools and animal bones was designated Context 1306 (Equivalent to WM context 1832; not shown in Fig. 2b). This layer directly underlies Context 866 with a ^{14}C date on charcoal of 13 820–14 116 cal. BP (OxA-16666), placing it in the Late Pleistocene.

3. Methodology

This study concentrates primarily on the mammal remains from the Terminal Pleistocene deposits (ca. 14 000 cal. BP) up to the mid-Holocene shell middens (5000–7000 cal. BP). The layers produced discrete, well-dated animal bone assemblages that presented an opportunity to identify a chronological sequence of change in the composition of the faunal community during these periods. The more recent phases of cave use involved the interment of several hundred people, which has reworked and mixed deposits in the upper part of the sequence, including the animal bones, and thus limits the resolution to which later remains can be studied. Nevertheless, the radiocarbon chronology suggests that all the material above the shell midden dates to within the last 5000 years, and though the resolution is not ideal, it does provide an indication of the faunal community in and around the cave during more recent millennia.

All the bones recovered from the late Pleistocene and early Holocene layers, and a sample from late Holocene contexts were sorted, counted, measured and analyzed for taphonomic modifications. Diagnostic skeletal elements were identified to genus or species using comparative osteological collections in the National Museum of the Philippines and the University of the Philippines. The determination of some mammal bones was hampered by the limited number of modern comparative specimens available in the Philippines. These important skeletal elements were transported by PJP and JO to the Field Museum of Natural History (FMNH) in Chicago, for comparison with their comprehensive collections of modern mammal skeletons from the Philippines.

To differentiate between closely-related taxa and identify morphometric changes over time, all molars and selected anatomical features of appendicular elements were measured, using methods following von den Driesch (1976). However, for deer and pig teeth, a standard measurement for the length of the tooth was taken, and then the width of each molar column was measured. Since cervid and suid molars change in shape as they wear, all measurements were taken at or as close to the enamel–root junction as possible, providing a point of reference to ensure comparability in measurements of archaeological and modern comparative specimens. The cervid teeth, mandibular and cranial elements from Ille Cave were compared with samples of the three native living deer in the Philippines – Calamian hog deer (*Axis calamianensis*), Philippine brown deer (*Cervus mariannus*) and Visayan spotted deer (*Cervus alfredi*). Comparisons were also made with Sambar deer (*Cervus unicolor*) and Muntjac (*Muntiacus muntjak*), which are inhabitants of mainland Southeast Asia and the adjacent island of Borneo. Pig remains were compared with the Palawan endemic wild boar (*Sus ahoenobarbus*) and Eurasian wild boar (*Sus scrofa*); the latter species is known to have been introduced from mainland Southeast Asia to the islands as a domesticated in the late Holocene (Larson et al., 2005, 2007; Dobney et al., 2008; Cucchi et al., 2009; Piper et al., 2009).

All small mammal mandibular and maxillary fragments (the most diagnostic elements) were identified to the highest taxonomic level possible using keys such as Cranbrook (1968) for bats and Musser and Newcomb (1983) for rat species with wide geographic ranges. No keys exist for the numerous endemic species from Palawan, and all identifications of these were made using the comparative collections at the Field Museum.

A modified version of the York System database (Harland et al., 2003), used to record the animal bones from Ille, generates unique identifying numbers for the individual or groups of bones entered for Ille Cave West Mouth (ICWM) and East Mouth (ICEM) assemblages, and these numbers are used in the text and illustrations here.

In this paper, taxonomic nomenclature for mammals follows Esselstyn et al. (2004), except for the native Palawan pig, which is now classified as a distinct species, *S. ahoenobarbus*, after Lucchini et al. (2005).

4. Taxonomic accounts

A total of 26 090 bone fragments were studied from Ille Cave; 28 mammal taxa from 19 families were identified from the Late Pleistocene and early–late Holocene deposits (Table 1). This includes the first identification of the tiger (Piper et al., 2008a), at least two species of deer and a canid. Discussion focuses on new identifications and not those already outlined in Reis and Garong (2001). Numbers preceded by the abbreviations “ICWM” and “ICEM” indicate bone identification numbers whereas numbers with “WM” and “EM” indicate context numbers.

4.1. Order Insectivora

4.1.1. Family Soricomorpha

4.1.1.1. *Crociodura cf. batakorum* (Batak shrew). A single left mandibular ramus (ICEM-19464) was recovered from a mid-Holocene midden context (EM-332). The specimen is substantially smaller than the endemic *Crociodura palawanensis* and the introduced commensal *Suncus murinus*. Reis and Garong (2001) discovered a humerus of a similarly small *Crociodura* in their studies in central Palawan. Recently, Hutterer (2007) described a new species of shrew from Palawan, *C. batakorum* sp. nov. based on collections stored at the Deutsches Museum, Bonn. The holotype was found in Puerto Princessa, in central Palawan, and is the smallest *Crociodura* species currently known in the Philippines. Comparison of scaled photos of the Ille specimen and of a modern specimen collected by J. Esselstyn (personal communication) show a comparable likeness in size and the specimen from Ille is tentatively allocated to this species.

4.2. Order Chiroptera

4.2.1. Suborder Megachiroptera

4.2.1.1. *Family Pteropodidae*. Two taxa were identified: the flying fox (*Pteropus* sp.), represented by a single posterior fragment of the right mandibular torus containing a heavily worn 2nd molar (ICEM-18420), and the short-nosed fruit bat (*Cynopterus cf. brachyotis*), with 16 mandibles from the Late Pleistocene to the mid-Holocene (EM-769, 784, 807, 1306; WM-1574, 1626, 2003). Both are common and widespread in Southeast Asia, and the latter still roosts on the outer fringes of Ille Cave today.

4.2.2. Suborder Microchiroptera

All identifications were initially based on teeth and alveoli morphology, and species were separated using dental biometrics. Four insectivorous bat species were identified, with *Hipposideros diadema* (diadem roundleaf bat) being the most common throughout the Holocene archaeological sequence (EM-784, 769, 807; WM-1530, 1530A, 1537, 1560, 1574, 1626, 2003). Three new fossil identifications are also presented here. *Rhinolophus cf. creaghi* (Creagh's horseshoe bat), is represented by three mandibles from Early Holocene to mid-Holocene contexts (EM-769, 784). A single fragment of mandibular body and ramus (ICEM-18312) from the early Holocene context EM-784 was designated as *Hipposideros* cf.

Table 1

A list of the mammal taxa recovered from Terminal Pleistocene (TP), early (EH), mid (MH) and late (LH) Holocene layers at Ille Cave. * denotes extinct on Palawan.

Order	Family	Genus/Species	Local names	English name	TP	EH	MH	LH	Status
Insectivora	Soricomorpha	<i>Crocidura cf. batakorum</i>	Bising	Shrew			×		Extant
Chiroptera	Pteropodidae	<i>Pteropus</i> sp.		Flying fox				×	Extant
	Rhinolophidae	<i>Cynopterus brachyotis</i>	Kabag	Short-nosed fruit bat	×	×	×		Extant
	Hipposideridae	<i>Rhinolophus cf. creaghi</i>	Kabatkabat/Kabag	Creagh's horseshoe bat		×	×		Extant
		<i>Hipposideros diadema</i>	Kabatkabat/Kabag	Diadem roundleaf bat	×	×	×	×	Extant
		<i>Hipposideros cf. ater</i>	Kabatkabat/Kabag	Dusky roundleaf bat		×			Extant
	Vespertilionidae	<i>Myotis cf. macrotarsus</i>		Phil. large-footed myotis		×	×		Extant
Primates	Cercopithecidae	<i>Macaca fascicularis</i>	Unggoy	Long-tailed macaque	×	×	×	×	Extant
Pholidota	Manidae	<i>Manis culionensis</i>	Balintong	Palawan pangolin	×	×	×	×	Endemic
Rodentia	Sciuridae	<i>Hylopetes nigripes</i>	Pula Tuka	Arrow-tailed flying squirrel		×	×	×	Endemic
		<i>Sundasciurus</i> sp(p).	Bising	Tree squirrels	×	×	×	×	Endemic
	Muridae	<i>Maxomys panglima</i>	Daga	Palawan spiny rat			×		Endemic
		<i>Rattus cf. tiomanicus</i>	Daga	Malaysian field rat		×	×		Extant
		<i>Sundamys muelleri</i>	Daga	Great Sunda rat	×	×	×		Extant
	Hystricidae	<i>Hystrix pumila</i>	Durian	Palawan porcupine	×	×	×	×	Endemic
Carnivora	Canidae	<i>Cuon/Canis</i> sp.		Wild dog?	×	×			Extinct*
		<i>Canis familiaris</i>	Aso	Domestic dog				×	Extant
	Mustelidae	<i>Aonyx (Aonyx) cinereus</i>	Dingguin	Oriental small-clawed otter		×	×		Extant
	Mephitidae	<i>Mydaus marchei</i>	Pantot	Palawan stink badger	×	×	×	×	Endemic
	Herpestidae	<i>Herpestes brachyurus</i>		Short-tailed mongoose	×	×	×	×	Extant
	Viverridae	<i>Arctictis binturong</i>	Binturong	Binturong		×	×	×	Extant
		<i>Paradoxurus hermaphroditus</i>	Musang	Common palm civet	×	×	×	×	Extant
	Felidae	<i>Panthera tigris</i>	Tiger	Tiger	×	×			Extinct*
		<i>Prionailurus bengalensis</i>	Maral	Leopard cat		×	×		Extant
Artiodactyla	Cervidae	<i>Axis calamianensis</i>	Usa	Calamian hog deer	×	×	×	×	Extinct*
		<i>Cervus</i> sp(p).	Usa	Deer	×	×	×		Extinct*
	Suidae	<i>Sus ahoenobarbus</i>	Baboy	Palawan bearded pig	×	×	×	×	Endemic

ater (dusky roundleaf bat). Lastly, a single left mandible (ICEM-20391) of early Holocene date (EM-784) was assigned to *Myotis cf. macrotarsus* (Philippine large-footed myotis). All bat species identified are known cave roosters in primary lowland forests (Heaney et al., 1998).

4.3. Order Rodentia

4.3.1. Family Sciuridae

Two squirrel taxa were identified from the Ille record. *Hylopetes nigripes* (arrow-tailed flying squirrel) is represented by seven mandibles and one maxillary fragment from early to late Holocene contexts (EM-769; WM-1530, 1626). This species can be readily

distinguished from other Palawan squirrels by their distinctive tooth morphology. The mandibular 4th premolar to 3rd molar becomes progressively larger and square in occlusal outline. The cusps are not so markedly separated by deep grooves as is evident in *Sundasciurus* spp. The teeth have pronounced 'crenellations' and an accessory cusplet on the antero-labial side of the anterior cusps. The paraconid is high and the hypoconid low. Toothrow length and molar dimensions show no variation in size between modern and archaeological populations (Table 2).

Eleven tree squirrel mandibles were identified as *Sundasciurus* sp(p), from Late Pleistocene and Holocene deposits (Table 2). Palawan has three known species from this genus, with *Sundasciurus juvenicus* (Northern Palawan tree squirrel) considered to be an endemic of the

Table 2

Comparative measurements of the mandibular toothrows and premolar and molar lengths and breadths of the *Hylopetes nigripes* and *Sundasciurus* sp(p.) recovered from Ille Cave and modern specimens from the Field Museum of Natural History, Chicago. The range of FMNH comparative measurements are shown as maximum and minimum values and the number of measured specimens for each species is in parentheses.

ARCHAEOLOGICAL SPECIMENS (mm)											
Bone ID	Taxon	Context/phase	Mand TRL	p4L	p4B	m1L	m1B	m2L	m2B	m3L	m3B
ICEM-19272	<i>Hylopetes nigripes</i>	769 EH	11.63	Broken	na	2.75	2.58	3.03	2.98	3.81	3.11
ICEM-20081	<i>H. nigripes</i>	LH	11.75	2.37	1.73	\	\	\	\	3.3	2.93
ICEM-19010	<i>H. nigripes</i>	332 MH	11.97	\	\	\	\	3.12	2.96	3.26	2.9
ICWM-2339	<i>H. nigripes</i>	1626 LH	11.97	2.34	2.17	2.59	2.35	3.01	2.75	3.56	2.99
ICWM-2321	<i>H. nigripes</i>	1626 LH	11.88	2.58	2.03	2.68	2.35	2.82	2.77	3.64	2.98
ICWM-2358	<i>H. nigripes</i>	1530 MH	11.64	\	\	2.53	2.49	\	\	\	\
ICWM-2363	<i>H. nigripes</i>	1626 LH	12.01	2.52	2.23	2.81	2.52	3.1	2.77	3.91	3
ICEM-19786	<i>Sundasciurus</i> sp.	784/EH	10.88	2.31	2.37	2.38	2.84	2.75	2.87	3.32	2.85
ICEM-20458	<i>Sundasciurus</i> sp.	1306/TP	10.1	2.32	2.37	2.18	2.55	2.33	2.64	2.84	2.56
ICEM-20459	<i>Sundasciurus</i> sp.	1306/TP	10.4	2.33	2.55	2.4	2.56	na	na	na	na
ICEM-20460	<i>Sundasciurus</i> sp.	1306/TP	10.97	2.4	2.49	2.14	2.56	2.58	2.87	3.44	2.99
ICWM-2336	<i>Sundasciurus</i> sp.	1530A/EH	\	\	\	2.36	2.54	\	\	\	\
ICWM-2333	<i>Sundasciurus</i> sp.	1530/EH	10.57	2.57	2.38	2.53	2.63	2.76	2.74	2.8	2.5
ICWM-2335	<i>Sundasciurus</i> sp.	1530/EH	10.8	\	\	2.52	2.42	2.56	2.73	3.05	2.59
ICWM-2331	<i>Sundasciurus</i> sp.	1626/EH	\	2.42	2.35	2.43	2.44	2.73	2.74	\	\
FMNH comparative measurements (ranges in mm)											
FMNH	<i>H. nigripes</i> (4)		10.76–12.08	2.4–2.72	2.0–2.38	2.54–2.93	2.43–2.88	2.64–3.34	2.78–3.15	3.2–3.83	2.88–3.21
FMNH	<i>Sundasciurus juvenicus</i> (9)		9.54–10.38	2.1–2.56	2.0–2.42	2.21–2.45	2.23–2.54	2.38–2.68	2.42–2.87	2.9–3.3	2.4–2.75
FMNH	<i>Sundasciurus steerii</i> (6)		10.0–10.33	2.23–2.56	2.2–2.5	2.3–2.66	2.3–2.42	2.41–2.64	2.5–2.67	2.93–3.16	2.36–2.46

central and northern regions of the island where Ille is situated. However, morphometric studies of the archaeological and modern skeletal material at FMNH show no differences between *Sundasciurus steeri* (Southern Palawan tree squirrel) and *S. juvencus*. (Ochoa, 2009). The other taxon known in the island is a smaller montane species *Sundasciurus rabori* (Palawan montane squirrel). At least five of the archaeological specimens from Terminal Pleistocene and early Holocene contexts at Ille exceed the size of the modern comparative specimens in all dental dimensions.

4.3.2. Family Muridae

Three murid taxa were identified, including the first identifications of *Rattus cf. tiomanicus* and *Sundamys muelleri* in Palawan. An unidentified murid, represented by a fragment of the right mandibular body (ICEM-18291), was also recovered from an early Holocene layer (EM-784). The specimen is considerably smaller than other taxa in the assemblage. The shape and size of the mandible corresponds well with modern *Chiropodomys calamianensis* (Palawan pencil-tailed tree mouse; Table 3), but identification cannot be secured due to lack of teeth.

4.3.2.1. *Rattus cf. tiomanicus* (Malayan field rat). Ten measurable mandibular specimens attributable to the genus *Rattus* were recovered from late Pleistocene and early Holocene deposits (Table 3). Two *Rattus* species are currently found on Palawan: *R. tiomanicus* and *Rattus tanezumi* (Oriental house rat). The former is considered a native and the latter an introduction in the late Holocene (Heaney et al., 1998). Biometric analyses of dentition indicate that the archaeological specimens from Ille are larger in size than the modern comparative collection of Malayan field rat, and in terms of length they fall within the range of the Oriental house rat (Table 3). However, labio-lingual measurements of the 1st molar indicate that all the archaeological specimens are narrower than those of the Oriental house rat modern comparatives. Interestingly, the archaeological specimens do fall within the range of a single modern comparative specimen of Malayan field rat from the island of Busuanga to the north of Palawan (Table 3). Metrical comparisons of molar tooththrow lengths and the size of the 1st mandibular molar between modern comparatives of the Malayan field rat and those recovered from the early Holocene on Palawan suggests there has been some diminution in size over the last few millennia (Fig. 3).

4.3.2.2. *Sundamys muelleri* (Great Sunda rat). Thirty-three measurable mandibles of the only large species of rat found on Palawan were recorded in numerous contexts throughout the Late

Pleistocene and Holocene sequence at Ille Cave. The Great Sunda rat can be found from Myanmar to Palawan and is present in lowland to montane forest today (Esselstyn et al., 2004). Even though only two modern comparative specimens from the island of Calamianes were available for size comparison with the archaeological collection, they showed a marked size difference encompassing the full range of zooarchaeological specimens, which suggests considerable variation in the body size of this taxon.

4.4. Order Carnivora

Except for *Amblonyx cinereus* (Asian small-clawed otter) which has been previously reported by Reis and Garong (2001) and *V. tangalunga* (Malay civet), this study presents the first fossil records of all other extant Palawan carnivores. These species are known to inhabit primary and secondary forest in a wide elevational range (Rabor, 1986; Heaney et al., 1998). *Mydaus marchei* (Palawan stink badger; Piper and Ochoa, 2007), is an extant endemic, while all other species are widespread in Southeast Asia, namely *P. hermaphroditus* (common palm civet), *Arctictis binturong* (Bear cat/binturong), *P. bengalensis* (leopard cat): and *Herpestes brachyotis* (short-tailed mongoose). The two viverrids and the leopard cat are also found in the oceanic Philippines, and they are known to have been translocated to Wallacean islands in the late Holocene (Heinsohn, 2001; van den Bergh et al., 2009).

The domestic dog (*Canis familiaris*) was also positively identified from late Holocene contexts based on three specimens: a partial canid skeleton (ICWM 2377), an isolated lower left carnassial (ICWM 1329) and a right mandible (ICEM 17955). The partial canid skeleton consisted of the cranium, mandibles and cervical vertebrae, with the rest of the skeleton reworked and disarticulated by a later human burial (Ochoa, 2005). In both mandibular specimens the double-posterior cusp on the carnassial clearly places them in the genus *Canis*. Comparisons of the length and breadth measurements of the carnassials indicate the Ille specimens are smaller than modern dingo and dhole (Table 4b). Comparisons with archaeological specimens of probable Metal Age date from Borneo (Clutton-Brock, 1959; Medway, 1977) show little difference between the Palawan and Bornean examples, and all fall well below the sizes of the modern dingo. This suggests the specimens from Palawan are unlikely to be directly related to the Australian dingo but represent a smaller domestic morphotype (breed).

This study also presents identifications of two extinct carnivore taxa, and these are detailed as follows.

Table 3

Comparative measurements of the mandibular tooththrows and the lengths and breadths 1st molars of *Rattus* specimens from Ille Cave and modern *Rattus* spp. and *Chiropodomys calamianensis* from FMNH, Chicago. The range of FMNH comparative measurements are shown as maximum and minimum values and the number of measured specimens for each species in parentheses.

Archaeological specimens (mm)					
Bone ID	Taxon	Context/phase	MandTRL	M1L	M1B
ICEM-18047	<i>Rattus cf. tiomanicus</i>	784/EH	6.17	2.66	1.52
ICEM-18179	<i>Rattus cf. tiomanicus</i>	784/EH	6.35	2.65	1.48
ICWM-2364	<i>Rattus cf. tiomanicus</i>	1626/EH	\	2.59	1.52
ICWM-2289	<i>Rattus cf. tiomanicus</i>	1626/EH	\	2.63	1.55
ICWM-2290	<i>Rattus cf. tiomanicus</i>	1626/EH	\	2.69	1.57
ICWM-2359	<i>Rattus cf. tiomanicus</i>	1530/EH	6.79	2.59	1.57
ICWM-2360	<i>Rattus cf. tiomanicus</i>	1530/EH	\	2.59	1.55
ICWM-2301	<i>Rattus cf. tiomanicus</i>	N4W15/EH	6.42	2.72	1.56
ICWM-2302	<i>Rattus cf. tiomanicus</i>	N4W15/EH	\	2.68	1.52
FMNH comparative measurements (mm)					
FMNH	<i>Rattus tanezumi</i> (9)		6.15–6.92	2.46–2.93	1.62–1.8
FMNH	<i>Rattus tiomanicus</i> (7)		5.7–6.06	2.35–2.46	1.41–1.61
FMNH	<i>Rattus exulans</i> (8)		4.7–5.27	1.9–2.21	1.24–1.38
FMNH	<i>C. calamianensis</i> (4)		4.06–4.35	1.66–1.85	1.07–1.27



Fig. 3. Occlusal view of the mandibular tooththrow of modern (FMNH-63154) and archaeological (ICEM-19227) specimens of *Rattus tiomanicus* from Palawan. Note the marked size difference between the early Holocene and modern specimens.

4.4.1. Family Canidae

The foot bones of a medium-sized carnivore were identified in the Late Pleistocene and early Holocene deposits (EM-1306, 807; Table 4a). Morphological examination attributes them to a member of the canid family and metrical analyses present two possible candidates: the dhole (*Cuon alpinus*) or a dingo-type domestic dog (*Canis familiaris dingo*). The two taxa can be distinguished on certain elements such as the lower carnassial and the presence of the 3rd lower molar in *Canis* (Tedford et al., 1995), but cannot be separated based on isolated bones of the extremities (see below for further discussion).

4.4.2. Family Felidae

4.4.2.1. *Panthera tigris* (Tiger). This big felid is represented by three specimens from Ille: a complete basal phalanx (ICEM-20034) and portion of a sub-terminal phalanx (ICEM-20086) both from the left manus, and a distal portion of a basal phalanx (ICWM-2376) of the 4th or 5th digit of either the manus or pes (Piper et al., 2008a). The first two fragments were recovered from the Terminal Pleistocene context EM-1306, dating to ca. 14 000 cal. BP (Piper et al., 2008a). The latter fragment was recovered from the early Holocene context WM-1839, and based on its stratigraphic and chronological position almost certainly represents a second individual. The tiger has been identified from Terminal Pleistocene and early Holocene deposits in Borneo (Harrison, 1998; Piper et al., 2007), but never before on Palawan.

4.5. Order Artiodactyla

4.5.1. Family Suidae

4.5.1.1. *Sus ahoenobarbus*. The endemic Palawan bearded pig is common throughout the archaeological record but becomes more abundant towards the mid-late Holocene as the frequency of deer bone diminishes (see below; Fig. 6). Bearded pigs inhabit many

environments, but are common in primary and secondary forest today, where they feed on fallen fruits, roots, herbs and other plant material as well as invertebrates and other small animals (Rabor, 1986). Very few measurable elements were recovered from either trench at Ille Cave, but the few teeth found fall within the size range of the Palawan bearded pig. However, pigs of the *scrofa/verrucosus* groups are notoriously difficult to differentiate by biometry alone and further geometric – morphometric studies of the molar cusp morphology might prove fruitful in the future (see Cucchi et al., 2009).

4.5.2. Family Cervidae

The skeletal elements of deer are common throughout the Late Pleistocene and early Holocene deposits at Ille Cave. Thereafter, they become progressively rare until they eventually disappear in the late Holocene. Two taxa, one 'large', the other 'small', can be clearly distinguished by the considerable variation in size observed in the dentition and postcranial elements (Table 5; Figs. 4–6).

4.5.2.1. *Axis calamianensis*. Comparisons of the labio–lingual and mesial–distal measurements of the mandibular tooththrow and individual fossil teeth with those of extant deer taxa in the Philippines and Island Southeast Asia suggest the most likely candidate for the small taxon is the Calamianes hog deer (Table 5). This species is still present on Busuanga and Culion, two islands that were part of the Greater Palawan landmass during the Pleistocene, but is no longer found on Palawan itself. The Calamianes hog deer inhabits forest edges and open grassland habitats today (Heaney et al., 1998).

4.5.2.2. *Cervus* (= *Rusa*) sp. Similar dental biometric comparisons of the 'large' deer taxon with extant species within the *C.* (= *Rusa*) *unicolor* group, which includes the widespread Southeast Asian *C. unicolor* (Sambar deer) and the two native Philippine taxa *C. mariannus* (Philippine brown deer) and *C. alfredi* (Philippine spotted

Table 4aComparative measurements (mm) of three of postcranial elements of the early Holocene canid recovered from Ille Cave with *Cuon alpinus* and *Canis familiaris dingo*.

CALCANEUM	Taxon	GL	Max medial width		
ICEM-18858	Ille canid	43.52	16.96		
FMNH 104389	<i>Cuon alpinus alpinus</i>	43.04	16.71		
FMNH 57807	<i>C. familiaris dingo</i>	49.33	18.6		
FMNH 119852	<i>C. familiaris dingo</i>	44	16.2		
FMNH 119851	Canid	42	15.3		
FMNH 57808	<i>C. familiaris dingo</i>	46.24	16.55		
METACARPAL III	Taxon	GL	Bp	Bd	
ICEM-18859	Ille canid	66.78	8.6	7.26	
FMNH 104389	<i>C. alpinus alpinus</i>	64.88	8.34	7.9	
FMNH 57807	<i>C. familiaris dingo</i>	64.19	8.12	9.3	
FMNH 119852	<i>C. familiaris dingo</i>	64.4	8.14	8.82	
FMNH 57808	<i>C. familiaris dingo</i>	68.12	7.82	8.48	
SCAPHO-LUNAR	Taxon	Maximum medio-lateral width	Maximum antero-posterior width	Minimum antero-posterior width	
ICEM- 20417	Ille canid	22.36	12.53	7.72	
FMNH 104389	<i>C. alpinus alpinus</i>	21.44	12.3	6.69	
FMNH 57807	<i>C. familiaris dingo</i>	25.92	13.53	8.54	
FMNH 52808	<i>C. familiaris dingo</i>	23.75	12.62	8.08	
FMNH 54203	<i>C. familiaris dingo</i>	20.31	11.23	7.56	

deer) suggests a close match with the Philippine brown deer from Luzon (Table 5). However, the Philippine brown deer shows considerable variation across its Philippine range, with those from Luzon being larger than populations on Mindanao Island. Thus, the overlap between the archaeological material and Philippine brown deer from Luzon might be coincidental and the fossils could possibly represent a different species of *Cervus* that formerly inhabited the island of Palawan. Taxonomic classification remains unresolved. Philippine *Cervus* spp. belong to the *Rusa* subgenus, along with the Sundaic *C. unicolor* and *Rusa timorensis* (Meijaard and Groves, 2004). *Cervus* are no longer found in the Palawan faunal region today.

5. Discussion

The zooarchaeological record from Ille Cave has produced evidence for seven orders, 25 genera and 23 species of mammals from the Terminal Pleistocene and Holocene sedimentary sequences. This assemblage provides a deeper temporal dataset for the study of macro-evolutionary and biogeographic processes on the

island, particularly those relating to colonization, environmental change and extirpation. Throughout the cave sequence, there are striking patterns in the distribution of certain taxa that allow us to document changes in the composition of the terrestrial vertebrate community and make inferences about the causes of such changes.

5.1. Colonization of Palawan

The close affinity of the Palawan mammal community with those of the Sundaic region to the west is a consequence of its geographic location on the north-eastern fringe of the shallow Sunda Shelf (Heaney, 1985, 1986). During glacial extremes over the past half a million years, when the oceans were lowered from –116 m during the terminal phase of the LGM (ca. 20 ka; Hanebuth et al., 2000) to as much as –139 m during MIS 12 (ca. 420 ka; Rohling et al., 1998), the gap between northern Borneo and the landmass of Greater Palawan was much reduced, possibly facilitating the migration of terrestrial vertebrates from one island to the other. A long-standing geographic question has been whether or not a land bridge connection existed

Table 4bComparative length and breadth measurements (mm) of the mandibular first (M1) and second (M2) molars of the Ille domestic dogs (*Canis familiaris*), *Canis familiaris dingo* and *Cuon alpinus* subsp. and archaeological specimens of Metal Age date from Sarawak in Borneo.

Modern comparative specimens					
LOWER M1	Taxon	M1 length	M1 breadth	M2 length	M2 breadth
FMNH 57807	<i>C. familiaris dingo</i>	21.84	10.41	10.33	7.65
FMNH 104389	<i>Cuon alpinus alpinus</i>	20.7	7.07	6.77	6.15
FMNH 39182	<i>Cuon alpinus adustus</i>	20.52	7.96	7.42	5.84
FMNH 36001	<i>Cuon alpinus lepturus</i>	20.6	8.17	8	5.68
FMNH 35813	<i>Cuon alpinus primaevus</i>	21.66	8.1	7.66	5.91
FMNH 33500	<i>C. alpinus adustus</i>	20.61	8.32	7.48	5.94
FMNH 38024	<i>C. alpinus adustus</i>	21.98	8.29	8.09	6.34
Ille cave specimens	Element	M1 length	M1 breadth	M2 length	M2 breadth
ICEM 17955	Right mandible	18.51	7.54	7.24	5.36
ICWM 1329	Left M1	18.34	7.36		
ICWM 2377	Right mandible	16.75	7	6.3	5.15
ICWM 2377	Left mandible	16.55	7.1		
Archaeological comparatives	Reference	M1 length	M1 breadth	M2 length	M2 breadth
Niah J/6	Clutton-Brock (1959)	17.2			5.3
Lobang Kudih, B1	Medway (1977)	16.8	6.2		
Lobang Kudih, D4	Medway (1977)	16	6.5		
Lobang Kudih, E1.EX	Medway (1977)	16.2	6.6	6.6	5.4
Lobang Kudih, E4	Medway (1977)	18.1	6.9		
Lobang Sirih	Medway (1977)	14.7	6		

Table 5
Comparative measurements of archaeological cervid teeth from Ille Cave and a range of extant deer taxa from the Philippines and Borneo: L = maximum length; B = maximum breadth; Ba = anterior breadth; Bm = breadth middle column (lower M3's only); Bp = posterior width. The range of FMNH comparative measurements are shown as maximum and minimum values and the number of available measured specimens for each species is in parentheses.

MAXILLA									
Taxon	Location	P4L	P4B	M1Ba	M2Ba	M1Bp	M2I		
<i>Axis calamianensis</i>	Calamianes	7.36–8.61 (3)	9.15–11.15 (3)	11.02–13.26 (6)	10.5–12.93 (6)	10.72–13.42 (6)	13.3–14.84 (4)		
<i>Cervus alfredi</i>	Negros	9.05–10.7 (3)	12.36–12.9 (3)	11.5–14.38 (5)	13.3–14.2 (5)	13.04–14.26 (5)	13.5–17.3 (4)		
<i>Cervus mariannus</i>	Mindanao	7.7–9.27 (5)	10.72–11.91 (5)	10.28–12.39 (8)	12.49–13.8 (8)	11.8–14.34 (8)	11.63–14.58 (7)		
<i>Cervus mariannus</i>	Luzon	9.03–11.17 (6)	13.4–15.2 (6)	12.4–15.12 (10)	13.75–17.03 (10)	13.95–17.04 (9)	15.06–18.28 (10)		
<i>Cervus unicolor</i>	SEA	12.34–13.76 (3)	15.99–17.56 (3)	15.59–17.24 (4)	19.72–21.42 (4)	19.62–21.18 (4)	19.74–21.13 (4)		
<i>Muntiacus muntjak</i>	Borneo	6.34–7.86 (3)	9.03–9.95 (3)	8.4–9.68 (4)	10.22–12.23 (4)	10.61–12.02 (4)	9.15–10.62 (3)		
Bone ID	Context/phase	Taxon	Element	P4L	P4W	M1I	M1Wa	M1Wp	M2I
ICEM-17512	1306/TP	<i>Cervus</i> sp.	RM3	\	\	\	\	\	\
ICEM-17827	807/EH	<i>Cervus</i> sp.	RM3	\	\	\	\	\	\
ICEM-17829	807/EH	<i>Cervus</i> sp.	M1	\	\	13.4	\	\	\
ICEM-20044	25/EH	<i>Cervus</i> sp.	L max	\	\	\	\	\	14.42
ICEM-20046	25/EH	<i>Cervus</i> sp.	L M3	\	\	\	\	\	\
ICWM-1171	N5W13	<i>Cervus</i> sp.	L P4	9.73	13.5	\	\	\	\
ICWM-1861	1626/EH	<i>Cervus</i> sp.	L max	9.63	12.73	13	15.7	15.78	\
ICWM-2088	1626/EH	<i>Cervus</i> sp.	L max	9.99	13.99	14.21	17.08	17.53	16.17
ICWM-2035	1626/EH	<i>Cervus</i> sp.	L M3	\	\	\	\	\	\
ICWM-1701	1626/EH	<i>Cervus</i> sp.	R M1	\	\	13.76	16.53	15.22	\
ICWM-831	1626/EH	<i>Cervus</i> sp.	R M1	\	\	13.6	12.7	12.9	\
ICWM-1700	1626/EH	<i>Cervus</i> sp.	L M1	\	\	13	13.94	14.02	\
MANDIBLE									
Taxon	Location	P4L	P4W	M1I	M1Wa	M1Wp	M2I		
<i>A. calamianensis</i>	Calamianes	8.85–10.16 (3)	6.28–6.8 (3)	9.82–11.93 (6)	7.35–8.02 (6)	7.15–8.52 (6)	14.06–14.76 (4)		
<i>C. alfredi</i>	Negros	10.7–12.14 (3)	6.91–8.2 (3)	11.22–13.78 (5)	8.45–9.5 (5)	8.77–10.47 (5)	14.25–16.48 (4)		
<i>C. mariannus</i>	Mindanao	10.08–12.07 (6)	6.36–7.12 (6)	10.24–12.96 (8)	7.76–8.7 (8)	8.5–9.44 (8)	12.34–14.53 (8)		
<i>C. mariannus</i>	Luzon	12.18–13.92 (5)	7.7–9.62 (5)	12.8–15.24 (8)	9.6–10.97 (7)	10.46–11.6 (8)	15.8–18.34 (8)		
<i>C. unicolor</i>	SEA	15.92–16.0 (2)	10.44–10.7 (2)	16.65–18.33 (3)	12.81–13.27 (4)	12.52–13.88 (3)	19.46–20.93 (2)		
<i>M. muntjak</i>	Borneo	7.97–8.72 (3)	5.43–5.84 (3)	9.32–9.77 (4)	6.67–7.04 (4)	6.9–7.72 (4)	10.05–11.0 (3)		
Bone ID	Context/phase	Taxon	Element	P4L	P4W	M1I	M1Wa	M1Wp	M2I
ICEM-18599	1306/TP	<i>A. calamianensis</i>	L mand	\	\	\	\	\	\
ICEM-18549	1306/TP	<i>Cervus</i> sp.	L mand	\	\	\	\	\	\
ICEM-20058	\	<i>A. calamianensis</i>	R mand	\	\	10.98	\	\	\
ICEM-18438	807/EH	<i>A. calamianensis</i>	M3	\	\	\	\	\	\
ICWM-1862	1626/EH	<i>Cervus</i> sp.	R mand	\	\	\	\	\	\
ICWM-2085	1626/EH	<i>Cervus</i> sp.	R mand	\	\	\	\	\	\
ICWM-2086	1626/EH	<i>Cervus</i> sp.	R mand	12.76	8.52	13.04	10.3	10.96	16.35
ICWM-2084	1626/EH	<i>Cervus</i> sp.	L M3	\	\	\	\	\	\
ICWM-818	1560	<i>Cervus</i> sp.	R M2	\	\	\	\	\	18.1
MAXILLA									
Taxon		M2Wa	M2Wp	M3I	M3Wa	M3Wm	M3Wp		
<i>A. calamianensis</i>		11.45–12.68 (4)	11.78–13.3 (4)	15.08–15.12 (2)	11.54–12.5 (2)	\	10.3–11.32 (2)		
<i>C. alfredi</i>		15.04–15.72 (4)	14.1–15.51 (3)	15.25–16.37 (3)	13.98–15.16 (3)	\	14.34–14.66 (2)		
<i>C. mariannus</i>		13.32–15.09 (8)	13.1–14.78 (7)	13.17–15.67 (7)	12.9–14.38 (7)	\	11.46–13.57 (5)		
<i>C. mariannus</i>		15.84–18.66 (9)	15.3–18.68 (8)	16.12–18.3 (7)	16.8–17.94 (5)	\	15.3–16.89 (5)		
<i>C. unicolor</i>		22.56–23.08 (4)	22.17–22.8 (4)	21.2–22.43 (3)	20.02–22.49 (3)	\	20.57–21.31 (2)		
<i>M. muntjak</i>		11.33–13.06 (3)	11.0–12.76 (3)	9.97–10.88 (3)	10.98–12.62 (3)	\	9.88–11.88 (3)		
Bone ID	Context/Phase	Taxon	M2Wa	M2Wp	M3I	M3Wa	M3Wm	M3Wp	
ICEM-17512	1306/TP	<i>Cervus</i> sp.	\	\	16.96	14.75	\	14.3	
ICEM-17827	807/EH	<i>Cervus</i> sp.	\	\	16.38	17.3	\	14.71	

ICEM-17829	807/EH	<i>Cervus</i> sp.	\	\	\	\	\	\
ICEM-20044	25/EH	<i>Cervus</i> sp.	16.21	16.53	\	\	\	\
ICEM-20046	25/EH	<i>Cervus</i> sp.	\	\	16.18	16.4	\	14.23
ICWM-1171	N5W13	<i>Cervus</i> sp.	\	\	\	\	\	\
ICWM-1861	1626/EH	<i>Cervus</i> sp.	\	\	\	\	\	\
ICWM-2088	1626/EH	<i>Cervus</i> sp.	17.9	17.94	\	\	\	\
ICWM-2035	1626/EH	<i>Cervus</i> sp.	\	\	16.73	17.84	\	18.61
ICWM-1701	1626/EH	<i>Cervus</i> sp.	\	\	\	\	\	\
ICWM-831	1626/EH	<i>Cervus</i> sp.	\	\	\	\	\	\
ICWM-1700	1626/EH	<i>Cervus</i> sp.	\	\	\	\	\	\
MANDIBLE								
Taxon			M2Wa	M2Wp	M3l	M3Wa	M3Wm	M3Wp
<i>A. calamianensis</i>			8.04–9.79 (4)	7.3–8.88 (4)	18.26–19.78 (2)	8.77–10.6 (2)	7.7–10.62 (2)	3.72 (1)
<i>C. alfredi</i>			10.14–11.38 (3)	10.43–11.32 (3)	20.49–20.9 (3)	9.78–11.04 (3)	10.17–11.24 (3)	5.49–5.88 (3)
<i>C. mariannus</i>			9–9.82 (8)	8.91–10.32 (8)	18.03–20.27 (7)	8.57–9.8 (7)	7.82–8.96 (7)	4.92–5.34 (5)
<i>C. mariannus</i>			11.05–13.18 (8)	11.12–12.46 (8)	23.3–25.28 (5)	11.4–12.77 (6)	10.52–12.94 (5)	5.86–7.46 (5)
<i>C. unicolor</i>			14.74–15.32 (3)	14.24–15.09 (3)	28.28–28.86 (2)	14.9–14.95 (2)	13.53–14.42 (2)	8.56–8.74 (2)
<i>M. muntjak</i>			7.97–8.56 (3)	8.11–8.28 (3)	14.64–15.2 (3)	7.65–8.15 (3)	7.23–7.78 (3)	4.41–4.76 (3)
Bone ID	Context/Phase	Taxon	M2Wa	M2Wp	M3l	M3Wa	M3Wm	M3Wp
ICEM-18599	1306/TP	<i>A. calamianensis</i>	\	\	19.50	\	\	\
ICEM-18549	1306/TP	<i>Cervus</i> sp.	\	\	24.18	11.32	9.96	\
ICEM-20058	\	<i>A. calamianensis</i>	\	\	\	\	\	\
ICEM-18438	807/EH	<i>A. calamianensis</i>	\	\	20.65	8.54	7.67	7.02
ICWM-1862	1626/EH	<i>Cervus</i> sp.	\	\	22.88	12.06	11.36	5.99
ICWM-2085	1626/EH	<i>Cervus</i> sp.	\	\	22.93	\	\	\
ICWM-2086	1626/EH	<i>Cervus</i> sp.	12.14	11.84	27.63	12.74	11.78	7.55
ICWM-2084	1626/EH	<i>Cervus</i> sp.	\	\	24.15	12.2	10.97	6.81
ICWM-818	1560	<i>Cervus</i> sp.	11.5	11.7	\	\	\	\

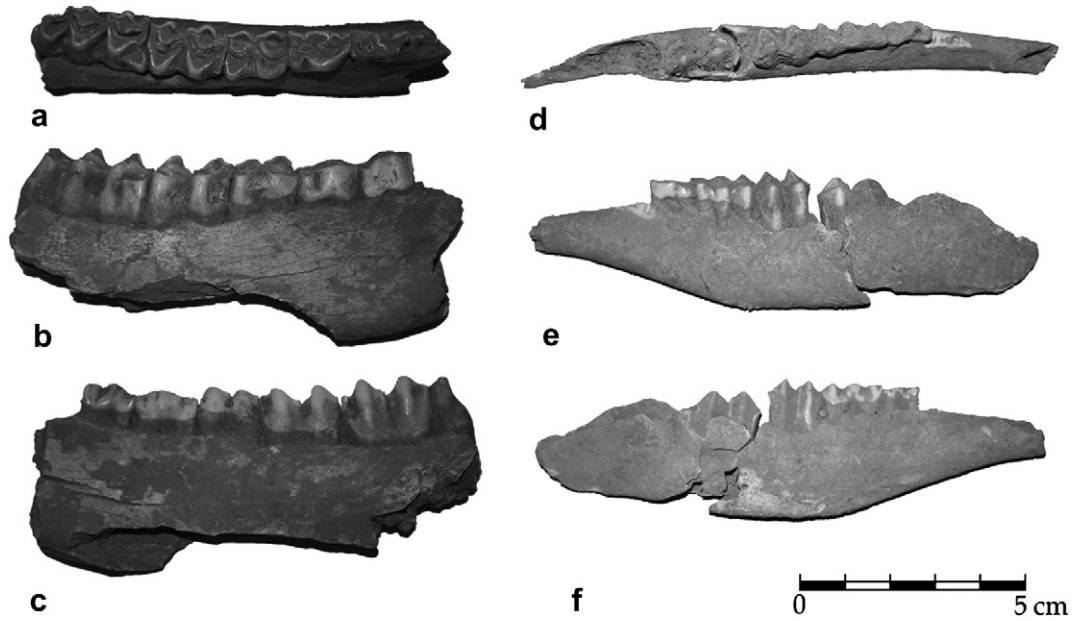


Fig. 4. The occlusal (top), labial (centre) and lingual (bottom) aspects of the partial right deer *Cervus* sp. mandible (ICWM-2086; a, b, c) from the early Holocene compared with an *Axis calamianensis* left mandible from the Terminal Pleistocene (ICEM-18599; d, e, f).

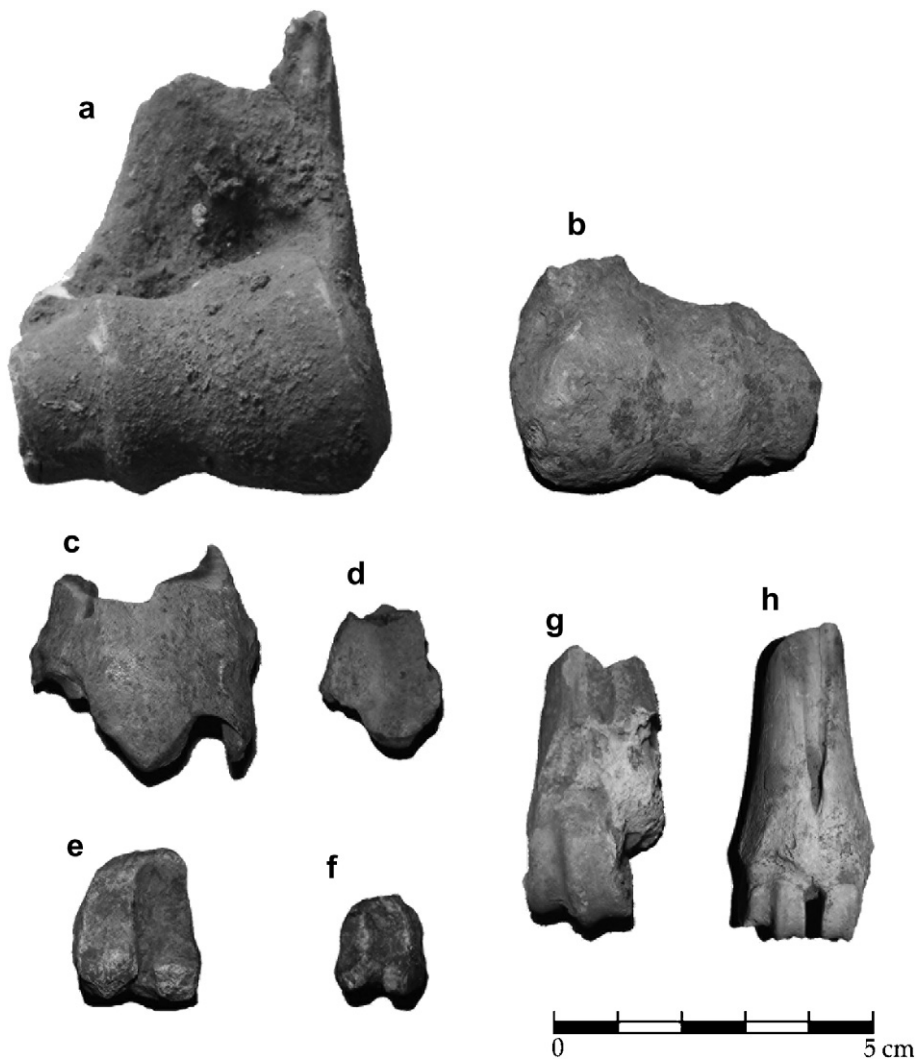


Fig. 5. a–b: Anterior/cranial view of distal humeri; c–d: caudal aspect of distal tibiae; e–f: proximal view of basal phalanges; g–h: cranial view of distal metatarsals. Specimens on the left of each element type are of the large cervid taxon and those on the right are of the small cervid taxon.

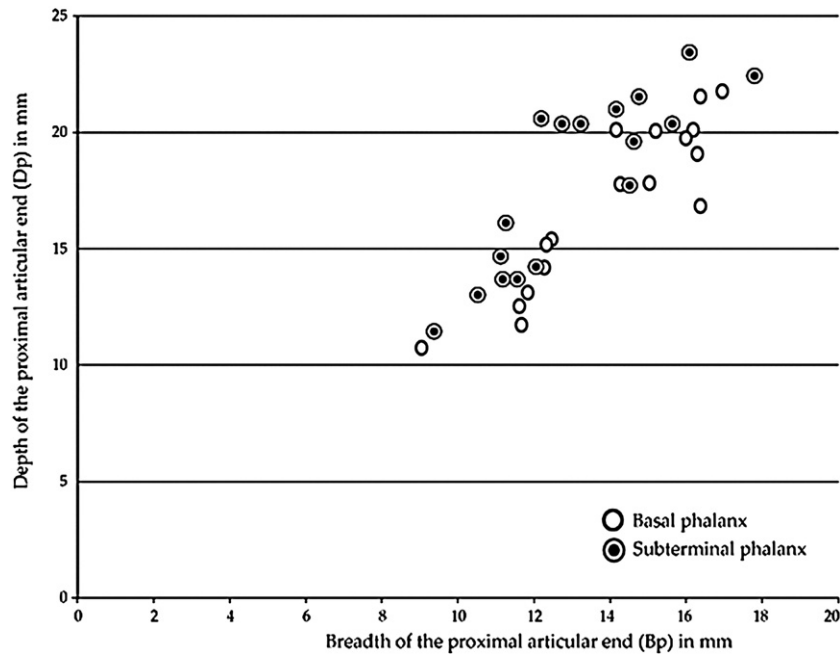


Fig. 6. Comparison of the breadths and depths of the proximal articular ends of the deer basal and sub-terminal phalanges (following von den Driesch, 1976) recovered from the East and West Mouths of Ille Cave. All epiphyses were fused to the diaphyses and thus from adult (full-sized) individuals.

between Palawan and Borneo, and if so, when this land bridge was last exposed. Cranbrook (2000) argues that the strong similarities between the mammal communities of Borneo and Palawan suggest that a land bridge between the two islands occurred during the LGM. Heaney (1986), on the other hand, suggests that the divergence of many of the Palawan species from their Sundaic relatives can only be explained by separation over hundreds of thousands of years, and proposes the last connection between the islands to have coincided with low sea stands during the Middle Pleistocene (ca. 420 and 620 ka).

The locally-extinct deer and tiger and the extant bearded pig are all known to have the capability to swim, and thus their migration to the island of Palawan could have been via a short open-sea crossing. Smaller mammals with Sundaic origins, however, such as the stink badger, pangolin, porcupine and squirrels have much lower dispersal abilities. Their presence on Palawan suggests the past existence of a land bridge connection. Thirteen of the native species of Palawan have been separated long enough from their Bornean conspecifics to diverge and become endemic island species. The same is true for the Palawan bearded pig (*S. ahoenobarbus*), implying that colonization by these animals must surely have taken place some considerable time prior to the LGM. Heaney (1986) suggests that the similarity of Palawan's non-bat mammal fauna with Borneo at the generic level is indicative of a Middle Pleistocene colonization, which would then have provided enough time for the divergence of these Palawan endemics. Fooden (1991) also argues that the Philippine subspecies of the long-tailed macaque *Macaca fascicularis philippinensis* represents isolated relict populations from an earlier dispersal into the Philippine archipelago; these have been replaced over much of their former range to the west by *M. f. fascicularis*. The timing of colonization proposed by Fooden was based on outdated sea level lowstand estimates of -160 m during the penultimate glacial period (van Couvering and Kukla, 1988; cited in Fooden, 1991), but more recent data estimate this at only ca. -125 m (Rohling et al., 1998), and such a decrease would not have been enough for a land bridge to emerge.

Furthermore, many tropical rainforest-adapted species such as the orangutan (*Pongo pygmaeus*), gibbons (*Hylobates* spp.), leaf monkeys (*Presbytis* spp.) and sun bear (*Helarctos malayanus*) found in Borneo are absent from Palawan. It is suggested that these taxa colonized the Sunda Shelf during the early Last Interglacial at around 120ka (van den Bergh et al., 2001; Westaway et al., 2007) and their absence in the later fossil record is in congruence with current palaeogeographic and biogeographic data (Reis and Garong, 2001), suggesting that a land connection was not present during the LGM. It must be noted that the nature of any land connection and the environment in southern Palawan would have had a profound effect on the abilities of these arboreal taxa to colonize the island. The absence of a land bridge is also supported by recent bathymetric sea-level reconstructions, which suggest that the last time lowered sea levels reached the reduction of ca. -140 m required to connect the two islands was probably during the Middle Pleistocene (Robles et al., in preparation).

Some local mammal species with low dispersal capabilities such as the bear cat, common palm civet, Malay civet, leopard cat, mongoose and otter are not considered to have diverged sufficiently from their Bornean conspecifics to merit an independent taxonomic status. Archaeological and historical evidence (Heinsohn, 2001; Bulbeck, 2008) indicates that the viverrids and mongoose may have been translocated by people to isolated oceanic islands in the past. Recent studies of the animal remains from the cave site of Liang Bua on Flores, Indonesia have shown that the common palm civet and long-tailed macaque were introduced to that island by at least 3500 cal. BP (van den Bergh et al., 2009). Furthermore there are the known translocations of cuscus (*Phalanger orientalis*) from New Guinea as far as Timor in the early Holocene (O'Connor and Aplin, 2007), the Sulawesi wild boar from Sulawesi to Flores and offshore islands around 7000 cal. BP (Dobney et al., 2008; van den Bergh et al., 2009) and the wild boar from the main Japanese islands to the Izu Islands by 9000 cal. BP (Yamazaki et al., 2005). These examples suggest that it is possible one or more of the civets and leopard cat could have been introduced to Palawan; only archaeological data of deeper antiquity will resolve this issue.

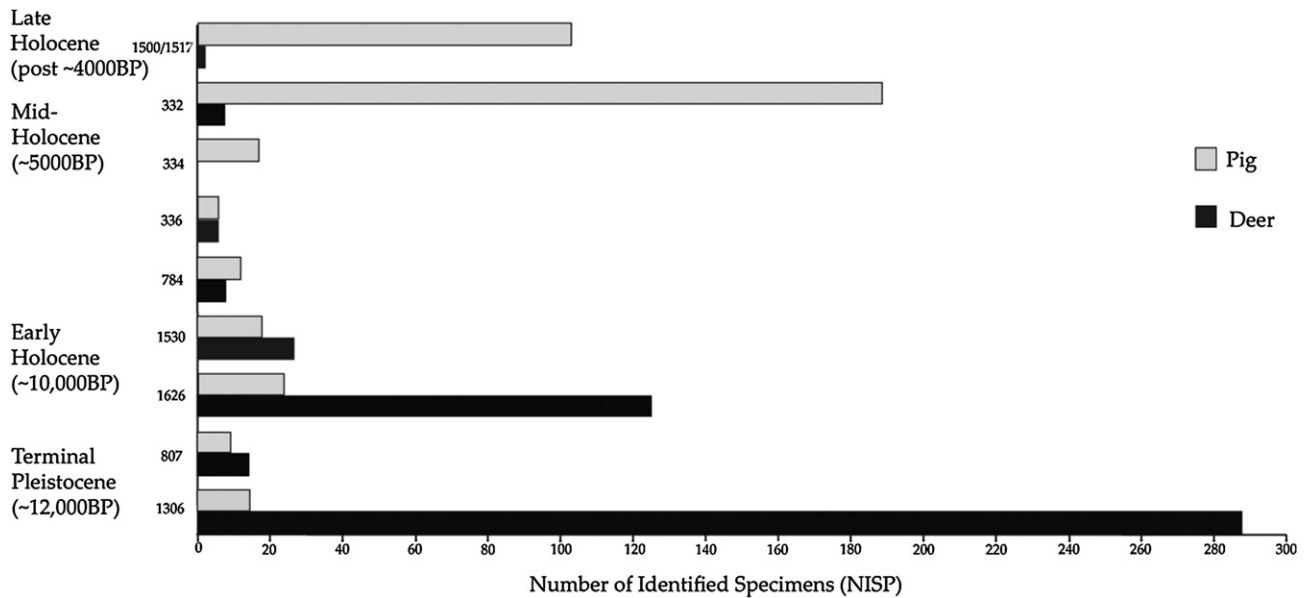


Fig. 7. Changes in frequency of occurrence of pig and deer from the Terminal Pleistocene to Late Holocene as represented by the Numbers of Identified Specimens (NISP) recorded in some of the key fossil-bearing layers (numbered contexts).

Two interesting cases are posed by the endemic hog deer (*A. calamianensis*) and the indigenous flying squirrel (*H. nigripes*), both of which have their closest relatives in the Indochinese region (see discussion of relict distribution of hog deer below). Curiously, the smooth-tailed tree shrew (*Dendrogale melanura*) and ferret badger (*Melogale orientalis*), confined to upland regions of north and northwest Borneo, also have their closest relatives in Indochina (Cranbrook and Piper, 2007), raising the possibility that the four species from Palawan and northern Borneo represent remnants of an 'earlier' migration from the Indochinese region into the islands of Southeast Asia.

5.2. Species representation and palaeoenvironmental reconstruction

The changing climatic conditions and palaeogeographic configuration of Southeast Asia throughout the Pleistocene have shaped the environments and evolution of its animal communities. The present biogeographic distribution of many vertebrate taxa in the region corresponds to boundaries of land masses defined by Pleistocene sea levels (Heaney, 1985). During glacial maxima, Greater Palawan (Heaney, 1985; Brown and Diesmos, 2001) would have had a landmass of approximately 78 000 km², seven times larger than its area at present (Robles et al., in preparation). Current palaeoenvironmental datasets suggest that an expanse of 'open' vegetation extended down from the Malaysian peninsula, into the presently inundated area between Java and Borneo, and further east to Palawan and the western flank of the Philippine archipelago (Heaney, 1991; Bird et al., 2005). For northern Palawan, carbon-isotope values from a bat guano sequence at Makangit Cave, near the Ille tower, indicate that a C₄-dominated grassland or sparsely wooded savanna was present in the locality during the LGM, and that this was eventually replaced by C₃-dominated closed tropical rainforest species in the Holocene (Bird et al., 2007).

Together, landscape, sea-level and palaeoenvironmental reconstructions suggest that at times during the Pleistocene, Palawan was a much larger island with an environment that consisted primarily of open woodland and savanna-like environments. The greater landmass and more open environments would have suited deer populations and provided enough territory to support the tiger and

wild dog. Recent studies of animal bones from Guri Cave in central Palawan also record the presence of both deer taxa proposed here, suggesting they were widespread throughout the early to mid-Holocene on Palawan (Piper and Bautista, forthcoming).

The smaller deer taxon in the archaeological record of Ille corresponds in size and morphology with the Calamianes hog deer (*A. calamianensis*), a species that still exists on the islands of Culion and Busuanga to the north, which were joined to Palawan during periods of sufficient sea-level regression in the Pleistocene. It is notable that the Calamianes hog deer still inhabits the grasslands that continue to exist in the landscapes of those islands but is now absent from the much larger, but tropical rainforest-covered Palawan. Although the impact of ecosystem change, perhaps in addition to human hunting impact, is unknown, the hog deer became locally extinct on Palawan largely due to changes in vegetation.

The larger deer taxon found in Ille, designated as a possible *Cervus* (= *Rusa*), may represent a grazing deer species that was also not well-adapted to dense tropical rainforests. Presently, sambar deer are found in both closed tall and secondary forest habitats, but they are known to thrive in breaks in the canopy, such as on very steep slopes and in swiddened or logged patches of forest (Rabor, 1986; Heaney et al., 1998). Among these species, only *R. timorensis* are grazers and glade-lovers, while the other species are browsers that can inhabit dense forest (Pitra et al., 2004). So perhaps in the case of the large deer, of which there is no evidence on Culion or Busuanga, where the Calamianes hog deer still exists, a different set of environmental/human variables combined to cause its extinction (Fig. 7).

The scarcity of pigs in the Terminal Pleistocene deposits at Ille – a species known in the archaeology and ethnohistory of the Philippines (and Southeast Asia in general) to be a key subsistence resource throughout the Late Pleistocene and Holocene (Pfeffer and Caldecott, 1986; Cranbrook and Piper, 2007; Piper and Rabett, 2009) – may be due to the proposed patchiness of suitable forest habitat in the Dewil Valley during the Late Pleistocene (Bird et al., 2007). A parallel may be seen with the faunal record from Lang Rongrien rock shelter in southern Thailand, which also has a low frequency of pig remains in the Late Pleistocene during a period interpreted drier and more seasonal climate (Mudar and Anderson, 2007). Wild pigs are versatile foragers, but they are primarily forest

species. Observations of modern Eurasian wild boar (*S. scrofa*) indicate that their distribution and reproductive biology are affected by forest density and the availability of water, food and shelter (Mudar and Anderson, 2007). If the landscape of Ille was dominated by more open habitat types and drier climate regimes, then pigs may have occurred in lower densities in the area and deer may have been more abundant and the preferred human prey during the Late Pleistocene-early Holocene (Fig. 7).

The Terminal Pleistocene context (1306) at Ille also has a small proportion of other terrestrial mammals, such as porcupines and tree squirrels. The latter are obligate forest dwellers, implying that there were patches of tree cover in the area. The absence of the arboreal bear cat and arrow-tailed flying squirrel at this early stage in the sequence (both are found in the early-late Holocene) might be significant, but absence of evidence may just represent the vagaries of the zooarchaeological record.

By the mid-Holocene, the Ille vertebrate record is dominated by lowland forest mammals; the tiger and dog are absent and deer are quite rare. Ground species, such as the pangolin, mongoose and stink badger are relatively versatile in their habitats, but the presence of arboreal species such as bear cat, squirrels and arrow-tailed flying squirrel indicate forested habitat similar to that seen in present times.

Some small mammal species in the Holocene levels – such as the Malaysian field rat and the short-nosed fruit bat – are currently known to prefer disturbed habitat types and are not closed-forest dwellers (Cranbrook and Piper, 2007), perhaps signalling the presence of a mosaic of environments in the vicinity of Ille, but perhaps with an increasing preponderance of closed forest cover.

Possible size diminution, perhaps related to climate change at the end of the Pleistocene, was observed in the Malaysian field rat (Table 3). Similar trends in size reduction have been recorded in a diverse range of mammals in Borneo including the Malaysian field rat, the giant long-tailed rat (*Leopoldamys sabanus*), Great Sunda rat, Bornean shrew (*Crocodyrus foetida* subsp.), macaque (*M. fascicularis*) and Sumatran rhinoceros (*Dicerorhinus sumatrensis*) (Hooijer, 1962; Medway, 1964; Cranbrook and Piper, 2007, 2008). Notably, the Great Sunda rat on Palawan, unlike its conspecific in Borneo, does not appear to have demonstrated similar size reduction, or at least not in the last 11 000 years.

A single modern comparative specimen of the Malaysian field rat (*R. tiomanicus*) from Busuanga is of similar dimensions to the early Holocene fossils, suggesting that the driving forces behind size reduction on Palawan were not acting on the rat populations of Busuanga (Table 3). These two examples illustrate that environmentally-driven evolutionary change does not necessarily act on the same species in the same ways in different climatic regimes and at varying geographic locations, even when these are in close proximity.

Five Terminal Pleistocene and early Holocene specimens of tree squirrel (*Sundasciurus* spp.) exceed the modern comparatives in tooththrow length and molar dimensions (Table 2). It is possible that the size disparities among the tree squirrels represent size diminution during the Holocene, but alternatively some of the archaeological specimens could represent an unknown, larger species of tree squirrel that inhabited Palawan in the past. Unfortunately, no archaeological examples of tree squirrels have been recovered from the mid-late Holocene deposits at Ille for comparison.

5.3. Extinction

Mega-faunal extinctions in Southeast Asia throughout the Pleistocene are said to have been influenced by environmental changes brought about by sea-level fluctuations and climate change (Louys et al., 2007). Extinction rates are directly correlated with island size, and species richness generally declines during

interglacial periods, when land bridges become submerged and islands subsequently become isolated (Heaney, 1986).

Reconstruction of northern Palawan's ancient coastlines from the LGM to the present indicates a tremendous landmass decrease (see Fig. 1; Robles, 2007). The extensive inundation of low-lying regions of Greater Palawan coincided with changes in local precipitation patterns, expansion of closed tropical rainforest and the disappearance of open woodland or savanna-like environments (Bird et al., 2005; Robles et al., in preparation). These dramatic changes would have inevitably had a knock-on effect on local faunal populations. The zooarchaeological record of Ille Cave chronicles the disappearance of the tiger, the deer and possibly the wild dog from Palawan in the Holocene. During the Terminal Pleistocene and early Holocene human hunting appears to have focused on deer, with cervid bones considerably out-numbering those of the wild pig (Fig. 6). From the mid-Holocene onwards, however, the human inhabitants of the cave slowly become more reliant on the forest-adapted pig and the remains of deer become rarer and eventually disappear from the archaeological record altogether.

The timing of the final disappearance of deer from Palawan is difficult to assess from the Ille record due to the considerable disturbance of the archaeological sequences by grave digging from ca. 4000 years ago onwards. Deer remains have been recovered from cultural contexts in many Late Pleistocene and Holocene cave sites in Palawan such as Tabon, Pilanduk, Sa'gung and Guri (Fox, 1970; Kress, 1977; Heng, 1988) implying that deer was certainly under human hunting pressure across the island. The impact of human predation on deer populations would have exacerbated selective pressures already acting on these populations due to island size reduction and habitat constriction. Environmental change is considered to be the major driving force for the disappearance of the hog deer on Palawan, as illustrated by its continuing survival on the much smaller islands of Culion and Busuanga to the north of Palawan. For the larger deer taxon that has completely disappeared from all of the Greater Palawan region, human hunting pressure may have been a deciding factor in its eventual extinction.

The relic distribution of Southeast Asian hog deer species across the region probably reflects large-scale habitat transformations and extinction patterns. Craniometric analyses of Southeast Asian deer link the Calamian hog deer with the Indochinese hog deer (*A. porcinus*) and the Bawean deer (*A. kuhli*), an endemic of the small island of Bawean located north of Java (Meijaard and Groves, 2004). The mainland Indochinese hog deer is considerably larger than either the Calamian or Bawean deer. Meijaard and Groves (2004) have argued that the Bawean deer is closely related to the Middle Pleistocene *Axis lydekkeri* of Java, and that they and the Indochinese hog deer should be included in a separate subgenus, *Hyelaphus* rather than *Axis*. Bawean Island would have been connected to Java and part of Sundaland when sea levels were at least ~70 m below present-day levels (Voris, 2000; Sathiamurthy and Voris, 2006). Like the Calamian hog deer on Palawan, the Bawean deer is recorded in the early Holocene fossil record of Java but is now extinct on the larger island (van den Brink, 1982). Thus, it is possible that both the Calamian hog deer and Bawean deer are relic populations of taxa that were once much more widely distributed throughout Southeast Asia.

The Ille record also tells the tale of extinction of a large carnivore that became isolated from its continental source. On Palawan, the tiger is currently only recorded in the Terminal Pleistocene to the early Holocene levels of the Ille faunal sequence. Carnivores are generally among those mammals most susceptible to extinction in interglacial island settings (Heaney, 1986). O'Regan et al. (2002) have modelled simulations for Southern Europe of the minimum range needed to sustain a large carnivore (*Panthera gombaszoegensis*) during periods of deglaciation, and concluded that Mediterranean islands were too small for its continued survival, and that for the animal to persist for over a thousand years, an area roughly

equivalent to the Italian peninsula was necessary. Lyman et al. (2007) roughly estimate the mean natural densities of tigers to be 0.67 ± 0.25 per 100 km² (see also Cranbrook, 2009). At the height of the last glaciation Palawan could have supported a viable population of perhaps 800–1000 tigers with the potential of intermittent recruitment from northern Borneo. However, island size and isolation alone cannot be invoked as the main cause of extinction – after all the tiger survived on the much smaller island of Bali into the 20th century (Seidensticker, 1987). More likely it was a combination of habitat loss, diminishing deer populations, and perhaps even hunting pressure that conspired to force the local extinction of the tiger on Palawan (Piper et al., 2008a).

Also observed in the Ille record is the enigmatic occurrence of canid remains from the Terminal Pleistocene and early Holocene. Morphometric comparisons indicate that the archaeological material falls within the overlapping limits of variation of the dhole (*Cuon alpinus*) and the dingo (*Canis familiaris dingo*). The dhole today inhabits dry and moist forests and thick jungles as well as scrub forest mosaics, and is widely distributed from India to China and down through the Thai-Malay Peninsula. The historic range of the dhole also included Java and Sumatra. Mitochondrial DNA analysis of dingoes indicates an origin ca. 5 ka in mainland Southeast Asia (Savolainen et al., 2004). Taking this divergence estimate into account, the temporal context of the Ille canid suggests that they are much older than dingo-type domesticated dogs. Cranbrook (1988) reported the discovery of dog bones within an early Holocene (ca. 10 000 cal. BP) layer at Madai Cave in Sabah, northern Borneo. On the basis of their age, the historical understanding of the former zoogeographic range of the dhole, and the knowledge that other large mammal taxa represented in the zooarchaeological record are now also extinct on Borneo, he attributes the remains to the former presence of the dhole on the island. The antiquity of the Ille canid specimens, combined with other taphonomic factors such as the lack of carnivore gnawing on mammal bones, hint that they are also of wild stock. In Southeast Asia, evidence for early dogs of assured domesticated status is sparse, and current archaeological evidence points to a late Holocene date for their earliest occurrence in the region (e.g. Veth et al., 2005; Bulbeck, 2008). In Ille, there is also evidence of domestic dogs in the late Holocene. These are much smaller than dingoes and correspond in size with other Metal Age archaeological dog remains in the region and correspond in size with other late archaeological dog remains in the region (Tables 4a and 4b; Clutton-Brock, 1959; Medway, 1977; Ochoa, 2005, 2009). In addition, canid remains are absent in the mid-Holocene, and so a curious gap exists during this period, after which a different type of dog appears in the late Holocene layers. This again suggests that the Terminal Pleistocene canid remains were of wild status, and that like the tiger and deer, the dhole on Palawan may have also succumbed to environmental and anthropic pressures during the early Holocene.

The Ille record of extinct large mammal species previously unknown on Palawan underscores the grave and pressing issue of Late Quaternary Extinctions (LQE). The current biotic crisis is said to be quite anomalous compared to other extinction events in the past 55 million years (Brook and Bowman, 2002; Koch and Barnosky, 2006). Studies on the causes of LQE have traditionally weighed the effects of environmental as opposed to anthropogenic impacts (see Martin and Klein, 1984; Burney and Flannery, 2005; Martin, 2005). It is nonetheless obvious that this pervasive nature-culture dichotomy can be quite delimiting, and in order to understand the driving forces behind the LQE, the specifics of the interaction among environmental and human-induced variables must be investigated (Koch and Barnosky, 2006). For Southeast Asia, the effects of sea-level rise were tremendously far-reaching (Louys

et al., 2007), but the magnitude of anthropic impacts on Sundaic and Wallacean faunas – whether from direct predation or other indirect means – still needs much more examination before the extent of its role can be confidently ascribed.

6. Conclusion

The zooarchaeological analysis of the Terminal Pleistocene and early Holocene animal remains from Ille Cave has produced fossil evidence for many extant mammals and for four taxa that are locally extinct on Palawan. This dataset includes new records of several small and intermediate mammals, such as the Palawan pangolin, stink badger, common palm civet and bear cat, and confirms their presence on the island since the end of the last glacial period.

The presence of the tiger and possibly the dhole in the Terminal Pleistocene and early Holocene archaeological record increases the known former range of both of these species. The occurrence of these species also strengthens the biogeographic affinities of Palawan with neighbouring Borneo and the Sundaic region generally. Along with the Calamian hog deer, their presence here also adds further support to radio-isotopic environmental reconstructions, suggesting that an open woodland/savanna-type environment existed towards the end of the Pleistocene in northern Palawan.

The authors concur with Heaney (1986) and Reis and Garong (2001) that the current biogeographic evidence shows that no land bridge existed between Palawan and Borneo during the LGM on the following grounds: 1) the high endemism observed in the mammal community of Palawan; 2) the fact that many of the endemic and extinct taxa represented are characteristic of the Middle Pleistocene; and 3) the absence on Palawan of large closed-forest species that are otherwise common on the Sunda Shelf. The most recent land connection between Palawan and Borneo probably existed during glacial maxima of the Middle Pleistocene, around 420 ka or 620 ka.

The extirpation of several large island species on Palawan during the early to mid-Holocene adds to the record of Late Quaternary extinctions documented throughout the world. In Southeast Asia, the nature of such extinctions is still little understood due to the scarcity and fragmented nature of the fossil record and other palaeoenvironmental data, and relative dearth of published, well-dated, stratified sites, but some appraisals indicate that the domino-like effects of sea-level change were profound (Louys et al., 2007). On the current evidence from Ille, the disappearances of the Calamian hog deer, a larger cervid species, the tiger and perhaps the dhole on Palawan were primarily a result of the dramatic reduction of available territory and changes in the local environment. The role of humans in the faunal changes in the early Holocene is still difficult to assess. As in Palawan, the disappearance of some large mammals in Borneo and other Sundaic islands coincided with the establishment and long presence of modern human populations (Cranbrook and Piper, 2007). Nonetheless, it can be inferred from the case of the Palawan cervids that these animals were clearly under human hunting pressure throughout the whole island, judging from their abundance in Late Pleistocene and early Holocene archaeological cave site assemblages, and this pressure likely took its toll on already dwindling deer populations affected by sea-level rise and environmental change.

The antiquity of Palawan's vertebrate fauna, with both Middle and Late Pleistocene components, should warrant the attention and consideration of conservationists, local government and other concerned organizations. It remains probable that large island species, such as deer and tiger, became extinct due to a combination of natural factors and anthropogenic impact. Many other species have shown resilience despite extensive environmental change throughout the LGM and the Pleistocene-Holocene transition, but the contemporary impacts of modern agricultural and industrial

society are severely threatening the island's animal habitats and communities. The need to protect the remaining members of this Philippine faunal region with its unique mix of continental affinities and oceanic characteristics cannot be over-emphasized.

Acknowledgments

The authors would like to thank Angel Bautista and the National Museum of the Philippines for access to zooarchaeological comparative assemblages, and the El Nido municipal government, Mayor Leonor Corral and the Palawan Council for Sustainable Development (PCSD) for their cooperation and assistance. Many thanks to Dr. Lawrence Heaney for his expert advice on Palawan biogeography and to Dr. Ryan Rabett and the Earl of Cranbrook for reading and commenting on an early draft of this paper, and the comments of a reviewer. Funding for the phases of the Ille Cave Project producing these data was provided by the British Academy, the NERC/Orads programme, Rio Tuba and Coral Bay Nickel Mines, Petroenergy Corporation, Nido Petroleum, Philodrill Corporation, Cybersoft Geoinformatics, Jonathan Kress, University of the Philippines Archaeological Studies Program, the Solheim Foundation for Philippine Archaeology, the Irish Research Council for the Humanities and Social Science and SEAir Airlines. For the preparation of this publication PJP was funded by the UP Office of the Vice Chancellor for Research and Development (OVCRD). A visit to the FMNH by Janine Ochoa to study the modern comparative skeletal remains from Palawan was supported by a visiting scholarship from the FMNH and logistical assistance from Northwest Airlines.

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