Records of the Western Australian Museum Supplement No. 57: 341–350 (1999).

The Pleistocene mammal fauna of Kelangurr Cave, central montane Irian Jaya, Indonesia

Timothy F. Flannery
Mammalogy, Australian Museum, 6 College St, Sydney, NSW 2000;
email: timf@amsg.austmus.gov.au

Abstract — Sixteen mammal taxa have been identified on craniodental material from a rich deposit of bones in the first chamber of Kelangurr Cave. The remains of all species except the largest (*Maokopia ronaldi* and *Protemnodon hopei*) and the smallest (*Miniopterus* sp. cf. *M. macrocneme*) and possibly a single tooth cap of *Anisomys imitator*, are considered to have been accumulated by Pleistocene Sooty Owls (*Tyto tenebricosa*). About a dozen bird bones representing species ranging in size from finch to medium-sized honeyeater, and currently unidentifiable, are the only non-mammalian remains from the deposit.

Kelangurr Cave is at an elevation of 2,950 m, and presently located in tall upper montane forest. Analysis of the habitat requirements of the fossil mammal fauna indicates that at the time of deposition (25-20,000 BP) the cave was surrounded by alpine tussock grassland and scrub similar to that occurring today at 4,000-4,200 m on Mt Carstensz and Mt Wilhelmina.

The age of faunal remains not accumulated by owls is uncertain. There is no evidence of non-analogue mammal communities, and no evidence of extinction among species under 2 kg in weight in the fauna.

INTRODUCTION

The Kwiyawagi area (Figure 1) is the only part of Irian Jaya that has proved to be rich in Pleistocene vertebrate fossils (Flannery 1994). Remains of giant extinct marsupials were first discovered there by Pastor Doug Hayward of the Unevangelised Fields Mission during or before the 1980s. In January 1990 Dr Geoffrey Hope walked in to the West Baliem valley from Wamena, and found bones to be abundant both in Kelangurr Cave and in sediments exposed in the banks of the West Baliem River. I returned to the area with Dr Hope in June 1990 and

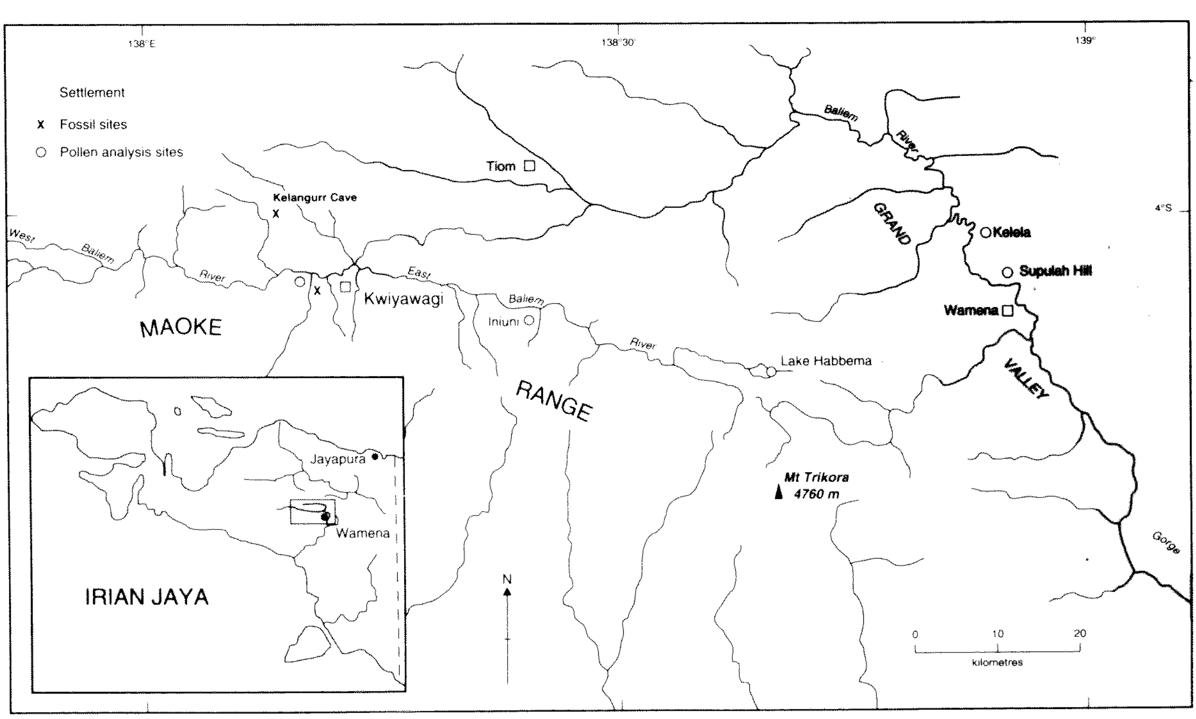

Figure 1 Location diagram, upper Baliem River catchment, Irian Jaya (inset).

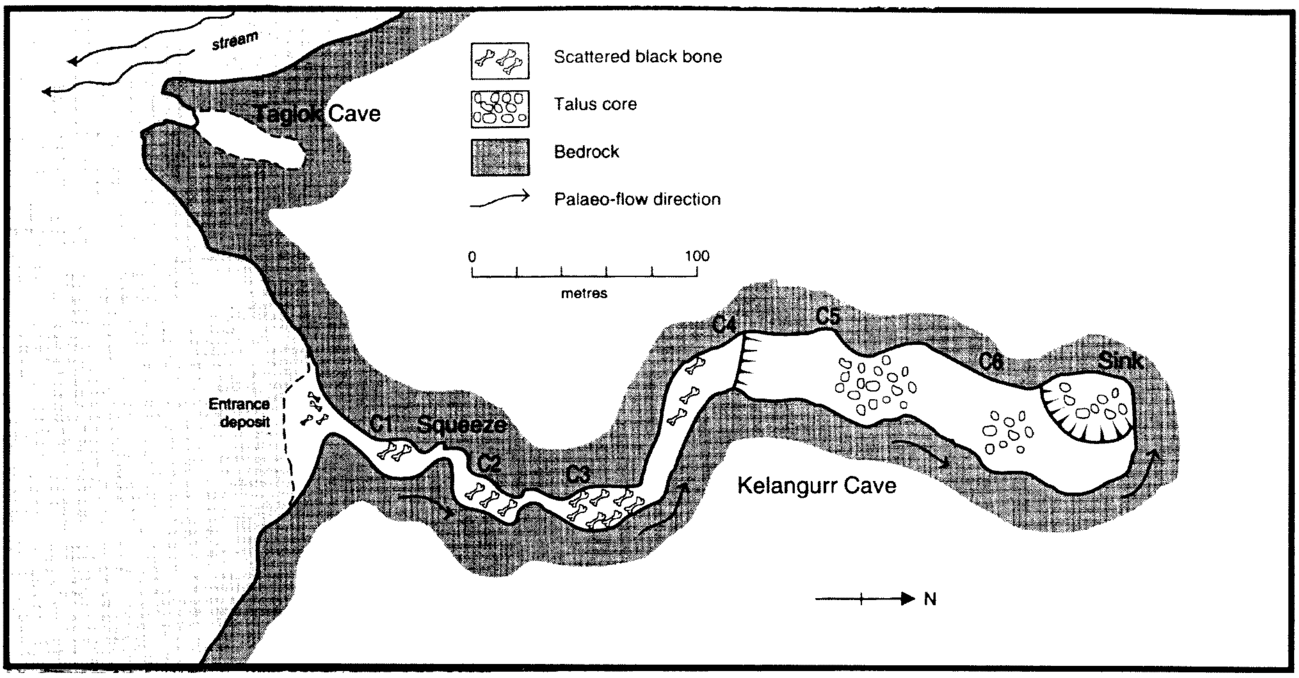

Figure 2 Plan of Kelangurr Cave showing location of Chambers and bone specimens.

made additional collections. The faunal remains included those of two large, extinct marsupials *Maokopia ronaldi* Flannery, 1992b and *Protemnodon hopei* Flannery, 1992b. The geology, palynology and dates obtained from the deposits have been described by Hope *et al.* (1993) and the sites are shown in Figure 1.

The Cave lies about 10 km west of the settlement of Kwiyawagi in a side valley leading to the West Baliem River. It consists of a passage about 350 m

Table 1 The fossil mammal fauna from Chamber 1, Kelangurr Cave: * possibly or certainly not accumulated by Pleistocene owls. MNI = minimum number of individuals; % = per cent of fauna; Wt = mean or estimated adult weight; E. r. = present elevational range (m a.s.l.); (weight and elevational range data for living species mainly from Flannery 1995); Survival: p = still present, np = not present in the area, ex = extinct. ? = no data.

Taxon	MNI	%	Wt	E. r.	Survival
Dasyuromorphia					
Neophascogale lorentzii	1	*0.2*	200 g	1500-3300	p
Peramelemorphia					
Microperoryctes longicauda	48	*8.7*	540 g	1000-3950	p
Diprotodontia					
Maokopia ronaldi *	1	*0.2*	100 kg	?	ex
Protemnodon hopei *	1	*0.2*	40 kg	?	ex
Thylogale christenseni	2	*0.4*	2 kg	?	ex
Thylogale sp.	1	*0.2*	6 kg	?	ex
Cercartetus caudatus	46	*8.3*	20 g	1500-3450	p
Pseudochirulus mayeri	290	*52.6*	150 g	1500-4200	p
Microchiroptera					
Miniopterus sp. cf. *M. macrocneme* *	1	*0.2*	9 g	0-3200	?
Rodentia					
Anisomys imitator *	1	*0.2*	500 g	*c.* 0 - 3500	p
Coccymys rümmleri	38	*6.9*	30 g	1900-3600	?
Coccymys sp.	2	*0.4*	*c.* 40 g	?	?
Hydromys habbema	1	*0.2*	*c.* 80 g	2800-3600	p
Mallomys gunung	6	*1.1*	2 kg	3500-4430	np
Stenomys richardsoni	101	*18.3*	70 g	3225-4500	np
Stenomys omlichodes	11	*2.0*	75 g	2950-3950	p
TOTALS	551	*100.1%*			

long averaging 3 m high, which slopes gently downward from a cliffed entrance (Figure 2). It is surrounded by diverse, tall upper montane forest, which includes species of *Podocarpus*, *Phyllocladus* and other gymnosperms. An area of swampy, valley floor vegetation is present approximately 1 km away.

During a visit to Kelangurr Cave in 1994 by the author and Alexandra Szalay, additional material was collected, including approximately 18 kg of matrix and lag deposit, rich in fossil bones, from the first chamber (Chamber 1). This material, which consists largely of the bones of small mammals, forms the focus of the present study.

MATERIALS AND METHODS

About 4 kg of primary matrix and 14 kg of lag deposit (consisting principally of mud and fossil bones) were removed from the walls and floor of Chamber 1 and taken to Kwiyawagi, where the lag material was washed and sieved through flywire (mesh approximately 1 mm). The bones and rock fragments were then dried, packed and transported to the Australian Museum, where the loose bones were sorted and the craniodental fragments separated from the rest. An attempt was made to acid prepare a small sample of matrix (approximately 2 kg), but with little success. The small sample of bones recovered from this attempt comprises only taxa recorded from the lag material.

The craniodental material was identified using the Australian Museum mammal collection as a reference. This collection includes examples of all extant species identified except *Coccymys* sp. Details of identification criteria are provided in the Mammal Systematics subsection of the Discussion, below. The megafaunal specimens (*Maokopia ronaldi* AM F100743 and *Protemnodon hopei* AM F83413) and four *Stenomys* specimens (*S. richardsoni* AM F100744 and *S. omlichodes* AM F100745) have already been accessed

Table 2 The present mammal fauna of the Kwiyawagi area, including the vicinity of Kelangurr Cave, as determined from faunal survey 4-10 June 1994. Data on body weight range (Wt), present elevational range in metres a.s.l. (E. r.), and primary habitat (Habitat) mainly from Flannery (1995). *Dendrolagus mbaiso* Flannery, Boeadi and Szalay, 1995 and *Mallomys gunung* were collected only high in the Prinz Wilhelm Range to the south of Kwiyawagi.

Taxon	Wt	E. r.	Habitat
Dasyuromorphia			
Dasyurus albopunctatus	580-710 g	0-3500	forest
Neophascogale lorentzii	212 g	1500-3300	forest
Peramelemorphia			
Microperoryctes longicauda	350-670 g	1000-3950	forest/alpine
Peroryctes raffrayana	650-1000 g	60-3900	forest
Diprotodontia			
Phalanger carmelitae	1700-2600 g	1400-3660	forest
Phalanger sericeus	1750-2405 g	1500-3900	forest
Dendrolagus dorianus	6.5-18 kg	600-3300	forest
Dendrolagus mbaiso	8.5-9 kg	3250-4200	alpine
Dorcopsulus vanheurni	1500-2340 g	800-3100	forest
Dactylopsila palpator	260-550 g	1200-2950	forest
Petaurus breviceps	69-114 g	0-3000	forest
Pseudochirops corinnae	925-1300 g	1200-2900	forest
Pseudochirops cupreus	1300-2250 g	1700-3996	forest/alpine
Pseudochirulus mayeri	105-206 g	1500-4200	forest/alpine
Microchiroptera			
Pipistrellus collinus	5.1-6.9 g	1700-2950	?
Tadarida kuboriensis	23-27.5 g	1900-2950	?
Rodentia			
Anisomys imitator	388-580 g	0-3500	forest
Hydromys sp. cf. *H. habbema*	*c.* 80 g	2800-3600	rivers/lakes
Mallomys gunung	2000 g	3500-4430	alpine
Mallomys rothschildi	925-1500 g	1550-3700	forest
Paramelomys rubex	31-57 g	900-3000	forest/alpine
Rattus steini	110-220 g	20-2800	gardens
Stenomys niobe	36-55.5 g	760-4050	forest/alpine
Stenomys omlichodes	69-78 g	2950-3950	swamps/alpine
Uromys anak	450-1020 g	850-2950	forest

into the Australian Museum palaeontological collection. The other material will be added to that collection in the near future.

RESULTS

For the modern mammal species, classification generally follows Flannery (1995), including recognizing *Stenomys* as a genus separate from *Rattus*. An exception is members of the *Melomys* complex, where Menzies (1996) is followed. The extinct *Thylogale*, previously identified as *T. brunii*, is here referred to as *Thylogale* sp. following Flannery (1992a). Authorities are only given for species not included in Flannery (1995) or Walton (1988). Higher category taxa of marsupials follow Aplin and Archer (1987).

Fossil Fauna from Kelangurr Cave

Sixteen species of mammals, ranging in estimated mean body weight from 9 g to 100 kg, have been identified in the fossil fauna from Chamber 1 of Kelangurr Cave (Table 1, overleaf). Minimum numbers of individuals were determined from the most abundant identified skeletal element of each species (Table 1 and Table 4, below). The only other vertebrate remains collected consist of about a dozen currently unidentifiable bones of birds, ranging in size from a finch to a medium-sized honeyeater.

Extant Mammal Fauna of the Kwiyawagi Area

A survey of the extant mammal fauna of the Kwiyawagi area was undertaken at the time of the 1994 visit. Results are given in Table 2, and indicate that the area today supports a fauna which is primarily forest dwelling. The alpine species listed in Table 2 were collected in the mountains which rise on the southern side of the West Baliem Valley.

Dating of the Deposit

New optically-stimulated luminescence (OSL) and uranium series dates, the details of which will be published elsewhere in conjunction with R.G. Roberts and J.M. Olley, indicate that the deposit in Chamber 1 accumulated between 25,000 and 20,000 BP. The OSL dating was undertaken on tiny sand grains which had probably made their way in to the deposit in the fur of prey items. These would presumably have been picked up from the surface of the ground where they would have been thoroughly bleached, so it seems reasonable to assume that the faunal remains derived from owl pellets are accurately dated by this technique. The background radiation dose rate, used to calibrate the OSL dates, was measured in the laboratory on the bulk sample of deposit.

As will be discussed below, a small proportion of the fossil material from Chamber 1 is probably reworked from an earlier fossil accumulation and may thus be considerably older than 25,000 BP. This material includes the remains of the extinct giant marsupials.

DISCUSSION

Mammal Systematics

The species identified from Kelangurr Cave can be divided into three categories according to their elevational and temporal distributions. A) Species unknown from the immediate area of Kwiyawagi today, being restricted to higher elevations, B) Species still occurring in the Kwiyawagi area, or known from similar elevations elsewhere in Irian Jaya, and C) extinct species.

A) Taxa unknown from the immediate area of Kwiyawagi today, being restricted to higher elevations (*Mallomys gunung, Stenomys richardsoni*).

The Kelangurr Cave sample of giant rats was identified as *Mallomys gunung* (rather than one of the other three species of *Mallomys* known to inhabit the Maokop, Flannery 1995), primarily on the basis of white incisor enamel, a characteristic unique to *M. gunung* in its genus.

The molars of the fossil *Mallomys* are comparable in size to those of *M. gunung*, and larger than those of *M. rothschildi* (the only species known to inhabit the area of the cave today; Table 3). They are also larger than those of *M. aroaensis*, but overlap considerably with *M. istapantap* (Table 3). None of the palatal remains from the Kelangurr sample has an ovoid choana (unique to *M. istapantap* in the genus), so despite the similarity in molar size, identification of palatal remains with this species was excluded.

The identification of the *Stenomys* sample proved more difficult. Three species of *Stenomys* are known from subalpine grassland on the Maokop (Flannery 1995). Their taxonomy is still poorly understood. *Stenomys omlichodes* has only recently been re-elevated to full specific status, distinct from *S. richardsoni* (Flannery 1995). Adequate craniodental diagnosis of these taxa based on examination of a large sample is still unavailable.

I was able to satisfy myself that *S. niobe* is absent from the Kelangurr Cave sample. Its molars are markedly smaller, more slender and more cuspidate that its congeners, and none resembling it was present in the fossil sample. I had difficulty, however, in distinguishing *S. richardsoni* from *S. omlichodes*.

One useful character for distinguishing these species is the colour of the incisor enamel; that of *S. richardsoni* is white, while that of *S. omlichodes* is yellow. Unfortunately, many fossil specimens do not include an incisor, so other criteria had to be used as well.

Table 3 Dental measurements of species of *Mallomys*. (a) = fossils identified as *M. gunung* from Chamber 1 deposit, Kelangurr Cave; (b) = single fossil identified as *M. gunung* from deeper inside Kelangurr Cave; (c) = modern sample *M. gunung* from all New Guinea; (d) = remains of recently dead individuals of *M. rothschildi* from Chambers 2-4, Kelangurr Cave; (e) = modern sample *M. rothschildi weylandi* from all New Guinea; (f) = modern sample *M. aroaensis aroaensis* from all New Guinea; (g) = modern sample *M. istapantap* from all New Guinea. Upper molar measurements of (c), (e), (f) and (g) from Flannery *et al.* (1989). All measurements in mm.

		M^{1-3} length	M^1 width	M_{1-3} length	M_1 width
(a) *M. gunung*	$\bar{x}$	18.8	5.8	18.1	5.0
	R	17.9-20.0	5.4-6.4	17.6-18.5	4.8-5.1
	n	3	3	4	8
	s	1.33	0.51	0.39	0.14
(b) *M. gunung*		19.2	6.0	-	-
	n	1	1	0	0
(c) *M. gunung*	$\bar{x}$	18.8	5.8	17.9	4.9
	R	17.4-20.0	5.6-6.0	17.7-18.0	4.8-5.0
	n	5	4	2	2
	s	0.96	0.18	-	-
(d) *M. rothschildi*	$\bar{x}$	16.8	5.5	16.2	4.5
	R	16.6-17.0	5.4-5.5	16.1-16.2	4.5
	n	2	2	2	2
(e) *M. rothschildi*	$\bar{x}$	16.5	5.2	16.3	4.5
	R	15.7-17.5	5.1-5.4	16.0-16.6	4.3-4.6
	n	11	9	2	2
	s	0.21	0.11	-	-
(f) *M. aroaensis*	$\bar{x}$	17.0	5.2	-	-
	R	16.3-18.0	4.9-5.4	-	-
	n	10	10	-	-
	s	0.67	0.13	-	-
(g) *M. istapantap*	$\bar{x}$	18.4	5.4	-	-
	R	17.4-19.1	5.0-6.0	-	-
	n	8	8	-	-
	s	0.57	0.35	-	-

My small sample of modern specimens of both species (about six of each) indicate that some *S. richardsoni* possess accessory buccal cusps on the lower molars (see Figure 3), but these are not invariably present. In addition, the molars of *S. richardsoni* are broader and more robust than those of *S. omlichodes* (see Figure 3 for examples). Although these differences did not always allow for unequivocal identification of each fragment, the fossil sample was divided into specimens more resembling *S. richardsoni* in molar robustness and morphology, and those resembling *S. omlichodes*.

The results of these comparisons (Table 4) suggest that whichever criteria are used, specimens referred to *S. richardsoni* are more abundant than those referred to *S. omlichodes* (in total about 74% of all

Table 4 The *Stenomys* dentary and dentary fragment sample (N = 123). Groups: (1) = identified as *S. richardsoni* on the basis of both molars and white incisors; (2) = identified as *S. richardsoni* on the basis of molars (incisors absent); (3) = identified as *S. richardsoni* on the basis of white incisors (molars absent); (4) = specimens with white incisors but *S. omlichodes*-like molars; (5) = specimens with yellow incisors, but *S. richardsoni*-like molars; (6) = identified as *S omlichodes* on the basis of molars (no incisors); (7) = identified as *S. omlichodes* on the basis of yellow incisors (no molars); (8) = identified as *S omlichodes* on the basis of both molars and yellow incisors; (9) = could be identified only to genus *Stenomys*. Per cent = percentage of sample in each of the four major categories.

	S. richardsoni			intermediate		*S. omlichodes*			*Stenomys* sp. indet.
Group	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Counts									
Left	44	35	20	3	4	0	7	1	14
Right	48	30	23	4	1	4	0	7	19
Per cent									
Left		*77.3*		*5.5*			*6.3*		*10.9*
Right		*74.3*		*3.7*			*8.1*		*14.0*

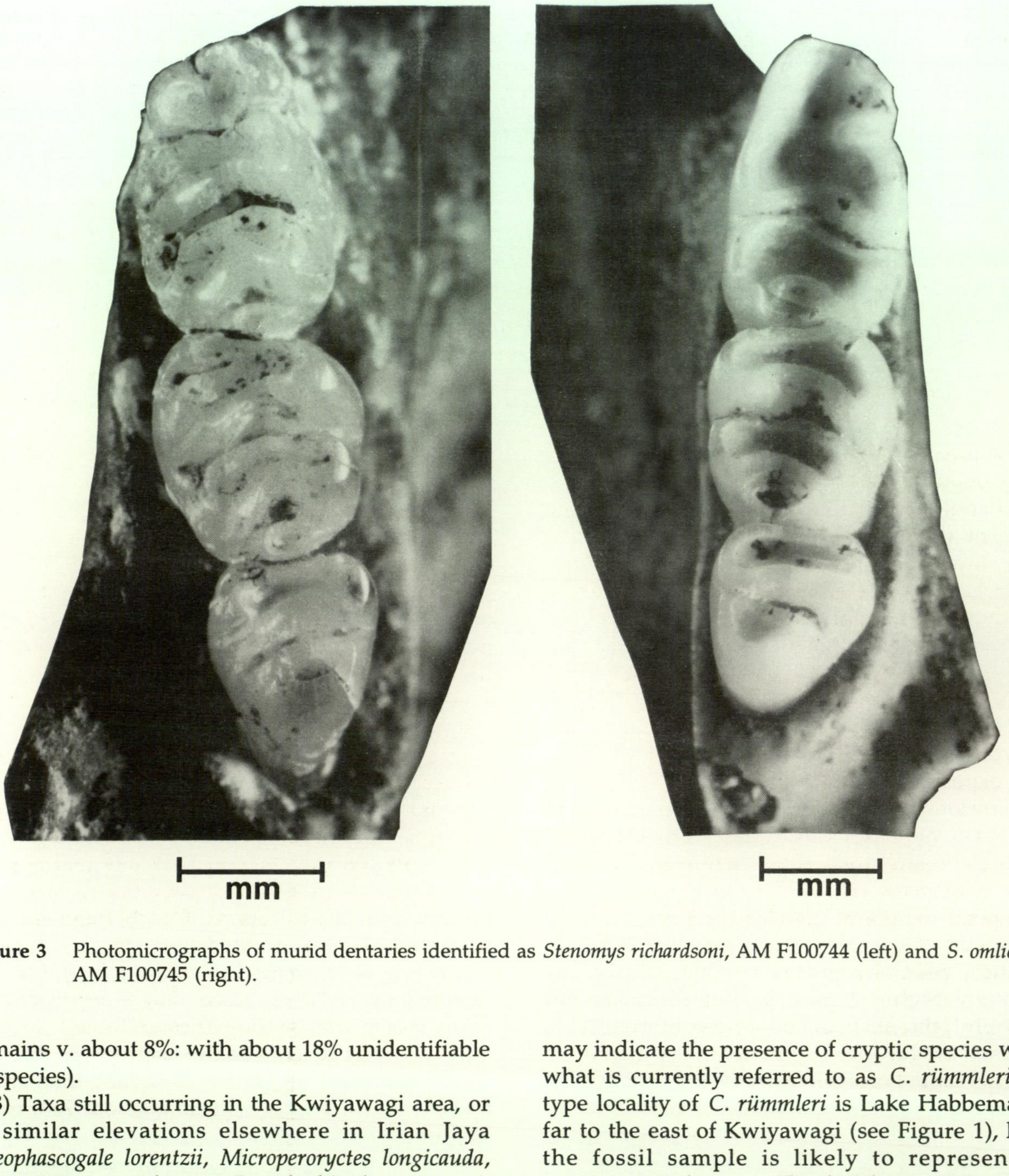

Figure 3 Photomicrographs of murid dentaries identified as *Stenomys richardsoni*, AM F100744 (left) and *S. omlichodes*, AM F100745 (right).

remains v. about 8%: with about 18% unidentifiable to species).

B) Taxa still occurring in the Kwiyawagi area, or at similar elevations elsewhere in Irian Jaya (*Neophascogale lorentzii*, *Microperoryctes longicauda*, *Cercartetus caudatus*, *Pseudochirulus mayeri*, *Miniopterus* sp. cf. *M. macrocneme*, *Anisomys imitator*, *Coccymys rümmleri*, *Hydromys habbema*, *Stenomys omlichodes*).

These nine species are all known to occur at around 2,900 m elevation in central Irian Jaya at present. Identification of all except *C. rümmleri*, which is in need of systematic revision, was straight forward. The Kelangurr Cave sample of *C. rümmleri* consisted of larger individuals than those (all from Papua New Guinea) which were available for comparison. Hope (1976) also noted that Holocene specimens of this species from the Carstensz area were larger than the modern specimens with which she compared them. The significance of this is presently unknown, but it may indicate the presence of cryptic species within what is currently referred to as *C. rümmleri*. The type locality of *C. rümmleri* is Lake Habbema, not far to the east of Kwiyawagi (see Figure 1), hence the fossil sample is likely to represent the nominotypical taxon. The fossil material referred to *Coccymys* sp. is extremely fragmentary. It appears to represent a species slightly larger than even the fossil *C. rümmleri*, but with less complex molars. It may be the poorly-known *C. albidens*, only recorded from the alpine zone on Mt Wilhelmina (Trikora).

The present elevational distributions of the eight taxa identified to species level vary, but all except *Anisomys imitator* (which is restricted to forest) are known to inhabit areas of subalpine scrub and to occur above the treeline; and all of the others except *Neophascogale lorentzii* and *Pseudochirulus mayeri* (the latter the most common species in the sample, see Table 1) can be found in tussock grassland. *Stenomys omlichodes* is not known to inhabit forest. The upper elevational limits of most species are poorly known. There is some doubt about the provenance of two of these taxa (*Miniopterus* sp. cf. *M. macrocneme*, *Anisomys imitator*). Both may represent modern contamination of the lag deposit (see below).

C) Extinct taxa (*Maokopia ronaldi*, *Protemnodon hopei*, *Thylogale* sp., *Thylogale christenseni* Hope, 1981).

The elevational ranges of all of these taxa are very poorly known. Fossils of *Maokopia ronaldi* and *Protemnodon hopei* are only recorded from the Kwiyawagi area (Flannery 1992b). Remains of both species have been found in sediments exposed along the West Baliem River. Fossil pollen and plant macrofossils from the same deposits suggest that the area was above or near the treeline at the time of deposition (Hope *et al.* 1993).

The dentitions of both *M. ronaldi* and *P. hopei* are consistent with a diet relatively rich in silica and other abrasive material (Flannery 1992b). Both species have higher crowns and more prominent links than related species whose fossils have been found at lower elevation. These data suggest that both consumed grasses and lived above the treeline, where grass is most abundant. As the remains of these taxa were clearly not accumulated by owls, their association with the rest of the fauna in the deposit is uncertain (see below).

Pademelons (genus *Thylogale*) are known from the Maokop only as fossils. Although their original elevational distribution is poorly known, remains of late Holocene age have been recorded from rockshelters in tussock grassland at 3,990 and 3,700 m elevation (Hope 1976; Hope *et al.* 1993). This evidence, plus the nature of their dentitions (relatively high crowned with well-developed links) and the ecology of related populations (Flannery 1992a) all suggest that they inhabited grassland and herbfield communities above the treeline.

The time of the extinction of these species is poorly known. The remains of *Maokopia ronaldi* and *Protemnodon hopei* have been found in association with peats dated to 39,860 ± 770 BP in the West Baliem River, and with wood, the cellulose fraction of which has been dated at 42,740 ± 1020 BP (Hope *et al.* 1993).

Thylogale sp. and *T. christenseni* are known from much more recent deposits, including Billingeek rockshelter in the Prinz Wilhelm V Range, where their remains are associated with charcoal dated as young as 3,250 ± 80 BP (Hope *et al.* 1993).

Agents of Accumulation

With the exception of the remains of the very large and very small taxa (see below), all of the other mammalian remains appear to have resulted from accumulation at an owl roost.

The bone accumulation present in Chamber 1 of Kelangurr Cave probably exceeds several cubic metres in volume. It is plastered on the sides and floor of the cave, and is most obvious about 5 m in from the cave entrance. It is currently in the twilight zone. It seems likely that the bulk of the deposit has already eroded away.

As Baird (1991) noted, owls are "by far the most frequent accumulators of vertebrate bone in caves". The only other obvious possibility is derivation from acciptrid pellets, but the high frequency of undamaged limb bones among the remains is inconsistent with this hypothesis.

Among the existing owl species of New Guinea, only the Sooty Owl (*Tyto tenebricosa*) occurs at elevations above 2,500 m (Beehler *et al.* 1986). This species also occurs in southeastern Australia, where its biology has been extensively studied. Australian Sooty Owls can reach 1 kg in weight and a total length of 51 cm (Schodde and Mason 1980). They have large talons and are capable predators, preying upon a wide variety of medium-sized to small mammals. Single or paired Sooty Owls forage over ranges of 200 to 800 hectares around their roost (Schodde and Mason 1980).

In Australia, the Sooty Owl has been found to feed upon animals ranging in size from the House Mouse (*Mus musculus*, mean weight 18 g) to the Common Ringtail Possum (*Pseudocheirus peregrinus*, mean weight 900 g). The prey species most commonly recorded in a series of five sites in New South Wales is the Sugar Glider (*Petaurus breviceps*, mean weight 128 g; Debus 1994). This general prey profile fits well with that observed at Kelangurr Cave, where the estimated mean weight of the smallest prey is 20 g, and the largest 1 kg (juveniles of *Mallomys gunung* and *Thylogale* sp.), with the most common prey species, *Pseudochirulus mayeri*, averaging 150 g.

New Guinean Sooty Owls average 36 cm in length (Beehler *et al.* 1986); only slightly larger than the Barn Owl. The biology of the New Guinean population is poorly understood, but it is known to hunt rodents and marsupials in forest and at the edge of alpine grassland (Beehler *et al.* 1986). It occurs from sea level to 4,000 m elevation. It is theoretically possible that another, as yet unknown owl species existed in New Guinea during the Pleistocene, and this species was responsible for the accumulation.

Ages and Provenance of the Faunas

As noted in Results, OSL and uranium series dates indicate that the deposit in Chamber 1, containing the fauna derived from owl pellets, accumulated between 25,000 and 20,000 BP. Four species, however, represented by just five fossil fragments, were probably not accumulated by

Pleistocene owls. The age and provenance of these remains needs to be separately assessed.

Two taxa (represented by just three fragments) may be recent remains that have been mixed with the Pleistocene lag deposit. These are *Miniopterus* sp. cf. *M. macrocneme* and *Anisomys imitator*.

The smallest species in the deposit is the cavernicolous bat *Miniopterus* sp. cf. *M. macrocneme* (weight about 9 g), which is represented by left and right dentary fragments, possibly from the same individual. This species has been recorded roosting in caves at 2,600 m elevation, and has been observed flying over alpine herbfield at 3,200 m elevation (Flannery 1995). The two bones of this species thus far identified may represent the remains of an individual which was roosting in Kelangurr Cave in recent times. The fact that the bone is light and fragile and the tooth enamel white, is consistent with this interpretation.

Anisomys imitator is represented in the deposit by a single M^1 enamel cap, which is white in colour. Many of the other specimens have variably stained enamel. The *Anisomys* tooth cap may differ in age and/or origin from the rest of the remains, although there is no way to test this empirically at present. It should be noted, however, that the remains of other large, recently deceased murids, have been found deeper in the cave.

Only two mammal bones found in Chamber 1 come from individuals estimated to have weighed more than 1 kg (see Table 1). Neither could have been preyed on by owls. These are a dentary of an adult *Protemnodon hopei* (estimated weight 40-60 kg) and a scapula of *Maokopia ronaldi* (estimated weight 100 kg). (Although the estimated adult weights of the two *Thylogale* species were also more than 1 kg, the species are represented in the sample by juveniles.) The left dentary of *Protemnodon hopei* (AM F83413), although exposed on one side, was actually embedded in the owl pellet deposit. The scapula of *Maokopia ronaldi* (AM F100743), was found lying loose on the chamber floor, with fragments of matrix adhering to it.

Hope *et al.* (1993) visualized Kelangurr Cave as consisting of six chambers (see Figure 2). Fossil remains were found in four of these, being most common in Chambers 1 and 2. The cave slopes downwards from its mouth, and Hope *et al.* (1993) hypothesized that the cave was once much larger, and that the majority of it (including the original entrance) was carried away in a prehistoric landslide. Some evidence suggests that megafaunal remains have been migrating downslope in the cave for some time. Some bones of *M. ronaldi* and *P. hopei* were found cemented into a flowstone in Chamber 3. These bones do not appear to be *in situ*, but to have been derived from some other primary deposit (Hope *et al.* 1993). Depending upon the past morphology of the cave, it is possible that Kelangurr Cave may have acted as a pitfall trap for larger marsupials, or megafauna may have used the cave as a shelter and died there.

Given the history of the cave and its deposition, and the fact that the megafaunal remains from Chamber 1 represent isolated, albeit well-preserved elements, I have no confidence that they are in fact contemporaneous with the owl pellet remains. They may be much older, having been washed into Chamber 1 from the now lost proximal region of the cave, in an already fossilized state.

The relationship between the owl pellet deposit in Chamber 1, and other deposits in the cave, remains uncertain. Hope *et al.* (1993) analysed the chemical compositions of bones of *Mallomys* collected in Chambers 2-4 of the Cave. Black-stained bones differed substantially in composition from the lighter coloured bones, suggesting an age differential (see below). Hope *et al.* (1993) also suggested that the black bones were contemporaneous with or slightly older than black flowstones found in the same chambers and measured by ESR at 68 ± 14 and 80 ± 40 Gray units. Unfortunately, in the absence of background dose rates for these deposits, it is impossible to convert these measurements into dates. Interestingly, the fluorine, organic nitrogen and apatite CO_2 contents of the bones and flowstone are similar. In the absence of obvious leaching, this argues for a stable depositional environment in which the black materials represent a groundwater chemistry different from that prevailing at present.

The strong correlation between the chemistry of the black flowstones and black bones from Chambers 2-4, suggests that both may be of similar age. The material from the deposit in Chamber 1 is variably stained, some bones being black, while others are much paler. Fragments of black-stained flowstone, apparently formed *in situ*, are also present in the Chamber 1 deposit.

Heavily mineralized bones, blackish in colour, of *Stenomys* sp. and *Mallomys gunung* were found lying loose in Chambers 2-3. Other faunal remains recovered from Chambers 2-4 appear to have a different origin and possibly a different age. These include less mineralized bones of *Microperoryctes longicauda, Phalanger sericeus, Thylogale* sp., *T. christenseni, Dactylopsila palpator, Mallomys rothschildi* and *Uromys anak*. Of these taxa *P. sericeus, D. palpator, M. rothschildi* and *U. anak* are obligate forest dwellers. Some remains of the last two species represented recently dead individuals. A living *U. anak* was found in the cave at the time of the 1990 visit, and all except the two species of *Thylogale* (which became extinct some time after 3,250 years ago) are still to be found around the cave (see Table 2).

Past Vegetation Formations Around Kelangurr Cave

A number of lines of evidence suggests that the fossil deposit preserved in Chamber 1 of Kelangurr Cave accumulated at a time when the surrounding area was vegetated with tussock grassland and some alpine scrub, the latter possibly confined to rocky slopes. Forest was almost certainly absent, as the remains of obligate forest dwelling mammals are almost entirely absent from the deposit.

The presence of *Mallomys gunung*, and apparently of no other *Mallomys* species, in the deposit, provides an important insight into palaeoecology. *Mallomys gunung* is the only member of its genus which is an obligate inhabitant of plant communities occurring above the treeline. All other *Mallomys* inhabit forest, although *M. istapantap* extends into alpine grassland in Papua New Guinea in the absence of *M. gunung* (Flannery 1995). The fact that all identifiable remains of *Mallomys* in the deposit are *M. gunung* is consistent with the hypothesis that at the time of accumulation, the treeline was below Kelangurr Cave.

Stenomys richardsoni has only been recorded from alpine tussock grassland near and on Mt Wilhelmina and Mt Carstensz, where it occurs at elevations of up to 4,500 m (Hope 1976). No mammal has been recorded at higher elevation in New Guinea, although *Mallomys gunung* has been recorded at 4,430 m.

Limited trapping which I undertook at 3,950 m elevation in the Meren Valley, revealed three species of *Stenomys* (*niobe*, *omlichodes* and *richardsoni*) in approximately equal abundance, although their preferred habitats differed (unpublished observations). *Stenomys richardsoni* was most commonly encountered in tussock grassland growing in the valley floor; *S. omlichodes* favoured the short scrub clinging to the rocky walls of the valley; and *S. niobe* was associated with a large, loose boulder slope and in particular with human camp sites in this area. At lower elevations *S. omlichodes* is associated with heath and boggy scrub (down to 2,900 m), and *S. niobe* is common in forest.

The high relative abundance of *S. richardsoni* in the Kelangurr Cave deposit provides further evidence that tussock grassland was an important component of the vegetation of the area at the time of the accumulation.

The absence of forest-dwelling species from the fossil deposit is unlikely to have resulted from the feeding preferences of the Sooty Owls, as they are well-known to take a wide variety of forest-dwelling mammal species, both arboreal and terrestrial, in Australia. The present foraging areas of Sooty Owls in Australia vary from about 2 km^2 to 8 km^2. On this basis, it seems likely that, at the time of deposition, forest communities lay at least this far and possibly even more distant from Kelangurr Cave.

Table 5 The fossil mammalian fauna from Mapala rockshelter. The left hand column lists taxa recognized by Hope (1976), and the right hand column the names used in this paper. [1] = taxonomic change, [2] = re-identification.

Hope (1976)	This paper
Zaglossus bruijnii (as *bruijni*)	*Zaglossus bruijnii*
Satanellus albopunctatus	*Dasyurus albopunctatus* [1]
Peroryctes longicauda	*Microperoryctes longicauda* [1]
Phalanger sp.	*Phalanger sericeus* [2]
Dendrolagus dorianus	*Dendrolagus* sp.[2]
Thylogale brunii (as *bruijni*)	*Thylogale* sp.[2]
Thylogale sp. nov	*Thylogale christenseni* [1]
Pseudocheirus cupreus	*Pseudochirops cupreus* [1]
Pseudocheirus mayeri	*Pseudochirulus mayeri* [1]
Mallomys rothschildi	*Mallomys gunung* [1]
Hyomys goliath	*Hyomys dammermani* [1]
Canis familiaris	*Canis familiaris*

The abundance of *Pseudochirulus mayeri* in the deposit suggests the presence of significant areas of alpine scrub in the vicinity of the Cave. This was most likely confined to rocky slopes.

Hope (1976) gave an account of the mammal fauna of Mt Carstensz, as well as a subfossil fauna recovered from Mapala rockshelter, which is located at 3,996 m elevation just above the treeline on the Kembau Plateau. The lower levels of the Mapala rockshelter deposits have been dated to 5,440 ± 130 BP (Hope 1976). I have re-examined the material from Mapala rockshelter and present in Table 5 a new faunal list for the site, based on modern systematic concepts. All of the extant taxa except *Dasyurus albopunctatus*, *Phalanger sericeus* and *Hyomys dammermani* are known to inhabit alpine scrub above the treeline. As the deposit results from human accumulation, the three exceptions may have been captured at lower elevations and carried up to the shelter.

Pseudochirops cupreus is abundant in the Mapala rockshelter fauna and is the most commonly encountered game item in alpine scrub in the area today (Flannery 1995). Yet, remarkably, it is entirely absent from both Kelangurr Cave and Billingeek rockshelter, dated at 3,250 ± 80 BP (Hope *et al.* 1993). It may be a recent arrival in this habitat.

Hope (1976) also gave an informative account of the contemporary, indigenous mammal fauna of the highest parts of the Jaya mountains. Very few species occur above 4,200 m elevation. She recorded only *Mallomys gunung* (as *M. rothschildi*), *Stenomys richardsoni* and *S. omlichodes* (the latter as *S. niobe*). To this list can probably be added *Pseudochirulus mayeri* (I have found skulls of freshly-killed individuals at about 4,200 m elevation in the Prinz Wilhelm V Range, unpublished observations) and *Zaglossus bruijnii*, which has been recorded at 4,150 m (Harrer 1964). The diversity of fossil mammalian taxa recorded from Kelangurr Cave is considerably higher than that found above 4,200 m today.

Overall, the closest match among contemporary environments to that represented by the fossil fauna in the Chamber 1 deposits from Kelangurr Cave, is that occurring between 4,000 and 4,200 m elevation on the Maokop. At these elevations, valley floors support tussock grassland, while rocky slopes support dense alpine scrub which grows to 1-2 m in height. These habitats support a moderately diverse mammal fauna. This interpretation is consistent with other palaeoenvironmental data, for the treeline in New Guinea dropped to as low as 2,100 m elevation during the last glacial maximum (Hope and Hope 1976). Today tall upper montane forest surrounds the site and the treeline lies at about 3,900 m elevation on the mountains to the south.

ACKNOWLEDGEMENTS

I am indebted to Alexandra Szalay for literally giving the shirt off her back to aid in the collection of the sample analysed here. Mr Edward Seeto and Mr Rui Lopes sorted and prepared the sample for analysis. Mr Lopes also attempted the acid preparation of the matrix sample, and carried out preliminary taxonomic classifications. Dr Geoff Hope kindly made available Figures 1 and 2 for use in this publication.

REFERENCES

Aplin, K.P. and Archer, M. (1987). Recent advances in marsupial systematics with a new syncretic classification. *In* Archer, M. (ed.), *Possums and opossums: studies in evolution*: xv-lxxii, Surrey Beatty & Sons Pty Ltd, Chipping Norton, N.S.W.

Baird R.F. (1991). The taphonomy of late Quaternary cave localities yielding vertebrate remains in Australia. *In* Vickers-Rich, P., Monaghan, J.M., Baird, R.F. and Rich, T.H. (eds), *Vertebrate palaeontology of Australasia*: 267-309, Pioneer Design Studios, Melbourne, Victoria.

Beehler, B., Pratt, T.K. and Zimmerman, D.A. (1986). *Birds of New Guinea.* Handbook No. 9, Wau Ecology Institute: 1-293, Princeton University Press, Princeton, New Jersey, U.S.A.

Debus, S.J.S. (1994). The Sooty Owl *Tyto tenebricosa* in New South Wales. *Australian Birds* **28**: 4-19.

Flannery, T.F. (1992a). Taxonomic revision of the *Thylogale brunii* complex (Macropodidae: Marsupialia) in Melanesia, with description of a new species. *Australian Mammalogy* **15**: 7-23.

Flannery, T.F. (1992b). New Pleistocene marsupials (Macropodidae, Diprotodontidae) from subalpine habitats in Irian Jaya, Indonesia. *Alcheringa* **16**: 321-331.

Flannery, T.F. (1994). The fossil land mammal record of New Guinea: a review. *Science in New Guinea* **20**: 39-48.

Flannery, T.F. (1995). *Mammals of New Guinea*, revised and unpdated edition: 1-568, Reed Books, Sydney, N.S.W.

Flannery, T.F., Aplin, K.P., Groves, C.P. and Adams, M. (1989). Revision of the New Guinea murid genus *Mallomys* (Muridae: Rodentia), with descriptions of two new species from subalpine habitats. *Records of the Australian Museum* **41**: 83-105.

Flannery, T.F., Boeadi and Szalay, A.L. (1995). A new tree-kangaroo (*Dendrolagus*: Marsupialia) from Irian Jaya, Indonesia, with notes on ethnography and the evolution of tree-kangaroos. *Mammalia* **59**: 65-84.

Harrer, H. (1964). *I come from the Stone Age*, Rupert Hart-Davis, London, U.K.

Hope, G.S., Flannery, T.F. and Boeardi (1993). A preliminary report of changing Quaternary mammal faunas in subalpine New Guinea. *Quaternary Research* **40**: 117-126.

Hope, G.S. and Hope, J.H. (1976). Palaeoenvironments for man in New Guinea. *In* Kirk, R.L. and Thorne, A.G. (eds), *The biological origins of the Australians*: 29-53, Australian Institute of Aboriginal Studies, Canberra, A.C.T.

Hope, J.H. (1976). Fauna. *In* Hope, G.S., Peterson, J.A., Radok, U. and Allison, I. (eds), *The equatorial glaciers of New Guinea. Results of the 1971-1973 Australian Universities' Expeditions to Irian Jaya: survey, glaciology, meteorology, biology and palaeoenvironments*: 207-224, A.A. Balkema, Rotterdam, The Netherlands.

Hope, J.H. (1981). A new species of *Thylogale* (Marsupialia: Macropodidae) from Mapala rock shelter, Jaya (Carstensz) Mountains, Irian Jaya (Western New Guinea), Indonesia. *Records of the Australian Museum* **33**: 369-387.

Menzies, J.I. (1996). A systematic revision of *Melomys* (Rodentia: Muridae) of New Guinea. *Australian Journal of Zoology* **44**: 367-427.

Schodde R. and Mason, I.J. (1980). *Nocturnal birds of Australia*, (illustrated by J. Boot): 1-136, Lansdowne Press, Melbourne, Victoria.

Walton, D.W. (ed.) (1988). *Zoological catalogue of Australia.* **5**: Mammalia: i-x, 1-274, Australian Government Publishing Service, Canberra, A.C.T.

Manuscript received 9 March 1998; accepted 19 August 1998.