Table 2

U-series isotopic data for GG4.1 *Hexaprotodon* molar from Ngalau Gupin, Sumatra (errors are 2σ).

Sample	U (ppm)	232Th (ppb)	230Th/232Th	230Th/238U	234U/238U	uncorr. 230Th Age (ka)	corr. 230Th Age (ka)	corr. Initial (234U/238U)
HIP-1 (enamel)	1.977 ± 0.002	19.2 ± 0.1	193 ± 2	0.618 ± 0.004	1.122 ± 0.002	85.5 ± 0.8	85.3 ± 0.8	1.156 ± 0.002
HIP-2 (dentine)	6.94 ± 0.04	102 ± 1	103 ± 1	0.50 ± 0.01	1.067 ± 0.006	68.4 ± 1.5	68.0 ± 1.5	1.081 ± 0.007
HIP-3 (dentine)	9.72 ± 0.04	1.25 ± 0.04	10272 ± 338	0.44 ± 0.01	1.080 ± 0.004	56.1 ± 0.9	56.1 ± 0.9	1.094 ± 0.005
HIP-4 (dentine)	12.52 ± 0.01	18.1 ± 0.1	1077 ± 8	0.514 ± 0.003	1.096 ± 0.002	68.3 ± 0.6	68.2 ± 0.6	1.117 ± 0.003
HIP-5 (dentine)	12.32 ± 0.01	13.0 ± 0.1	1544 ± 13	0.539 ± 0.003	1.097 ± 0.002	72.8 ± 0.7	72.7 ± 0.7	1.119 ± 0.002

Note: Ratios in parentheses are activity ratios calculated from the atomic ratios, but normalized to measured values of secular-equilibrium HU-1 Pike et al. (2002). All errors are given at the 2σ level. 230Th ages are calculated using Isoplot EX 3.0 (Ludwig, 2003) with decay constants $\lambda_{238} = 1.551 \times 10^{-10}$ yr^{-1} (for 238U), $\lambda_{234} = 2.826 \times 10^{-6}$ yr^{-1} (for 234U) and $\lambda_{230} = 9.158 \times 10^{-6}$ yr^{-1} (for 230 Th), respectively (Cheng et al. 2000). 2σ errors in the uncorrected (uncorr.) ages were propagated directly from the uncertainties in the (230Th/238U) and (234U/238U). The corrected (corr.) 230Th age was calculated using the assumed bulk earth or upper crust value equivalent to the detrital 230Th/232Th activity ratio of 0.83 (Cheng et al., 2000; Pike et al., 2002; Ludwig et al., 2003).

leaching. This is confirmed by the finite AU-ESR ages obtained for all of them. In particular, the other two teeth from NG-A (SUM18-26a and SUM18-27a) yield much younger age estimates of around 40–50 ka compared with SUM18-21a. However, AU-ESR, EU-ESR and CSUS-ESR estimates are systematically within error for all samples, indicating that the potential occurrence of uranium leaching, or any other types of uranium uptake, has only a minimum influence on the calculated ESR results. This is because the dose rate is dominated by the contribution from the sediment. When considering both beta and gamma dose rate components coming from sediment sample SUM18-11 (scenario b), the resulting US-ESR age for SUM18-21b gets much younger by a factor >2 (57 +5–4 ka) and becomes consistent with SUM1826a & SUM18-27a

(Table 1). A somewhat similar observation can be made when using the sediment attached to SUM18-21 instead: all ages get much older, SUM18-21a and SUM18-26b being consistent (134 vs 130 ka), while SUM18-27b is younger by about 30 ka, but nevertheless 2σ consistent. This tooth displays the smallest D_E of the data set (15% and 37% lower than SUM18-21 & SUM18-26), which might be due to a locally less radioactive environment around the tooth in comparison with the other fossils. The significant age gap between scenario a and b for NG-A samples is simply due to the massive difference in the gamma dose rate derived from sediment associated to SUM18-21 (173 ± 14 Gy/a) and SUM18-11 (460 ± 35 Gy/a). Since SUM18-21a is the only tooth for which the original sediment attached to the tooth was collected, we may

Table 3

The representation of each taxa in NISP of the NG-A and NG-B assemblages.

Class	Order	Family	Taxon	Common name	NG-A NISP	NG-B NISP
Reptilia	Squamata	Varanidae	gen. et sp. indet.	Lizard	0	1
Aves	gen. et sp. indet.	gen. et sp. indet.	gen. et sp. indet.	Bird	0	3
Mammalia	Artiodactyla	Suidae	*Sus* sp.	Pig	23	77
			Sus scrofa	Crested pig	12	43
			Sus barbatus	Bearded pig	13	18
		Hippopotamidae	*Hexaprotodon*	Pygmy Hippo	1	1
			gen. et sp. indet.	Hippo	6	0
		Tragulidae	gen et sp. indet.	Mouse deer	1	0
		Cervidae	*Rusa* sp.	Sambar deer	0	4
			Muntiacus sp.	Muntjak	1	2
			gen. et sp. indet.	Deer	4	43
		Bovidae	gen. et sp. indet.	Cow	4	11
			Capricornis sumatraensis	Serow	0	1
		Moschidae	gen. et sp. indet.	Mouse deer	0	1
	Primates	Hominidae	*Pongo* sp.	Orangutan	13	40
		Cercocipithedae	*Presbytis*	Surili	0	16
			Macaca sp.	Macaque	3	25
		Colobinae	*Nasalis* sp.	Proboscis monkey	1	0
		Hylobatidae	*Symphalangus syndactylus*	Siamang	0	19
			Hylobates sp.	Gibbon	0	2
	Perissodactyla	Rhinocerotidae	*Rhinoceros unicornis*	Indian rhino	0	1
			Rhinoceros sondaicus	Javan rhino	0	1
			Dicerorhinus sumatrensis	Sumatran rhino	0	3
			gen. et sp. indet.	Rhino	6	8
		Tapiridae	*Tapirus indicus*	Tapir	4	7
	Carnivora	Ursidae	*Helarctos*	Sun bear	2	6
		Felidae	gen. et sp. indet.	Wild cat	0	9
			Panthera	Tiger	1	7
		Mustelidae	gen. et sp. indet.	Mustela	0	3
		Viverridae	*Paradoxurus*	Palm civet	0	6
	Chiroptera	Microchiroptera	gen. et sp. indet.	Bat	5	13
	Rodentia	Hystricidae	*Hystrix* sp.	Porcupine	14	56
			gen. et sp. indet.	Rat	0	3
	Proboscidea	Elephantidae	*Elephas* sp.	Elephant	1	2

reasonably consider it as being the most reliable age estimate for NG-A, and it is possible that sediment SUM18-11 has been collected from a locally weathered breccia within NG-A and may thus not provide an accurate estimate of the true gamma dose rate. The very similar radio-activity levels measured in SUM18-11 and SUM18-12 from NG-B, and the heavily weathered state of the breccia at NG-A, indirectly support this hypothesis.

Teeth SUM18-22a and SUM18-24a from NG-B return very close AU-ESR age estimates (60 ± 10 and 61 ± 2 ka). Although these results indicate that dental tissues have experienced uranium leaching, the uranium uptake modelling has only a very limited impact on the calculated ESR ages: EU-, AU- and CUS-ESR results are virtually the same (Table 1) for a given sample. Again, the dose rate is dominantly, and almost exclusively, driven by the external beta and gamma dose rate from the sediment. However, because the teeth were found at NG-B within the first 10 cm below ground surface, it may reasonably be considered that the infinite matrix assumption was not fulfilled, At a 10-cm depth, the tooth would receive about 88% of the gamma dose rate instead (Aitken, 1985). New age calculations based on this scenario (labelled "b" in Table 1), return results older by about 8 ka (+13%). Interestingly, a finite US-ESR age result of 68 + 7–6 ka (Table 1) may be obtained for SUM18-22b, while SUM18-24b yield ages of around 68 ka, whatever the uranium uptake model considered. We acknowledge that scenario b most likely underestimates the true dose rate: the contribu-tion of the air component in the gamma dose rate is not null, as it may include a non-negligible contribution from the Rn gas present in the cave, and from the gamma-rays from the sediment that are reflected by the limestone wall. Consequently, the true gamma dose rate is most likely somewhere between the two values used for scenarios a and b. The resulting ages may bracket the true age of the fossils assuming they have not been reworked from other deposits.

4.3. Taphonomic analysis

4.3.1. Taxonomic representation

In the NG-A assemblage, a total of 141 fossils were recovered, rep-resenting 17 genera and a minimum of 26 individuals (Table 3). In the NG-B assemblage, a total of 1313 fossils were recovered, representing 30 genera and a minimum of 80 individuals. Both loci produced a diverse suite of small to large herbivorous, omnivorous, carnivorous and dur-ophagous (bone feeding) animals. Mammals dominate both assem-blages, and a small number of bird, reptile and mollusc remains were recovered from NG-B. The bird, reptile and mollusc remains were not included in the taphonomic analysis. Fifteen taxa are shared between the NG-A and NG-B assemblages (*Pongo, Macaca, Sus scrofa, Sus barba-tus*, Rhinocerotidae, Cervidae, *Hexaprotodon, Muntiacus*, Bovidae, *Ele-phas, Helarctos, Hystrix, Tapirus indicus, Panthera tigris* and Chiroptera). Only two taxon are found exclusively in the NG-A assemblage (Trag-ulidae and *Nasalis*), while sixteen taxa were found exclusively in the NG-B assemblage (Felidae, *Rusa, Capricornis sumatraensis, Dicerorhinus sumatrensis, Rhinoceros unicornis, Rhinoceros sondaicus, Hylobates, Sym-phalangus, Presbytis, Paradoxurus*, Mustelidae, Rodentia, Varanidae, Viverridae, Moschidae and Aves; Fig. 10).

The representation of taxa in each deposit is provided in Tables 3–4 and Figure S2 & S3. In the NG-A assemblage, artiodactyls are the most abundant taxon (53.2% NISP), followed by primates (15.6% NISP), ro-dents (12.8% NISP), perissodactyls (10.1% NISP), bats (4.5% NISP), carnivores (2.8% NISP) and proboscideans (1% NISP). In the NG-B
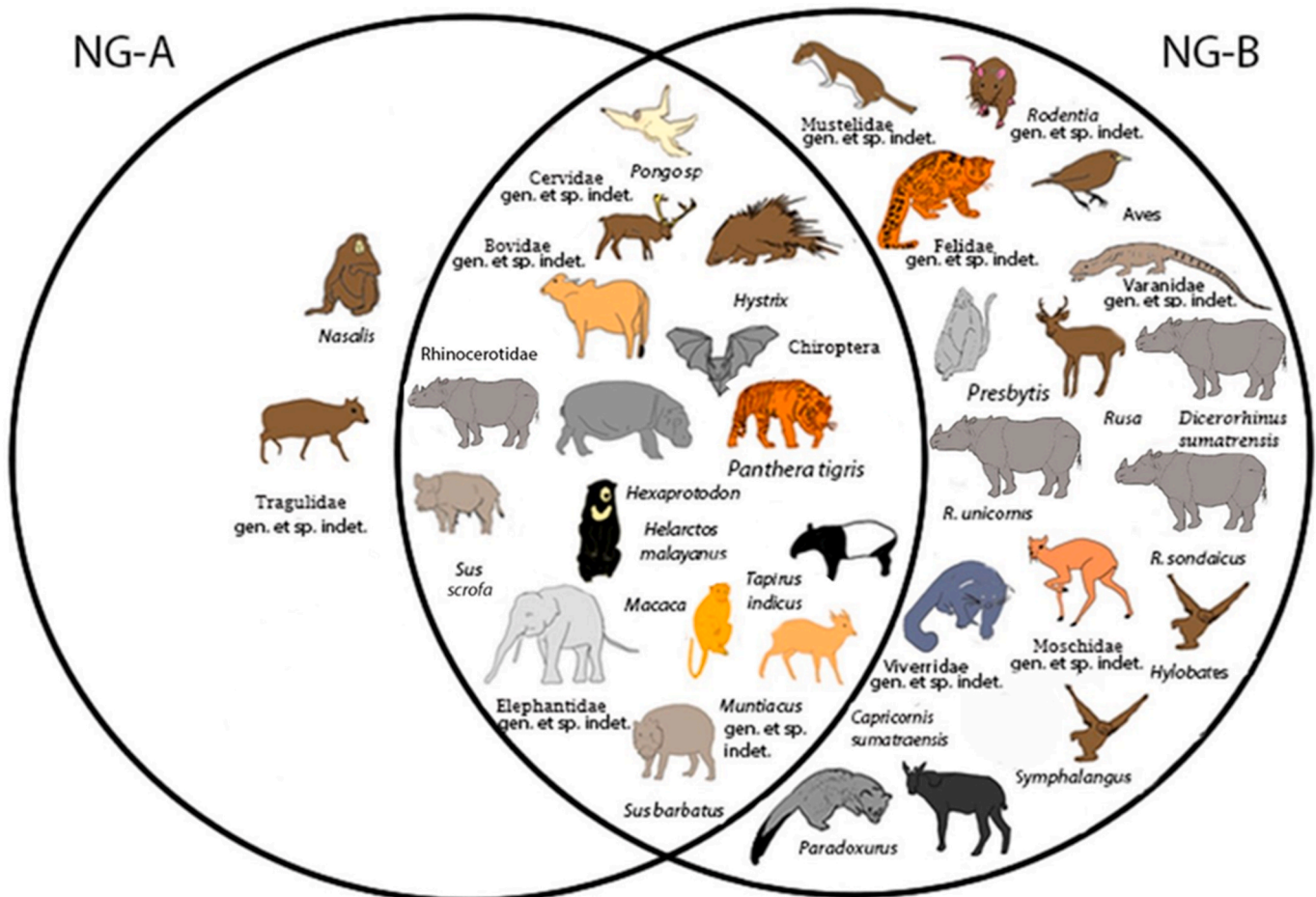

Fig. 10. Venn diagram of the relationship between the faunal representations in the NG-A and NG-B assemblages.

Table 4
Abundance of NISP of taxonomically identifiable teeth in the Ngalau Gupin collection according to taxon.

	NG-A molar NISP	NG-A premolar NISP	NG-A incisor NISP	NG-A canine NISP	NG-B molar NISP	NG-B premolar NISP	NG-B incisor NISP	NG-B canine NISP
Artiodactyl	22	16	3	2	107	61	9	5
Primates	12	1	1	1	49	26	15	6
Rodentia	4	0	5	3	42	8	21	0
Carnivora	1	2	0	0	8	18	0	0
Perissodactyl	1	2	0	1	12	2	0	0
Chiroptera	0	0	0	0	5	4	0	0
Total NISP	40	22	9	7	223	119	45	11

assemblage, artiodactyls are once again the most abundant (46.3% NISP), followed by primates (24.1% NISP), rodents (13% NISP), carnivores (7.6% NISP), perissodactyls (4.6% NISP), bats (3% NISP), birds (0.7% NISP) and proboscideans (0.5% NISP) and varanids (0.2% NISP). There is no difference in mammalian NISP between the two deposits (X^2 (6, N = 97,99.1) = 7.01, p = 0.32).

The most abundant taxon classified in the identifiable tooth specimens of the NG-B assemblage are artiodactyls (n = 200, 48% of NISP), followed by primates (n = 102, 24.4% of NISP), rodents (n = 53, 12.7% of NISP), carnivores (n = 30, 7.2%), perissodactyls (n = 20, 4.9% of NISP) bats (n = 9, 2.1% of NISP) and finally proboscideans (n = 2, 0.5% of NISP). Based on identifiable teeth, taxa are similarly represented in the NG-A assemblage (X^2 (7, N = 104,416) = 13.137, p = 0.07), with artiodactyls being best represented (n = 58, 55.7% NISP), followed by primates (n = 17, 16.3% of NISP), rodents (n = 14, 13.5% of NISP), perissodactyls (n = 12, 10.6% of NISP), carnivores (n = 3, 3% of NISP) and proboscideans (n = 1, 1% of NISP) (Fig. 12).

Given their proximity and the significant overlap in represented taxa, an interpretation that the NG-B assemblage originated from the NG-A breccias is our null hypothesis. This hypothesis is consistent with the favoured interpretation of the ESR/U-series data suggesting the two deposits are of a similar age. The greater species richness in the NG-B assemblage could simply be explained by its larger sample size.

4.3.2. Skeletal part representation

Isolated bone and tooth fragments dominate and make up 98% (n = 117) and 63% (n = 539) of the NG-A and NG-B total assemblages, respectively. Only 29 complete bones were recovered: 24 from NG-B and five from NG-A. The surviving complete elements from NG-B comprise phalanxes (n = 6), vertebrae (n = 4), and radii (n = 3), followed by calcanei, metatarsals, and humeri (n = 2) and a single metacarpal, rib, tibia, clavicle and scapula. Identifiable skeletal fragments from NG-B include two partial mandibles, one partial maxilla, three partial

vertebrae, 27 cranial fragments, three partial ribs and 38 long bone midshaft fragments. A single petrosal and four long bones attributed to the wings of Chiroptera were recovered from the NG-A breccias. All (n = 5) post-cranial elements in the NG-A deposit and 87.5% (n = 60) of those in the NG-B deposit belong to small mammals (e.g. bats, rodents, felids) and birds. Only three post-cranial remains from the NG-B assemblage can be assigned to larger mammals; a juvenile pig metatarsal and two primate phalanxes.

Teeth are abundant in both loci from Ngalau Gupin, and 87.4% (n = 104) and 72% (n = 417) of the dental material from the NG-A and NG-B deposits can be assigned to taxon. Molars, premolars, incisors, and canines make up 55% (n = 214), 30.6% (n = 119), 11.6% (n = 45), and 2.8% (n = 11) of all taxonomically identifiable teeth in the NG-B assemblage, and 50.6% (n = 40), 28.6% (n = 22), 11.7% (n = 9), and 9.1% (n = 7) of all taxonomically identifiable teeth in the NG-A assemblage (See Table 4 and Fig. 11). There is no statistical difference in the representation of tooth types between these the two deposits (X^2 (4, N = 389,77) = 4.54, p = 0.34), consistent with our null hypothesis.

4.3.3. Bone breakage

Most limb bone fragments in the NG-A assemblage exhibit right (n = 1, 6%), jagged (n = 3, 20%) and transverse (n = 5, 33%) fracture patterns consistent with fracturing of dry bones. Still, oblique (n = 5, 33%) and curved (n = 2, 13%) fracture patterns indicate that breakage also occurred while still fresh. Likewise, the NG-B long bones exhibit fracture patterns that indicate breakage occurred while the bones were fresh as well as dry. Many bones exhibit right (n = 21, 36.25%), jagged (n = 19, 49%) and transverse (25.5%, n = 11) fractures consistent with dry fracturing, while a number of oblique (27.5%, n = 16), smooth (n = 21, 51%) and curved (n = 11, 25.5%) fractures suggest fresh breakage of bones. Oblique/right (n = 21, 36.25%) and intermediate (n = 21, 49%) fractures were also recorded.
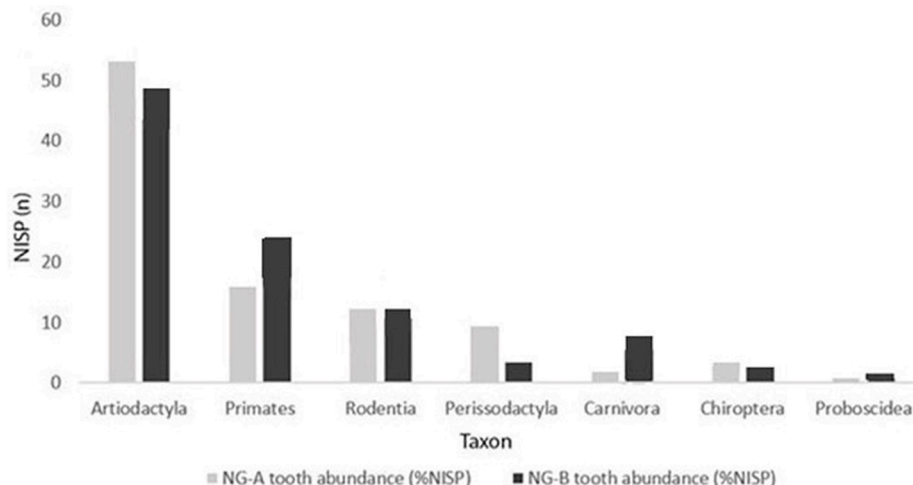

Fig. 11. The %NISP tooth abundance in each biological order of the NG-A and NG-B assemblages.
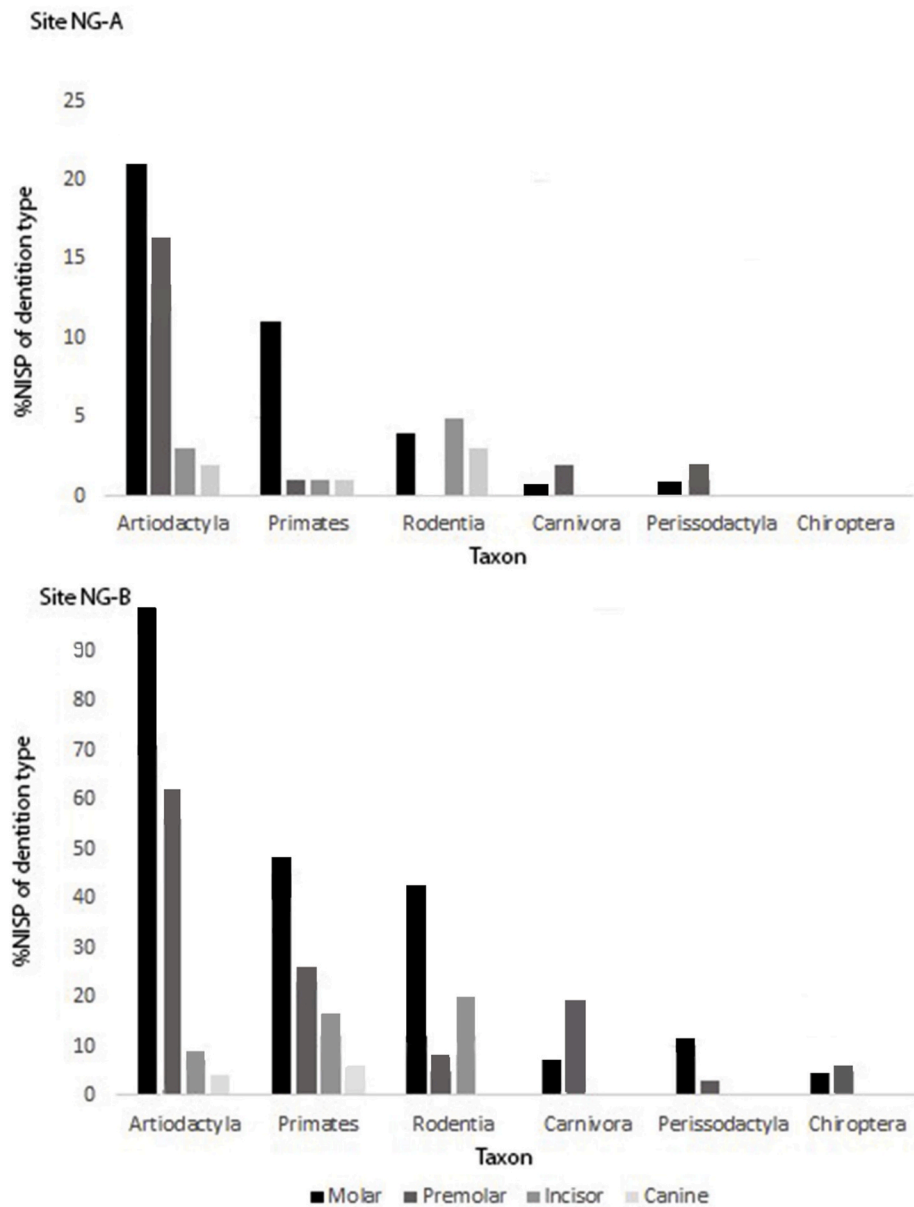
Site NG-A

Site NG-B

Fig. 12. The %NISP of each dentition type in each biological order of the NG-A and NG-B assemblage.

4.3.4. Nature of accumulation

There are no cut marks or intentional bone breakage, marks or modification, so we cannot relate the bone assemblage to human activities or bone collecting behaviours such as scavenging or hunting by humans nor stone tools. Three bones from loci NG-B exhibit marks that might be consistent with burning, but confirmation requires chemical testing not yet attempted. Nine species from Ngalau Gupin could theoretically have modified the assemblages: tigers (Brain, 1981; Haynes, 1983), porcupines (Thomas, 1971; Behrensmeyer and Hill, 1988), pigs (Olsen and Shipman, 1988), macaques (Sugiyama et al., 2009; De Marco, 2018), gibbons, felids (Andrés et al., 2012), palm civets, mustelids and rodents (Denys, 2002; Klippel and Synstelien, 2007; Pokines et al., 2017). A small blackened long bone fragment from the NG-B assemblage exhibits numerous small carnivore tooth pits and punctures across the midshaft (Fig. 13). These perforations average 1.1 mm in width and are prolific across the midshaft of the long bone. These perforations can be related to a small carnivore. There are numerous small carnivores present in the Ngalau Gupin deposits that are plausible agents for this damage, including mustelids, viverrids, felids, and varanids.

The second definitive biotic agent that can be confirmed in the Ngalau Gupin collections is the porcupine. Four specimens (2.9%) from the NG-A deposit exhibit gnawing, whereas a much greater proportion of 443 (35.3%) of the total specimens from the NG-B deposit exhibit gnawing. If these assemblages are distinct, it is possible this disparity is due to a much greater porcupine presence during the formation of the NG-B assemblage in comparison to NG-A. However, if NG-B formed as a result of the erosion and redeposition of material from NG-A it is more likely that porcupines only had access to scavenge NG-B specimens on the surface of soft sediments after erosion occurred, as NG-A specimens were shielded by a hard, indurate $CaCO_3$ deposit.

Four specimens from the NG-B deposit and a single specimen from the NG-A deposit display measurable trough marks which range from 2.6 to 6.0 mm, consistent with porcupine gnawing marks (Table S4; Fig. 13). Gnawing is restricted to the periphery of the teeth (partly due to the smaller size of the teeth) and bones. The trough marks are specifically located on the enamel-dentine junction on the sides of the teeth and the articular ends of long bones. Only seven teeth (2%) were missing
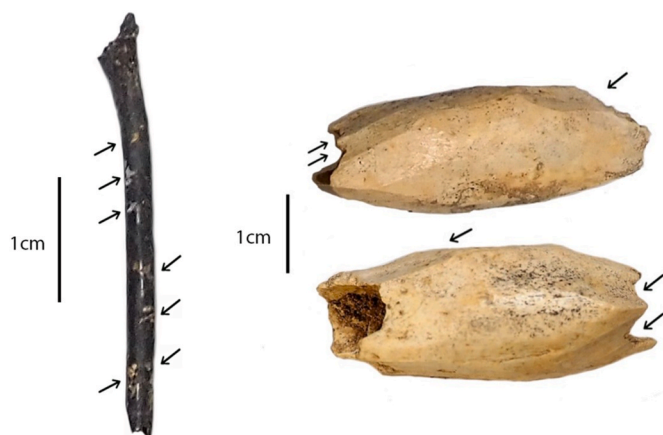
Fig. 13. (Left) Photograph of blackened long bone fragment NG4.16 from the NG-B assemblage exhibiting numerous tiny carnivore tooth pits, scores and punctures; (right) Photograph of visible gnawing marks on bone fragment NG27.10.

roots in the NG-A assemblage. In contrast, all but 80 (98%) teeth in the NG-B assemblage have a complete or partial absence of roots, and this is likely evidence of the preferential gnawing of tooth roots by porcupines (de Vos and Ciochon, 1996). The evidence of porcupine activity is further supported by the presence of this rodent's dental remains in both assemblages.

4.3.5. Depositional setting

Overall, 4% (n = 7) of all specimens from the NG-A assemblage and 24.24% (n = 311) of all specimens from the NG-B assemblage have partial mineral staining or discoloration on their surface area. The staining occurs in dull black and orange-yellow tones, which suggests mineral staining is caused by the presence of manganese oxide and iron (Dupras and Schultz, 2013). The superficial coating is derived from circulating water, dissolved by groundwater in the presence of CO_2 and precipitated by CO_2 loss, oxidation, and evaporation (López-González, 2006). Weathering of bone and tooth specimens was observed in both assemblages. Most specimens in the NG-A assemblage exhibit stage one weathering (98.2%, n = 575) and a small number reach maximally stage three (1.8%, n = 10). In the NG-B assemblage, 59% (n = 256) exhibit stage one weathering, followed by 37.8% (n = 163) in stage three and 3.2% (n = 12) in stage four. Only 3% (n = 16) of the weathered specimens from site NG-B exhibit cortical exfoliation. Abrasion is also evident in both assemblages. In the NG-A assemblage, 17% (n = 31) of remains have first stage abrasion, and no other stages are evident. In the NG-B assemblage, 19% (n = 245) of the NG-B assemblage exhibits first stage abrasion, and a single specimen exhibits third stage abrasion.

4.3.6. Age category

In the NG-A assemblage, ungulates (i.e., suids, cervids, bovids) are best represented by adults (MNI = 7), followed by seniors (MNI = 3) and juveniles (MNI = 1), although it's worth noting the very small sample size. Primates are best represented by adults (MNI = 4), a single senior, and no juveniles. In the NG-B assemblage, ungulates are best represented by adults (MNI = 14), followed by seniors (MNI = 7) and juveniles (MNI = 3). Likewise, primates are best represented by adults (MNI = 10), followed by seniors (MNI = 6) and no juveniles. The most abundant age class evident in the taxonomically identifiable teeth are significantly different between the localities (X^2 (3, N = 389, 104) = 22.13, p = <0.001), with the number of adult teeth proportionally less represented in NG-B, (adults, n = 258; seniors, n = 122; juveniles, n = 9) compared to NG-A (adults, n = 93; seniors, n = 9; juveniles, n = 2). In the NG-A assemblage, carnivores (e.g. felids, viverrids and ursids) are best represented by adults (MNI = 2), with no seniors and juveniles

present. In the NG-B assemblage, carnivores are once again best represented by adults (MNI = 9), followed by seniors (MNI = 5) and no juveniles. In the NG-A assemblage, rodents are best represented by adults (MNI = 1) and no juveniles or seniors. In the NG-B assemblage, rodents are best represented by adults (MNI = 3) and seniors (MNI = 3), and no juveniles. Taken together, adults are best represented at Ngalau Gupin, followed by seniors, and very few juveniles. The underrepresentation of juvenile teeth may, however, be due to a greater susceptibility of juvenile bones and teeth to destruction (Lyman, 1994; Munson, 2000; Munson and Gariewicz, 2003). Indeed, all surviving deciduous teeth originate from large animals with thick enamel and dentine such as *Tapirus indicus*, Cervidae, Rhinocerotidae and Elephantidae.

5. Discussion

This study represents the first taxonomic, taphonomic, and chronological study of fossil faunal assemblages from Ngalau Gupin Cave in the Padang Highlands, Sumatra, and one of only several such studies for the entire island. This research acts as an important contribution to elucidating the processes of site formation that determine fossil preservation state in this tropical sub-region. Our taphonomic assessment of the assemblages revealed a complex history of carnivore and porcupine accumulation and post-depositional attrition.

5.1. Comparative study of NG-A and NG-B

The fossils from the NG-B unconsolidated sediments on the cave floor were recovered from directly below the NG-A fossiliferous breccia and there is a remarkable amount of taxonomic overlap between the two deposits. Furthermore, the taxa are similarly represented in terms of abundance, necessitating a consideration of whether these are distinct fossil assemblages, or if NG-B formed because of the erosion and redeposition of material from NG-A (our null hypothesis).

Combined observations of speleology, geology, taphonomy and species presence suggest that the NG-B locus is most likely the result of erosion from the NG-A breccias. The fauna in both sites consists of predominantly modern taxa, with most representatives still living in the area (e.g., *Macaca*, *Pongo*, *Panthera tigris*, and *Elephas*) or elsewhere in Southeast Asia (e.g., *Rhinoceros unicornis* and *Rhinoceros sondaicus*). The sole exception to this is the presence of *Hexaprotodon*, which represents the first time hippos have been recovered from Sumatra.

Both assemblages are comprised mostly of isolated dental remains and heavily fragmented bone specimens. Wolff (1973) suggested that assemblages dominated by isolated teeth and fragmented bone have often undergone hydrodynamic sorting. Despite the evidence for wet conditions, the presence of complete small mammals remains suggests that water flow through the cave was neither regular nor particularly strong. High energy waterflow, combined with the angular limestone clasts that characterise the Ngalau Gupin sediments, is likely to have destroyed fragile small animal remains (e.g. Andrews and Cook, 1990).

Water action, however, is not the only process that can create this bias of isolated dental remains. Prevalently in Southeast Asia, rodents, and in particular porcupines, are renowned accumulators of bones and teeth, and there is evidence for porcupine gnawing, as well as porcupine fossils, at Ngalau Gupin. The degree of transformation in the NG-B assemblage suggests that porcupines are likely to play a significant role in the modification and probably in the accumulation of the assemblage. Prolific gnawing behaviour is related to honing porcupine incisors and may also provide some essential nutrients (Brain, 1981). Porcupine accumulations can be abundant in the vicinity of a carnivore lair and bones can be collected from many different predators to reveal a broad spectrum of plausible prey animals and predators (Brain, 1981; O'Regan et al., 2011).

Adult ungulates and primates are most common in Ngalau Gupin deposits. Size of the prey is correlated with the size of carnivores. Regarding ungulates, this may reflect predation by large carnivores such

as tigers. Tigers have a broad diet that includes a variety of ungulates and primates (O'Brien et al., 2003) and they are known to preferentially target adults averaging 91.5 kg (Karanth and Sunquist, 1995). Hominins are also known to preferentially target adult individuals (e.g. Bar-Oz et al., 2005; Zhang et al., 2009) but a hominin role in the accumulation of bones at Ngalau Gupin can be excluded based on (1) the lack of anthropogenically modified bone and (2) the age of the Ngalau Gupin material, which pre-dates the earliest known hominin presence in Sumatra. However, we acknowledge that due to the elements preserved in this assemblage and the reconstructed taphonomic pathways, anthropogenic modifications and/or tools, if they had been present, would be very unlikely to preserve. There are several potential predators of these species in SE Asia including birds of prey and cats (e.g. Van Schaik and Van Noordwijk, 1985; McGraw and Berger, 2013). Given the scarcity of bone remains and associated bone surface modifications it remains difficult to confidently comment on the likely contributor of the death assemblage leading to the Ngalau Gupin collection; however, the ungulate and primate age profiles are most consistent with the hunting behaviour of a large carnivore.

Small animals like rodents and birds tend to have very different preservational pathways compared to larger animals (Andrews and Cook, 1990). One of the main accumulating agents of small animal remains in cave deposits are raptors (e.g., owls) which deposit dense concentrations of small animal bones at their nesting sites in the form of pellets (Andrews and Cook, 1990; Hawkins et al. 2017, 2018). Perhaps the clearest sign of raptor predation is acid corrosion resulting from gastric acid acting on bones following consumption (Fernández-Jalvo et al., 2016). However, none of the Ngalau Gupin small animal remains exhibit acid corrosion and therefore accumulation by a raptor appears unlikely.

The bones in the Ngalau Gupin collection exhibit fracture patterns consistent with both green and dry fracturing of bone. The green fractures may be the result of carnivore processing, further evident in the small carnivore punctures seen on one of the small mammal specimens. The dry fracturing may have occurred at a later time, and may have been caused by trampling, rock fall, and/or burial. In some karstic sites (like Ma U'Oi in Vietnam; Bacon et al., 2004, 2006), two types of assemblages can be observed: one of only large mammals, and another of only microfauna. This is due to different dynamics of deposition: the assemblage can be a mixture of large mammal fossils and more recent microfauna from the surface. Our observations suggest the very small mammal bones in Ngalau Gupin (i.e. bats) looked fresh and were probably more recent than the other taxa.

Tropical caves are prone to inundation by water and high levels of humidity, making them less-than-ideal places for the long-term preservation of bones (Andrews and Cook, 1985; Fernández-Jalvo et al., 2010; Morley and Goldberg, 2017). The precipitation of manganese oxide on fossil surfaces in both assemblages indicates the cave environment was wet and mildly alkaline, which is supported by the presence of fossil molluscs. In addition, a small number of NG-B fossils exhibit cortical exfoliation, a common indicator that fossils were exposed to repeated cycles of wet-dry conditions. Staining is less common in the NG-A assemblage and this may be because these fossils were protected by the calcium carbonate cement.

Taken together, our data suggests that the mammal remains were initially deposited in the landscape surrounding the cave, perhaps as the result of large carnivore predation. Following this, animal remains were modified in the cave by porcupine gnawing, leaving mostly teeth. The remains were then cemented into the NG-A assemblage forming consolidated breccia. The significant overlap in the faunal representation in both assemblages, as well as evidence for more pronounced staining, damage, and weathering of the specimens from NG-B, suggest that fossils eroded out of NG-A and were redeposited into the unconsolidated NG-B sediments directly below, following a small amount of lateral and vertical movement aided by low energy water flow. Most small animal remains, however, may have been deposited by small

carnivores, although positive evidence for this is based on a single specimen and so it is unclear precisely how small mammal remains accumulated.

5.2. Age of Ngalau Gupin

In the first instance, the significant age difference between SUM18-21a from NG-A and SUM18-22a from NG-B (i.e., the two samples providing finite combined US-ESR age estimates), might be used as evidence suggesting that the fossil assemblages from the two loci are not coeval. However, this may also be a calculation artefact due to the very specific features displayed by the teeth. When using the sediment sample SUM18-11 collected from NG-A, the resulting age (SUM18-21b) of about 60 ka becomes very close to those obtained from NG-B. In other words, the apparent age difference is only due to the sediment samples used in the dose rate evaluation. Although sediment samples collected at NG-A and NG-B display very different radioelement concentrations, the overall gamma dose rate that may be derived are virtually the same (465 vs 460 µGy/a). Additionally, although the ESR data do not show any major differences between NG-A and NG-B teeth, the U-series instead seem to indicate slightly different uranium uptakes (See Table 1).

This may well originate from different depositional histories, or simply be the results of a more recent change in the geochemistry of the surrounding environment, as the result of erosion and reworking from NG-A. If reworking can be unambiguously demonstrated, then the ESR age results obtained for NG-B fossils should be taken with extreme caution. By principle, the ESR dose rate reconstruction is based on the assumption that the current sedimentary environment has prevailed throughout the sample's burial history. If not, then it is virtually impossible to properly and accurately evaluate the gamma dose rate associated to the tooth that is being dated. This issue is even more crucial in the present case, where the dose rate from the sediment represents >90% of the total dose rate.

SUM18-21a most likely provides the most reliable chronological constraint for Ngalau Gupin fossil assemblage because (i) it comes from the original breccia deposits of NG-A, which is less likely to have been impacted by sedimentary reworking processes, and (ii) it was the only tooth for which the sediment was directly attached. Dental tissues represent <10% of the total dose rate, which is thus mostly dominated by the component from the sediment. Consequently, sources of uncertainty associated with the external dose rate evaluation may significantly impact the calculated ESR ages. In particular, we have identified two crucial parameters in that regard: (i) the water content and (ii) the vicinity of the limestone wall.

Age calculations were initially performed using the current water content (25 $\pm$ 5%) measured in sediment samples SUM18-11 and SUM18-12. However, one may reasonably consider that humidity conditions may have changed over time. Consequently, some sensitivity tests were performed in order to evaluate the impact of the assumed water content on the calculated ESR ages (Fig. 14a). For sample SUM18-21a, increasing the water content (WC) by +5% and 10% would make the age older by +8% and 18%, respectively. The age estimates would increase from ca. 134 ka (25% WC) to ca. 145 ka (30% WC) and ca. 158 ka (35% WC). The latter would still overlap within 2-σ with the initial US-ESR age calculation performed for sample SUM18-21a and considering water content values > 35% seems presently purely speculative. Instead, when using a value of 15%, which approximately corresponds to the value measured in the breccia deposits from the nearby Sumatran site of Lida Ajer (Westaway et al., 2017), the combined US-ESR age result decreases by about 13% and reaches 116 + 10–9 ka.

Initial age calculations were performed assuming that 100% of the gamma dose rate was coming from the breccia. However, field observations suggest that the limestone wall was <30 cm from the tooth, most likely around 15 cm. This may impact the accuracy of the gamma dose rate, as limestone is typically not very radioactive compared to sediment, which may be approximated in first instance as a virtually inert
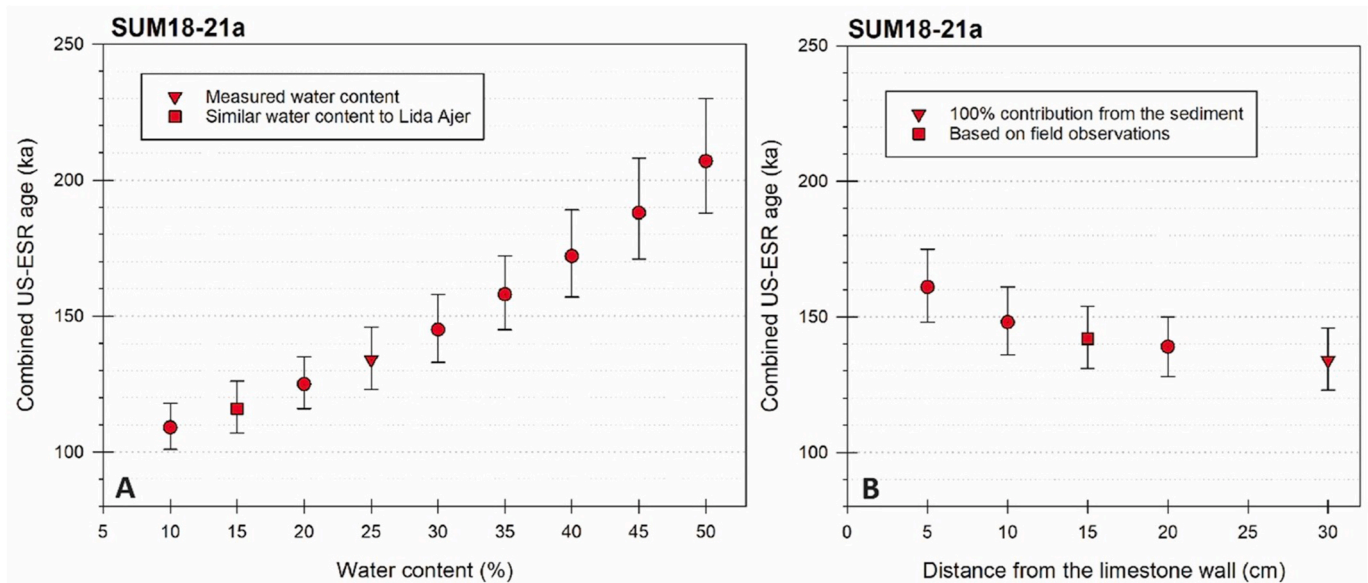
Fig. 14. Age sensitivity tests for tooth SUM18-21a. A: Impact of water content (% wet weight) on calculated combined US-ESR age estimates. The measured water content is 25% (values corresponding to the SUM1821a age calculation displayed in Table 1). The 15% (% wet weight) correspond approximately to the value measured in Lida Ajer (Westaway et al., 2017). B: impact of the distance from limestone on the calculated combined US-ESR age estimates. The 30-cm distance corresponds to the calculation displayed in Table 1 for SUM1821a.

material. Consequently, some age simulations were performed by considering the relative distance to limestone and correcting the gamma dose rate accordingly using Aitken (1985). As expected, the closer to the limestone wall and the older the age gets (Fig. 14b). However, when considering the 15 cm distance, the combined US-ESR age gets slightly older by only about 8 ka (+6%) but remains nevertheless within error. Although we acknowledge an inherent uncertainty around the gamma dose rate, given the heterogeneity of the deposits and the absence of *in situ* measurements, these calculations illustrate the limited impact of the limestone wall vicinity on the calculated ages.

In summary, combined US-ESR dating of SUM18-21 sample indicate that the age of fossil assemblage at Ngalau Gupin lies somewhere between ~160 ka and ~115 ka, depending on the long-term water content value selected for the dose rate evaluation.

5.3. Implications of Ngalau Gupin study

Our results correlate the Ngalau Gupin fauna with either the second half of the MIS 5 or the beginning of MIS 6. The faunas from this site are essentially modern, and most likely represents a rainforest environment much like found locally today. Nevertheless, the site records several important extirpations of large bodied taxa. This study indicates that the Indian and Javan rhinos *Rhinoceros unicornis* and *Rhinoceros sondaicus* and the proboscis monkey *Nasalis* were present in the Pleistocene of the Padang Highlands. It also provides the first evidence of *Hexaprotodon* from Sumatra. A detailed and quantitative analysis of the palaeoenvironments represented by the Ngalau Gupin assemblage is needed to provide insights into plausible extinction mechanisms operating on the island; however, it is interesting to note that neither *Hexaprotodon*, *Nasalis,* nor *Rhinoceros unicornis* have been recovered from the younger site of Lida Ajer, which incidentally hosts the earliest record of *Homo sapiens* on the island (Westaway et al., 2017).

Within the wider context of the Southeast Asian faunal assemblage, Ngalau Gupin shares similar faunal elements with other near-contemporaneous sites such as Punung in Java (Westaway et al., 2007), Tham Wiman Nakin in Thailand (Tougard, 1994, 1996, 1998; Suraprasit et al. 2016, 2020), Tam Hang South in Laos (Bacon et al., 2015), and Nam Lot and Coc Muoi (Bacon et al., 2018) in Vietnam. Lowered sea levels during the latter part of MIS 6 and into MIS 5 may

have promoted connections, faunal migrations, and faunal turnovers between these different regions (Long et al., 1996).

When compared to the site of Ngandong in Java, Ngalau Gupin differs considerably in terms of the fauna present and environments that were likely present. While several modern taxa are found in both Ngalau Gupin and Ngandong, including *Macaca fascicularis, Panthera tigris, Tapirus indicus* and *Rhinoceros sondaicus*, Ngandong nevertheless contains several extinct species that are not seen in Ngalau Gupin including *Stegodon trigonocephalus, Bubalus palaeokerabau, Sus macrognathus*, and *Homo erectus* (Rizal et al., 2020). The traditional view has been that modern rainforests appeared in Java, and by inference Sumatra, around the time of the deposition of Punung, and following on from the open woodlands associated with Ngandong (de Vos et al., 1983; Westaway et al., 2007). The Ngalau Gupin record, however, indicates a largely modern rainforest fauna existed in Sumatra prior to Ngandong. This suggests that rainforest persisted at least at the periphery of Sundaland (Ngalua Gupin, Punung) during periods when open woodland environments dominated the interior of the exposed Sunda shelf.

6. Conclusion

Ngalau Gupin represents a significant new palaeontological locality in Southeast Asia. Excavation of the NG-A and NG-B loci within the cave produced a rich, diverse suite of faunal remains, and produced the first evidence of *Hexaprotodon* in the Sumatran fossil record. Our results indicate that the NG-B assemblage was redeposited after being eroded from the NG-A breccias. Direct dating of the faunal assemblages suggests a late MIS 6 or early MIS 5 age. Additionally, our results provide an important case study on the limitations of dating in the complex cave environments, a subject that has important implications for interpreting fossil records from the region (e.g. Westaway et al., 2007; Bacon et al., 2008; O'Connor et al., 2010, 2017; Louys et al., 2017). The taphonomic data indicate that the Ngalau Gupin collection is composed of an assemblage with at least two different taphonomic pathways. The medium-to large sized mammal dental remains appear to represent a prime-dominated death assemblage accumulated by large carnivores and subsequently gathered by porcupines, whereas the small mammal post-cranial material may have been accumulated by smaller carnivores. Our analysis of the taphonomic and depositional history of Ngalau

Gupin fossil remains, within a detailed speleological and geochronological framework, provides important first insights into a diverse Pleistocene megafauna community from before human arrival in Sumatra.

Author contributions

Data availability

The data used to support the findings of this study are available with the paper and its supplementary files.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2021.05.005.

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