



An evaluation of evidence for utilization of cave habitats by terrestrial mammals in Meghalaya, northeast India

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Abstract: Based on evidence collected over the last three decades of speleological explorations in Meghalaya, the present study evaluates records of terrestrial mammals (i.e. non-bats) from within Meghalayan caves. Specifically, it looks for evidence of a distinct cavernicolous association. Such associations are likely to be linked to species accessing resources offered by caves in terms of refuge or shelter, access to water or opportunities for foraging. Over 100 records covering about 80 separate caves were collated and evaluated to distinguish evidence of presence due to direct cave association from mere accidental presence (e.g. carcasses washed in on floods). A rat species (*Leopoldamys edwardsi*) was found to have a very close association with caves with evidence of nesting and feeding underground. Porcupines also utilize the caves regularly, and we assume that they do so primarily for shelter and predator avoidance. The disproportionate frequency of occurrence of primate skeletal remains within caves suggests that their presence is not due purely to chance. We speculate that the steep rock in and around cave entrances may be used by primates as a refuge from ground-based predators and increase their vulnerability to entrapment within the caves. Other evidence suggests that various carnivorous mammals (including cats, civets and mongooses) enter caves occasionally, presumably for the purpose of hunting. Besides being attracted by the prey available at bat colonies they may also gain access to aquatic prey in the pools and streams of the caves.

Keywords: Edwards’s Long-tailed Giant Rat; Malayan Porcupine; Asiatic Brush-tailed Porcupine; Rhesus Macaque; Capped Langur; Indian Civet; Palm Civet; Fishing Cat; Leopard Cat; Asiatic Black Bear.

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Introduction

Meghalaya State in the northeastern corner of India (Fig.1) falls within the Indo-Burma biodiversity hotspot (Mittermier *et al.*, 2004) and supports correspondingly high levels of biodiversity (e.g. Pawar *et al.*, 2007). The combination of unusually high rainfall and the presence of a well-developed band of Eocene limestone along the southern fringe of the elevated Meghalaya plateau has resulted in extensive karstification (Prokop, 2014), with the most extensive cave development known in the Indian Subcontinent (Gebauer, 2008; Tewari, 2011; Arbenz, 2013; Arbenz, 2016; Lamare and Singh, 2016; Arbenz, 2017). The scientific interest of the Meghalayan caves is exemplified by the recent recognition of the Meghalayan Age/Stage within the Holocene Epoch/Series (Walker *et al.*, 2018).

The use of natural limestone caves as roost sites by bats is known to be widespread globally (MacSwiney *et al.*, 2007; Perry, 2013), and many Meghalayan caves support abundant and diverse bat populations (Harries *et al.*, 2008; Saikia *et al.*, 2018). Habitual usage of cave habitats by mammal species other than bats is, however, far less commonly recorded.

Although no troglobitic mammal species are known, various species are reported to utilize caves regularly. Potential reasons for mammals accessing caves may include shelter, nesting, hibernation, predator avoidance, access to water or the opportunity to forage for food. Examples of mammals known to utilize caves globally include bats, rats, skunks, raccoons, opossums, bears, leopard, porcupines, primates and badgers (Redmond and Shoshani, 1987; McGrew *et al.*, 2003; Montalvo, 2017; Vernes and Devos, 2022).

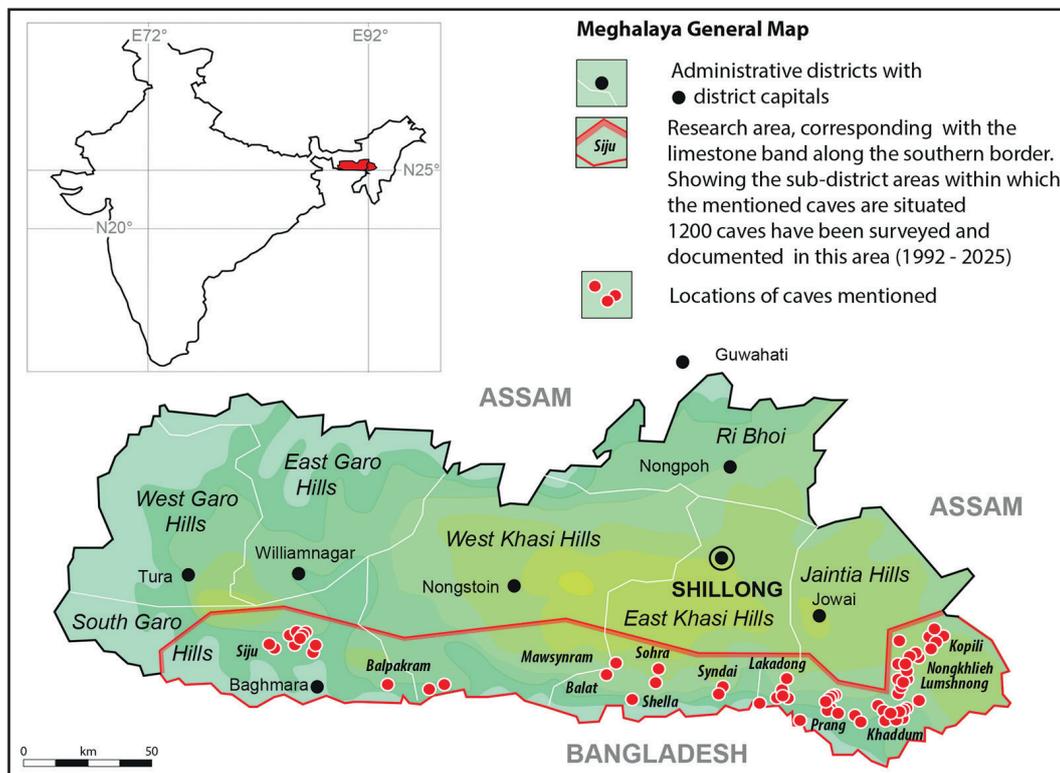


Figure 1: Overview map indicating location of Meghalaya, the southern limestone band (outlined in red) and the caves featured in this report.

There is limited documentation of terrestrial (non-bat) mammals in Indian caves. One study relates to Dandak Cave in Chhattisgarh (Biswas and Shrotriya, 2011). This provides evidence that Small Indian Civet (*Viverricula indica*) are regular visitors to the cave entrance area and predate the bats present in the cave. The study also reveals evidence of Indian Crested Porcupine (*Hystrix indica*) habitation, specifically dens and quills, within the cave’s interior. Another study, from caves in the Andaman Islands (Mane and Manchi, 2018), shows the common presence of Masked or Himalayan Palm Civet (*Peguma larvata*) and Large Indian Civet (*Viverra zibetha*) within the caves. An examination of civet scat within the caves indicated a primarily vegetarian diet. Civets are, however, opportunistic omnivores and Mane and Manchi (2018) note the possibility that they were also feeding on fallen bats or swiftlets within the caves.

The seminal 1922 study of Siju Cave in Meghalaya (Kemp and Chopra, 1924) reported the presence of rats and a cat (Kemp, 1924). Rats were noted as being ‘common’, with footprints frequently seen deep within the cave. They attributed the species to the Himalayan Field Rat (*Rattus nitidus*). Prints of a small unidentified cat species were noted at various locations deep within the cave. More recent publications are based on opportunistic records gathered during speleological explorations in Meghalaya. Little detail on mammals is provided by Harries *et al.* (2008), although they highlight the presence of rats and porcupines associated with caves, and mention that a range of mammalian skeletal remains has been found. According to Saikia *et al.* (2023) records exist of eight species of non-flying mammals from the Meghalayan caves. The current study draws upon the same resource of cave exploration records, with the aim of providing a more-comprehensive account of the utilization of Meghalayan caves by non-flying mammals.

Methods

Evidence of mammal occurrence within Meghalayan caves was gathered from an extensive archive of cave mapping reports and photographs. Many of these records were collected on an opportunistic basis by explorers focussed on cave mapping rather than on systematic recording of biological data. It should be recognized that this raises the possibility of under-reporting of inconspicuous signs of mammal presence. In total, there are 123 separate records spanning a 33-year period from 1992 to 2025 and including about 80 separate caves (Fig.1).

Records of mammals in the caves can be viewed as falling into two broad categories. First there are records that indicate current or recent animal presence in the caves. Such records might include sightings of live animals, prints, scat or nest material. The second category consists of records of bones, found within caves, that could be of recent or of ancient origin and might have occurred due to chance wash-in from surface habitats.

The primary interest of the current study was in seeking evidence of species having a specific association with caves, rather than those accidentally present. Evidence of cavernicolous behaviour would be strong where there was a high frequency of records indicating current or recent presence in the caves. Skeletal remains would become significant where the frequency of records of the species is higher than would be expected purely from chance wash-in from surface habitats.

Results

Overview

The records were grouped into major categories as shown in Table 1. This shows total number of records per category and gives a breakdown of the number of records indicative of current / recent presence in the caves as opposed to presence of skeletal remains.

Category	Recent (e.g. live animals, nests, prints, etc.)	Skeletal remains only	Total records
Rat	35	7	42
Porcupine	16	3	19
Primate	4	12	16
Small carnivore	13	6	19
Large herbivore	0	14	14
Bear	2	4	6
Other taxa	1	6	7
		Total	123

Table 1: Number of records of mammals associated with caves, broken down to major categories and indicating whether the records indicate recent presence or only the presence of skeletal remains.



Figure 2: A pair of live Giant Rats (*Leopoldamys edwardsi*) in Krem Khlaw Song, Jaintia Hills, 2011. [Photo: Thomas Arbenz.]

Rats

Records of rats constitute slightly more than a third of the records of mammals in Meghalayan caves and over 80% of the rat records indicate current or recent occupancy of the caves. Where positive species identification was possible from photographic evidence or examination of skulls (12 of 42 records) all were recognized as Edwards’s Long-tailed Giant Rat (*Leopoldamys edwardsi*). A further 7 visual records are also regarded as consistent with this species, although 2 visual records reported a smaller rat, consistent with the Himalayan White-bellied Rat (*Niviventer niviventer*).

The records include 20 where live individuals were sighted within a cave (Fig.2). In 11 of the 20 cases 2 or more individuals were present. Nests built by the giant rats were commonly encountered (17 records). These nests are highly distinctive in appearance, with the form of neat, bowl-shaped structures lined with leaves (Fig.3). Less commonly recorded evidence of rat presence includes footprints (3 records), scratch marks from claws (3 records) and faeces (5 records). Foraging scrapes provide another indication of rat presence.



Figure 3: Giant Rat nest in Krem Bsein, Jaintia Hills (Assam border), 2011. [Photo: Manuel Ruedi.]

These consist of small shallow excavations typically seen in banks of sediment containing vegetation deposited by floods; they occur widely but are rarely noted (3 records). Camera trap footage within a cave has provided evidence of *L. edwardsi* apparently foraging on such sediment banks. Another camera trap, deployed outside a cave entrance, however, showed a pair of *L. edwardsi* leaving the cave regularly each night, presumably to forage in the surrounding forest. Rat skeletal remains were also recorded more rarely (7 records), including 3 cases where examination confirmed the species identity as *L. edwardsi*.

Notes on location within the caves indicate that giant rats are by no means restricted to areas close to cave entrances, and evidence of rat presence has been noted hundreds of metres from the nearest known entrance. Records indicate their common occurrence in caves and include at least 35 distinct caves with rat records confirmed. They show a broad distribution within Meghalaya, with records representing all three main ranges of the Jaintia, Khasi and Garo hills. A list of all records relating to rats is presented in Table 2.

Nature of record (with ID where practicable)	Location	Source
Live animals (2 individuals), nest and faeces. Consistent with <i>Leopoldamys</i> .	Synrang Pamiang, Jaintia Hills.	1999. Note by Christian Fischer.
Nest. Confirmed as <i>Leopoldamys edwardsi</i> .	Krem Shrieh (Tangnub), Jaintia Hills.	2000. Written record and photograph, Tony Jarratt and Mark Tringham.
Skull.	Krem Shynrong Labbit, Jaintia Hills.	12/02/2001. Written record, Dan Harries.
Skull.	Krem Umthloo, Jaintia Hills.	13/02/2001. Written record, Dan Harries.
Live animals (2 individuals) and nest.	Krem Umblei, East Khasi Hills.	2002. Written record, Tony Jarratt.
Live animal seen on leaf nest. Consistent with <i>Leopoldamys</i> .	Et Hati entrance, Synrang Pamiang, Jaintia Hills.	2003. Note by Tony Jarratt.
Live animal seen on leaf nest. Consistent with <i>Leopoldamys</i> .	Teteng Kol, Garo Hills.	2003. Note by Tony Jarratt.
Skull. (uncertain record "large rodent")	Saisidung Khur, Jaintia Hills.	2005. Written record, Georg Baeumler.
Nest. Confirmed as <i>Leopoldamys edwardsi</i> .	Krem Lawkhlieng, East Khasi Hills.	04/03/2007. Written record and photograph, Daniel Gebauer.
Live animal. Consistent with <i>Leopoldamys</i> .	Krem Khnai Um Krypong, Jaintia Hills.	2010. Written record, Estelle Sandford.
Live animals (3 individuals). Confirmed as <i>Leopoldamys edwardsi</i> .	Krem Khlaw Song, Jaintia Hills (Assam border).	2011. Written record and photograph, Oana Chachula.
Nest.	Krem Bsein 1, Jaintia Hills (Assam border).	2011. Written record, Nicola Bayley.
Skull. Confirmed as <i>Leopoldamys edwardsi</i> .	Krem Bsein II, Jaintia Hills (Assam border).	17/02/2011. Photograph, Manuel Ruedi.
Live animal and leaf nest. Confirmed as <i>Leopoldamys edwardsi</i> .	Krem Bsein, Jaintia Hills (Assam border).	17/02/2011. Written record and photograph, Manuel Ruedi.
Live animal. Consistent with <i>Niviventer</i> .	Krem Khung, Jaintia Hills.	2013. Written record, Khlor Mukhim.
Skull. Confirmed as <i>Leopoldamys edwardsi</i> .	Krem Lymbiat, Jaintia Hills.	20/02/2014. Written record and photograph, Manuel Ruedi.
Nest and faeces. Consistent with <i>Leopoldamys</i> .	Krang Lapad (upstream), Jaintia Hills.	21/02/2014. Written record, Dan Harries.

Table 2 (part): Records indicating evidence of rats in Meghalayan caves, including summary details of record, location and source of information. [Continued below...]

Nature of record (with ID where practicable)	Location	Source
Live animal. Consistent with <i>Leopoldamys</i> .	Krang Lapad, Jaintia Hills.	21/02/2014. Written record, Dan Harries.
Live animal. Consistent with <i>Niviventer</i> .	Krem Lymbiat, Jaintia Hills.	2015. Written record, Khlur Mukhim.
Sighting of live animal. Confirmed on observation as <i>Leopoldamys edwardsi</i> .	Within unspecified cave, Jaintia Hills.	28/02/2015. Written record, Manuel Ruedi.
Prints.	Sait Shyrba, Jaintia Hills.	20/02/2015. Written record and photograph, Dan Harries.
Scratch marks on walls.	Krem Puri, East Khasi Hills.	2017. Written record and photograph, Marcel Dijkstra.
Scratch marks on walls.	Krem Puri, East Khasi Hills.	2018. Written record and photograph, Marcel Dijkstra.
Apparent foraging scrapes in mudbank (consistent with rats).	Tui Khur Lut, Jaintia Hills.	20/02/2019. Written record, Dan Harries.
Live animal, prints and foraging scrapes. Confirmed as <i>Leopoldamys edwardsi</i> .	Krem Sakwa, Jaintia Hills.	22/02/2019. Written record and camera trap video, Dan Harries.
Faeces.	Saisi River Cave, Jaintia Hills.	2020. Photograph, David Cooke.
Prints and foraging scrapes.	Mawmluh, East Khasi Hills.	11/01/2023. Written record and photograph, Dan Harries.
Live animals (two individuals) and nest. Confirmed as <i>Leopoldamys edwardsi</i> .	Nakama 2, Garo Hills.	2024. Written record, camera trap and photograph, Manuel Ruedi.
Nest.	Ribung Khung Khur, Jaintia Hills.	2024. Written record, Rowena Sheen.
Skull and skeleton.	Ram Khur, Jaintia Hills.	2024. Written record and photograph, Marcel Dijkstra.
Nest. Confirmed as <i>Leopoldamys edwardsi</i> .	Bolsil Kol 2, Garo Hills.	13/03/2024. Written record and photograph, Jean Marc Jutzet.
Live animals (several individuals) and nest.	Chiabol Kol 2, Garo Hills.	09/03/2024. Written record, Thomas Arbenz.
Live animals (two individuals).	Dopanggal Kol, Garo Hills.	11/03/2024. Written record, Jean Marc Jutzet.
Live animals (2 individuals) and nest. Confirmed as <i>Leopoldamys edwardsi</i> .	Nakama Kol 1, Garo Hills.	12/03/2024. Written record and photograph, Manuel Ruedi.
Live animals (2 individuals) and nest. Consistent with <i>Leopoldamys</i> .	Gambari Kol, Garo Hills.	16/03/2024. Written record, Tudor Tamas.
Live animals (2 individuals) and nest.	Makbil Kol Gatabilgre, Garo Hills.	17/03/2024. Written record, Rich Hudson.
Live animals (several individuals) and faeces.	Narong Chakram, Garo Hills.	2025. Written record, Tudor Tamas.
Live animals (several individuals), carcass and nest.	Sawe Kol, Garo Hills.	2025. Written record, Tudor Tamas.
Faeces.	Rongsep Kol, Garo Hills.	2025. Written record, Rich Hudson.
Carcass.	Papa Udari Kol, Garo Hills.	2025. Written record, Chris Scaife.
Scratch marks on walls (uncertain record).	Lijung Khur, Jaintia Hills.	2025. Written record, Marcel Dijkstra.
Skull and skeleton. Confirmed as <i>Leopoldamys edwardsi</i> .	Narong Chakram, Garo Hills.	2025. Written record and photograph, Tudor Tamas.

Table 2 (part): Records indicating evidence of rats in Meghalayan caves, including summary details of record, location and source of information. [...Continued from above.]

Porcupine

There are 19 records (Table 3) reporting the presence of porcupines in Meghalayan caves. More than 80% of these records indicate current or recent occupancy of the caves (e.g. fresh quills, piles of faeces, nests, prints, and polished cave walls). Considering the large size and banding pattern of the quills (Fig.4) it is highly probable that most records relate to Malayan Porcupine (*Hystrix brachyura*).

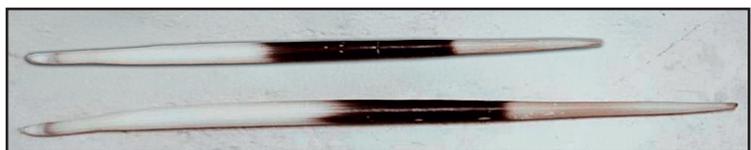


Figure 4: Malayan Porcupine (*Hystrix brachyura*) quills from Krem Umlawan, Jaintia Hills, 2013. The approximate length of the longer quill is c. 25cm [Photo: Uttam Saikia.]

Nature of record (with ID where practicable)	Location	Source
Dead animal and polished rock.	Krem Umkhang – Kharasniang, Jaintia Hills.	1997. Written record in Cave Registry 2000.
Nest.	Krem Thangshunai, Jaintia Hills.	2000. Written record, Paul Wilkinson.
Bones. (uncertain record).	Liat Prah, Jaintia Hills.	2002. Note by Dan Harries.
Mandibles. Identified as <i>Atherurus macrourus</i> .	Unknown cave, Jaintia Hills.	2003. Photograph, Dan Harries.
Quills, scrapes and polishing on rock.	Rubong 2, Jaintia Hills.	2005. Written record, Christian Fischer.
Faeces pile.	Krem Umthloo, Jaintia Hills.	16/2/2005. Written record and photograph, Dan Harries.
Quill.	Krem Wah Ser, Jaintia Hills.	18/02/2005. Written record, Dan Harries.
Unclear. "Porcupine presence".	AA Cave 15, Garo Hills.	2008. Written record, Keith Anderson.
Quills. Identified as <i>Hystrix</i> sp.	Krem Lymmoh, Jaintia Hills.	2010. Written record, Thomas Arbenz.
Quills, nest and prints.	Krem Khung, Jaintia Hills.	2012. Written record, Nicola Bayley.
Quills. Identified as <i>Hystrix brachyura</i> .	Krem Umlawan, Jaintia Hills.	2013. Written record, Uttam Saikia.
Quills and bone fragments. Possible <i>Atherurus macrourus</i> .	Krem Lymbiat, Jaintia Hills.	2014. Photograph, Dan Harries.
Prints and quills. Identified as <i>Hystrix brachyura</i> .	Krem Khung, Jaintia Hills.	12/12/2015. Written record and photograph, Khlur Mukhim.
Mandibles. Identified as <i>Hystrix</i> sp.	Krem Puri, East Khasi Hills.	2018. Written record and photograph, Marcel Dijkstra.
Scratch marks.	Chidobak Kol, Garo Hills.	2024. Written record and photograph, Ayush Singh.
Nest and prints.	Diphi Kol, Garo Hills.	2024. Written record, Roman Hapka.
Prints.	Chiabol Kol 2, Garo Hills.	11/03/2024. Written record, Tudor Tamas.
Prints.	Bolsil Kol 1, Garo Hills.	13/03/2024. Written record, Jean Marc Jutzet.
Quills, prints and scratch marks.	Misibakchong 1 Kol, Garo Hills.	2025. Written record, Mike Topso.

Table 3: Records indicating evidence of porcupines in Meghalayan caves, including summary details of record, location and source of information.

Nature of record (with ID where practicable)	Location	Source
Faeces (in cave entrance).	Krem Wah Ryngo, Jaintia Hills.	2000. Written record, Simon Brooks.
Faeces (in cave entrance).	Mahadeo Makkrekol, Garo Hills.	2001. Written record, Andy Tyler.
Skulls (2 individuals). Identified as a male and female macaque (<i>Macaca sp.</i>).	Krem Jynhaw, Jaintia Hills.	25/02/2001. Written record and photograph, Dan Harries.
Prints.	Krem Liat Prah, Jaintia Hills.	2002. Written record, Dave Hodgson.
Skull. Identified as a juvenile macaque (<i>Macaca sp.</i>).	Krem Lanshat/Swiftlet Pot, Jaintia Hills.	15/02/2002. Written record and photograph, Dan Harries.
Skull.	Saisidung Khur, Jaintia Hills.	2005. Written record, Georg Bäuml.
Skulls and bones (2 individuals). Identified as a macaque (<i>Macaca sp.</i>).	Krem Shynrong Shrieh, Jaintia Hills.	2008. Written record and photograph, Hugh Penney.
Skulls and bones (2 individuals). Consistent with macaque (<i>Macaca sp.</i>).	Krem Sim Suk / Syiem, Jaintia Hills.	2009. Written record and photograph, Bridget Hall.
Skull and skeleton. Identified as a Capped Langur (<i>Trachypithecus pileatus</i>).	Pdein Daharai, Jaintia Hills.	23/02/2014. Written record and photograph, Manuel Ruedi.
Skull fragments.	Lymbiat Cliff Cave, Jaintia Hills.	2015. Written record and photograph, Barbara Boesch.
Faeces (cliff above cave entrance).	Krem Knah Shrieh, Jaintia Hills.	2017. Written record, Simon Brooks.
Skull and skeleton. Identified as a macaque (<i>Macaca sp.</i>).	Krem Shrieh Songket, Jaintia Hills.	08/01/2020. Written record and photograph, Tudor Tamas.
Skulls and skeletons (2 individuals). Identified as a macaque (<i>Macaca sp.</i>).	Krem Ram Khur, Jaintia Hills.	2022. Written record and photograph, Marcel Dijkstra.
Skulls and skeletons (5 individuals). Consistent with macaque (<i>Macaca sp.</i>).	James Khur, Jaintia Hills.	2024. Written record and photograph, Yoxz Burgers.
Skull fragments.	Canyon Sink, Jaintia Hills.	2025. Written record and photograph, Marcel Dijkstra.
Tooth.	Lungchung Khur, Jaintia Hills.	2025. Photograph, David Cooke.

Table 4: Records indicating evidence of primates in Meghalayan caves, including summary details of record, location, and source of information.

Although no first-hand records of live porcupine are held, accounts from local guides in the Garo Hills suggest the presence of the smaller, Asiatic Brush-tailed Porcupine (*Atherurus macrourus*) living deep within caves. Signs attributed to porcupine within caves include quills (8 records), polished rock surfaces (2 records), nests (3 records), faeces (1 record), prints / scrape marks (8 records) and skeletal remains (4 records). Confident *a posteriori* species identification of all signs was not possible, but four were attributed with reasonable confidence to the larger *Hystrix* (e.g. Fig.4) and two were attributed to the far smaller *Atherurus* porcupines.

Those few records that specify a location within a cave tend to refer to areas within 100m of a known entrance. The records cover 18 distinct caves from all 3 hill ranges. A list of all records relating to porcupine is presented in Table 3.

Primates

There are 16 records relating to primates associated with caves. Of these, 12 refer to skeletal remains from 12 separate caves in the Jaintia Hills. Interestingly, 5 of these records document the presence of 2 or more individuals, and in one case remains of as many as 5 individuals were found together in one cave. Four records that are not associated with skeletal remains include 3 that refer to monkey faeces close to cave entrances. It was suggested that the monkeys were using the entrances or the surrounding rocks as shelter. The final record refers to monkey paw prints within a cave, but no photographic evidence is available.

Most of the photographed primate skulls are consistent anatomically with those of macaques (*Macaca sp.*), with Rhesus Macaque (*Macaca mulatta*) being the most likely source (Fig.5). A Capped Langur (*Trachypithecus pileatus*) skeleton was, however, also recorded at one location (Fig.6). A list of all current records that relate to primates is presented in Table 4.



Figure 5: Skull of a macaque (*Macaca sp.*) from Krem Jynhaw, Jaintia Hills, 2001. [Photo: Dan Harries.]



Figure 6: Skull of a Capped Langur (*Trachypithecus pileatus*) from Pdein Daharai, Jaintia Hills, 2014. [Photo: Manuel Ruedi.]



Figure 7: Remains of small carnivore (Palm Civet?) with rat nest, from Krem Shrieh, Jaintia Hills, 2000. [Photo: Mark Tringham.]



Figure 9: Fishing Cat prints from Krem Chympe / Pielkieng Pouk, Jaintia Hills, 2007. [Photo: Rainer Hoss.]

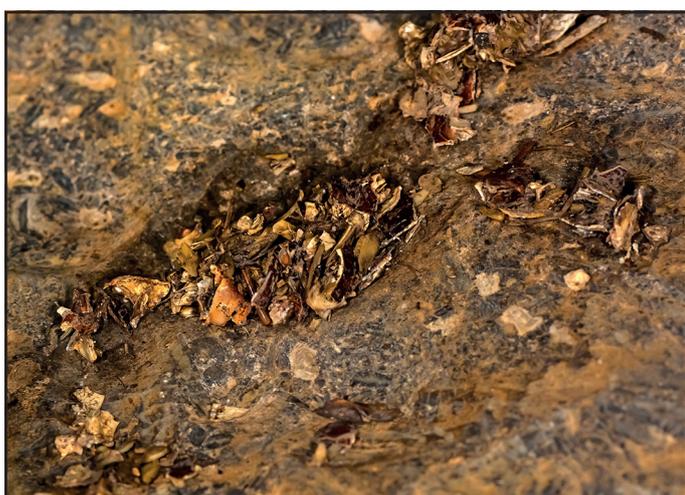


Figure 8: Faecal remains with crab fragments from Retdungkhur, Jaintia Hills, 2019. [Photo: Dan Harries.]

Small carnivores

There are 19 records relating to small carnivores associated with caves. Of these, one record was of a sighting of a live animal, 12 records were of traces indicating recent occupancy, and 6 records were of skeletal remains.

The description of the live animal was consistent with that of an Indian Civet (*Viverra* sp.). There are 9 records of prints from the caves. Of these, 4 originated from animals with visible claw prints and these might also relate to civets (the remaining 5 print records were from cats). Further evidence for the presence of civets includes a partly mummified body resembling a Palm Civet (subfamily Paradoxurinae) (Fig.7) and a skull, consistent in structure with those of Palm Civets, that was found in a separate cave.

Some of the clawed prints might, however, have been produced by mongooses. Supporting evidence includes faecal deposits containing the remains of freshwater crabs found on a rock ledge next to a streamway (Fig.8). The size of the droppings was consistent with those of a mongoose-sized animal, and they might be attributable to a Crab-eating Mongoose (*Urva urva*). A separate record reports a skull, suggested to be a mongoose, but without photographic evidence.

Three of the records relating to cats are consistent with a Fishing Cat (*Prionailurus viverrinus*). They include a record of a cat skull from a cave entrance area and 2 records of large cat prints within caves (Fig.9). The remaining 3 records of cat prints were smaller, and one set appears consistent in size with those of a Leopard Cat (*Prionailurus bengalensis*).

The remaining 3 skeletal records are of less significance and appear to originate from domestic dogs and a domestic cat. A list of all records relating to small carnivores is presented in Table 5.

Nature of record (with ID where practicable)	Location	Source
Prints. Cat.	Krem Dam, East Khasi Hills.	1992. Written record, Chris Smart.
Carcass semi-mummified. Civet?	Krem Shrieh (Tangnub), Jaintia Hills.	2000. Written record and photograph, Mark Tringham.
Skull. Mongoose?	Krem Um Thloo, Jaintia Hills.	2001. Written record, Tony Jarratt.
Mandible. Cat.	Krem Um Thloo, Jaintia Hills.	24/02/2001. Written record, Dan Harries.
Skull. Palm civet.	Liat Prah, Jaintia Hills.	2002. Written record and photograph, Dan Harries.
Skull. Consistent in size with Fishing Cat.	Ronga Cave, Khasi Hills.	2003. Written record and photograph, Dan Harries.
Faeces.	Krem Pyrda, Jaintia Hills.	2005. Photograph, Georg Bäumlner.
Skull. Dog.	Um Im 5, Jaintia Hills.	15/02/2005. Note (anon.).
Prints. Cat (consistent in size with Fishing Cat).	Krem Chympe / Pielkieng Pouk, Jaintia Hills.	2007. Written record and photograph, Kate Janossy and Rainer Hoss.
Live animal. Appearance consistent with civet.	Krem Lawklieng, East Khasi Hills.	04/03/2007. Written record, Daniel Gebauer.
Prints. Visible claws.	Krem Blang, Jaintia Hills.	2010. Written record and photograph, Thomas Arbenz.
Prints. Visible claws.	Krem Khung, Jaintia Hills.	2012. Written record and photograph, Thomas Arbenz.
Prints. Visible claws.	Krang Lapad, Jaintia Hills.	21/02/2014. Written record and photograph, Dan Harries.
Prints. Visible claws.	Krang Lapad, Jaintia Hills.	24/02/2014. Written record and photograph, Dan Harries.
Prints. Cat (consistent in size with Fishing Cat).	Sait Shyrba, Jaintia Hills.	20/02/2015. Written record and photograph, Dan Harries.
Skull. Dog.	Dead Dog Cave, Jaintia Hills.	2017. Written record and photograph, Paul Mackrill.
Faeces. Containing crab fragments.	Retdungkhur, Jaintia Hills.	16/2/2019. Written record and photograph, Dan Harries.
Prints. Cat.	Retdungkhur, Jaintia Hills.	16/02/2019. Written record and photograph, Dan Harries.
Prints. Cat (consistent in size with Leopard Cat).	Krem Pakse, Jaintia Hills.	2025. Written record and photograph, Marcel Dijkstra.

Table 5: Records indicating evidence of small carnivores in Meghalayan caves, including summary details of record, location, and source of information.

Nature of record (with ID where practicable)	Location	Source
Bones. Unidentified ungulate.	Krem Shynrang Labbit, Jaintia Hills.	05/02/2001. Written record, Dan Harries.
Tooth. Pig.	Krem Um Thloo, Jaintia Hills.	24/02/2001. Written record, Dan Harries.
Skull and bones. Himalayan Serow (<i>Capricornis sumatraensis</i>).	Krem Lanshat / Swiftlet Pot, Jaintia Hills.	15/02/2002. Written record and photograph, Dan Harries.
Bones. Cow?	Liat Prah, Jaintia Hills.	11/02/2003. Written record, Nigel Robertson.
Bones. Unidentified ungulate.	Um Im 5, Jaintia Hills.	15/02/2005. Written record, Dan Harries.
Tooth. Deer.	Mondil Kol, West Khasi Hills.	24/02/2005. Written record, Dan Harries.
Bones and skull fragments. Cow.	Krem Khnai Um Kyrpong, Jaintia Hills.	2010. Written record and photograph, Estelle Sandford.
Bones. Deer (<i>Cervidae</i> indet.)	Dead Dog Cave, Jaintia Hills.	2017. Written record and photograph, Paul Mackrill.
Bones. Unidentified ungulate.	Krem Puri, East Khasi Hills.	2018. Written record and photograph, Marcel Dijkstra.
Skull fragments. Cow.	Krem Khlieh Um Soh Jew, Jaintia Hills.	08/11/2022. Written record and photograph, Marcel Dijkstra.
Bones. Cow?	Ram Khur, Jaintia Hills.	2024. Written record and photograph, Marcel Dijkstra.
Tooth. Pig.	Chiginap Kol 1, Garo Hills.	07/03/2024. Garo 2024 diary.
Tooth and bone. Pig?	Mandal Kol, Garo Hills.	18/03/2024. Written record and photograph, Tudor Tamas.
Bones and partial skull. Cow.	Simina Kol, Garo Hills.	2025. Written record and photograph, Bartek Biela.

Table 6: Records indicating evidence of large herbivores in Meghalayan caves, including summary details, location and source of information.

Large herbivores

There are 14 records of ‘large herbivores’ noted from within caves and all relate to skeletal fragments. In most cases no skulls were present, and identification was not possible. A number of these records might originate from domestic livestock, and their presence within caves is certainly accidental. In 5 cases there was reasonable confidence that the bones were from cattle and in 3 cases they were attributed to pigs. For 3 further cases it was noted only that the bones indicate a large (at least deer-sized) animal, so some of these might also be domestic livestock. The remaining 3 cases were attributed with greater certainty to non-domestic species. These included the skull of a Himalayan Serow (*Capricornis sumatraensis*) (Fig.10) and 2 records that were attributed to species of deer. A list of all records relating to large herbivores is presented in Table 6.

Bear

Records relating to bear are available from 6 locations. Four relate to skeletal remains and one involves a claw scrape mark on a cave wall consistent to that of a bear in terms of size. The final record relates to a paw print attributed to bear (Fig.11). Three of the skulls have been identified as Asiatic Black Bear (*Ursus thibetanus*) (Fig.12). A list of all records relating to bears is presented in Table 7.

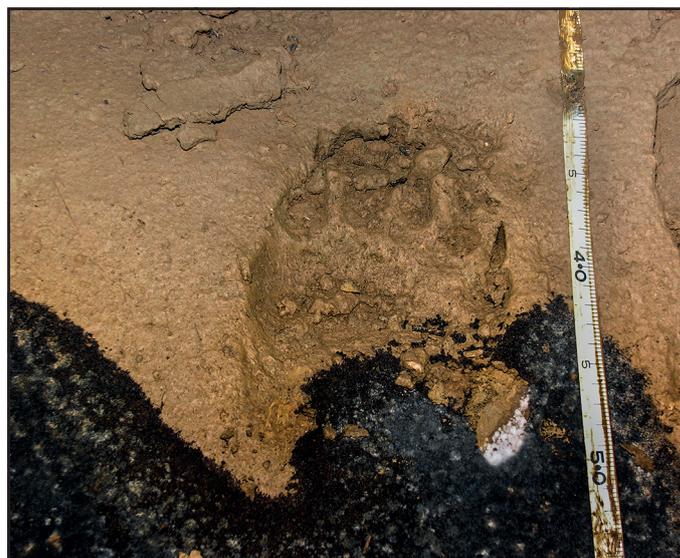


Figure 11: Bear print in Krem Chympe / Pielkieng Pouk, Jaintia Hills, 2007. [Photo: Rainer Hoss.]



Figure 10: Skull of Himalayan Serow (*Capricornis sumatraensis*) from Swiftlet Pot, Jaintia Hills, 2015. [Photo: Elena Buduran.]



Figure 12: Asiatic Black Bear (*Ursus thibetanus*) skull from Krem Sakwa, Jaintia Hills, 2005. [Photo: Georg Bäumlner.]

Nature of record (with ID where practicable)	Location	Source
Skull fragments.	Krem Umpyrjaw, Jaintia Hills.	2002. Written record and photograph, Dan Harries.
Skull. Tentative identification as juvenile Asian Black Bear (<i>Ursus thibetanus</i>).	Synrang Labbit, Jaintia Hills.	26/02/2003. Written record and photograph, Dan Harries.
Skull. Identified as Asian Black Bear (<i>Ursus thibetanus</i>).	Krem Sakwa, Jaintia Hills.	2005. Written record and photograph, Georg Bäumlner.
Print.	Krem Chympe / Pielkieng Pouk, Jaintia Hills.	2007. Written record and photograph, Rainer Hoss.
Scrape mark. Uncertain record but size consistent with bear.	Krem Puri, East Khasi Hills.	2016. Written record and photograph, Tony Hamnett.
Skull and bones. Consistent with Asian Black Bear (<i>Ursus thibetanus</i>).	Makbil Kol Gatabilgre, Garo Hills.	17/03/2024. Written record and photograph, Richard Hudson.

Table 7: Records indicating evidence of bears in Meghalayan caves, including summary details of record, location, and source of information.



Figure 13: Skull of Asian Grey Shrew (*Crocidura attenuata*) from Krem Lymbiat, Jaintia Hills, 2015. [Photo: Manuel Ruedi.]

Other records

Seven additional records do not correspond to any of the categories considered above. These include an account of a cave entrance in the Garo Hills where there was a ‘strong smell of cat’ and ‘a lot of golden-brown hairs’. A large cat print noted contemporaneously in the neighbouring forest was attributed to Common Leopard (*Panthera pardus*). Two records were of skull fragments of shrews from the genus *Crocidura* (Fig.13). There is one record of a squirrel skull and two records of unidentified rodent teeth. The final record is of an elephant limb bone in a cave streamway. A list of all other records is presented in Table 8.

Nature of record (with ID where practicable)	Location	Source
Prints and hairs. Leopard?	Chiring Kol, Garo Hills.	1995. Written record and photograph, Chris Smart.
Incisor. Rodent indet.	Krem Lymbiat, Jaintia Hills.	2014. Photograph, Thomas Arbenz.
Skull fragments. Shrew (<i>Crocidura</i> sp.).	Krem Lumjintep, Jaintia Hills.	2014. Photograph, Oana Chachula.
Molar. Rodent indet.	Krem Lumjintep, Jaintia Hills.	2014. Photograph, Oana Chachula.
Skull. Asian Grey Shrew (<i>Crocidura attenuata</i>).	Krem Lymbiat, Jaintia Hills.	12/2/2015. Written record and photograph, Manuel Ruedi.
Skull. Squirrel.	James Khur, Jaintia Hills.	2024. Written record and photograph, Yoxz Burgers.
Bone. Elephant.	Asim Kol, Garo Hills.	2025. Written record and photograph, Pynshai Syiemjong.

Table 8: Other records of mammals in Meghalayan caves, including summary details of record, location, and source of information.

Discussion

Rats

The frequency of nest records and several observations of pairs of live individuals indicate that the Edwards’s Long-tailed Giant Rat reproduce underground, and the foraging scrapes show evidence of occasional feeding within caves. Feeding opportunities for rats within caves would include vegetation deposited by seasonal floods and the abundant invertebrate fauna. However, studies of other Giant Rats in caves elsewhere in Southeast Asia (Latinne *et al.*, 2014) indicate that they generally shelter within the caves during daylight hours and emerge to feed in the surrounding forest during the night. This pattern of behaviour was also observed on camera trap footage – from the South Garo Hills – that showed a pair of Giant Rats emerging from the cave regularly each night, presumably to forage in the forest. It cannot be discounted that other species of rats might also visit caves opportunistically. The records of the 1922 Siju Cave survey noted that rats were common (Kemp, 1924). These were considered to be Himalayan field rats (*Rattus nitidus*) rather than the *Leopoldamys edwardsi* recognized in this report. Additionally, visual observations in Krem Khung and Krem Lymbiat noted rats consistent with *Niviventer niviventer* in terms of size and appearance. *Leopoldamys edwardsi* clearly has a well-established association with caves, but the opportunistic behaviour of rats might result in other species visiting caves occasionally.

Porcupines

Records presented here suggest that two species of porcupines, the larger *Hystrix brachyura* and the smaller *Atherurus macrourus*, use caves actively. Presence of *Hystrix* sp. is demonstrated by records of skull remains and typical quills found within 4 separate caves. In addition to the evidence provided in the Results section there is also a third-hand account from a local guide, who reported hunting a large porcupine within a cave entrance in the Jaintia Hills. There is evidence from several parts of the world of porcupines using caves as dens (Montalvo *et al.*, 2021). A published report on Dandak Cave in Chhattisgarh State in India also recorded the presence of Indian Crested Porcupine *Hystrix indica* (Biswas and Shrotriya, 2011) It is probable that caves offer shelter and protection from predators and are a convenient alternative to digging burrows. Due to their weight and size, it is probable that porcupines are less adept than rats at climbing vertical rock, so their distribution within caves might be more limited. Being predominantly herbivores, they presumably leave the caves regularly to forage outside. Consequently, it is also probable that porcupines will be restricted to areas close to cave entrances and more likely to the frequent horizontal entrances rather than those with vertical entrance pitches.

Primates

The primate skeletal records found within caves could be dismissed as being of accidental occurrence related to carcasses or living animals being swept into caves by flood waters., Primate skulls, however, are disproportionately common amongst skeletal remains found in Meghalayan caves, accounting for more than half of the skeletal remains of larger animals recorded from the caves. This suggests that they might have a greater susceptibility to being deposited within caves. The use of cave entrances for shelter and predator avoidance is a possible trait that would increase the chance of monkey bones being deposited in caves following accidental falls or sudden floods. It should also be noted that the condition of the bones from some sites indicates considerable antiquity, so these might have been deposited when monkeys were more abundant than is currently the case. Monkeys are rarely encountered in these areas nowadays but, despite this, 3 sites are recorded (Table 4) where live monkeys appeared to be actively associated with cave entrances. Another notable feature of the primate records is that many of them feature multiple individuals, commonly in close proximity. Whereas this might relate to accidental wash-in of different individuals from the cave entrance area on separate occasions, it is perhaps more likely that social groups were trapped simultaneously by floodwater. Overall, the evidence of an association with cave entrances is reasonably persuasive.

Utilization of caves by non-human primates is an uncommon phenomenon but a few examples exist from Madagascar, China and Japan (Grueter and Wei, 2006; Wang *et al.*, 2011; Sauther *et al.*, 2013; Kasiwagi *et al.*, 2018). Although most of the Meghalayan records were from macaques, at least one was a Capped Langur (*Trachypithecus pileatus*). It is noteworthy that members of this arboreal genus are known to favour forests in karstic landscapes and roost in limestone caves in Vietnam and China (Huang *et al.*, 2004; Grueter and Wei, 2006).

Small carnivores

It is likely that small carnivores frequent the caves more often than the current evidence might suggest. The noise, lights and disturbance caused by cave explorers makes it unlikely that the animals will be seen directly. Footprints of small carnivores are commonly present, but these are easy to overlook and are likely to be under-recorded.

The most plausible explanation of the presence of such animals within caves is that they are in search of food. During the dry winter months many surface riverbeds and pools tend to become dry, but pools of standing water and active streams remain available within many caves. Commonly these water bodies contain small fish, shrimp and crabs, which would offer a valuable resource to species of small carnivores able to hunt in water in darkness. The evidence of faecal deposits containing crab-remains

at one site indicates that active aquatic hunting does occur within some caves. It is also likely that some species hunt bats and/or the abundant invertebrate prey associated with piles of bat guano. Cavers have reported seeing bat carcasses where the body appeared to have been consumed and only the wings remained. Larger species of carnivore could also predate rats, although no direct evidence of this has been recorded. Gathering further evidence of such behaviour is challenging but a possible approach would be to place baited camera traps at suitable locations within caves to gauge the frequency of visits by species of small carnivore.

Several small- to medium-sized carnivores are plausible candidates for the records noted from the caves. Crab-eating Mongoose (*Urva urva*) are known to hunt for fish and crabs, so it is possible that they might forage inside caves where these resources are abundant. Some of the records of small prints with claw marks would be consistent with mongoose. Such prints would, however, also be consistent with civet, and there is further evidence of civet from skeletal remains. In other parts of India, large caves with downward facing openings are reportedly used by both Himalayan Palm Civet (*Paguma larvata*) and Large Indian Civet (*Viverra zibetha*) in the Andaman Islands (Mane and Manchi, 2018) or by Small Indian Civets (*Viverricula indica*) in the Dandak Cave of Chhattisgarh State (Biswas and Shrotriya, 2011).

Other recorded prints suggest the presence of cats. The relatively large prints seen in two Jaintia caves (and a skull in a different cave) were consistent in size with those of a Fishing Cat (*Prionailurus viverrinus*). It is entirely plausible that cats might occasionally hunt within caves. Besides fish and crustaceans inhabiting subterranean streams and pools, their attention might also be attracted by the presence of rats, as well as large colonies of bats, which could likewise serve as a food source.

Large herbivores

Skeletal remains of large herbivores present within caves do not constitute evidence that these animals had a specific association with the caves. It is possible that some herbivores might use cave entrances as places of shelter under certain circumstances, but there is no indication of this among the records considered here. Instead, the condition and location of the bones suggest the animals either fell into vertical entrances or that they, or their remains, were washed in by flood waters.

The main significance of the herbivore records is in comparison with primate remains. Each of the 14 records of herbivores appears to represent a partial skeleton of a single individual, and only 4 had recognizable skulls. This is consistent with carcasses having been washed in by flood waters. In contrast, 9 of the 16 primate records featured more complete skeletons and skulls were present. Additionally, those 9 records represent at least 16 distinct individuals. The high frequency of primate remains, the occurrence of multiple individuals at deposition sites and the more intact remains relative to those of herbivores suggest a different mechanism for occurrence to that of the herbivores, and this is consistent with a specific association with cave entrances in the case of the primates.

Bear

There is no strong and convincing physical evidence of active use of caves by bears in Meghalaya, although this lack of evidence might be a result of the scarcity of bears in the region in modern times. Additional to the evidence presented in the preceding section, however, two reports by local guides suggest that bears might indeed use certain caves, but the direct evidence is limited to a paw print at one site and a wall scrape at another. These signs might indicate active use, but such observations are too rare to discount the possibility that the signs were due to the accidental presence of stray individuals. None of the 4 records of skeletal remains includes noted evidence (such as scrape marks) that the sites were bear dens. Some appear to be from water-washed rocky sites, and dark colouration of the bones suggests that some were of considerable antiquity. It is probable that these constitute accidental bear presence, perhaps due to carcasses washed in by flood waters.

Other records

The record from the Garo Hills indicates a cave entrance being used as a shelter or den by a large cat. This is an isolated record, but it should be noted that many cave entrances are unsuitable for providing shelter because they are both steep and wet. It might be that where dry horizontal entrances are more common there is a greater chance of them being utilized by large predators. Limited significance can be attached to the isolated records of skeletal remains of the squirrel and shrew. Nevertheless, considering the insectivorous diet of shrews suggests the possibility that they might exploit the plentiful food resource provided by the small invertebrates that are abundant in bat guano piles.

Conclusion

This study presents a range of evidence demonstrating that the cave habitats in Meghalaya are commonly utilized by a number of terrestrial mammalian taxa. Much of the visible physical evidence is, however, fragmentary and difficult to interpret. Emerging techniques of environmental DNA sampling (e.g. Saccò *et al.*, 2022; Rishan *et al.*, 2023; Van Leeuwen and Michaux, 2023) might offer a means of gaining a more holistic understanding of which mammalian species frequent caves on a regular basis.

Foremost amongst the Meghalayan cavernicolous mammal species is Edwards's Long-tailed Giant Rat (*Leopoldamys edwardsi*), which appears to have a notably close association with caves. These rats are frequently encountered within the caves and there is clear evidence of nesting and of occasional underground feeding. The species is reportedly an inhabitant of lowland and montane forest and known to make nests of leaves on the ground (Figs 2 and 7). Fossil remains of the species have previously been reported from Cave of Mulan Mountain, Chongzuo, Guangxi, China (Denys *et al.*, 2017). No other previous records of this species from inside caves are known to the authors, however.

Whereas porcupines are considerably less commonly encountered than Giant Rats, they too appear to make frequent use of caves. It is assumed here that they do so primarily for shelter and avoidance of predators, although this is assumption is based purely on their reported dietary preferences rather than direct evidence. As noted above, *Hystrix* porcupines are known denizens of caves in other parts of the world, so their occurrence in Meghalayan caves is unremarkable.

Evidence in relation to primates (predominantly macaques) in the Meghalayan caves is more unexpected. Use of caves by non-human primates is reportedly rare but has been noted for baboons and langurs (Wang *et al.*, 2011). Macaques, however, are also known to use caves for shelter in Japan (Kasiwagi *et al.*, 2018) and known to frequent steep rock in the vicinity of cave entrances in Malaysia and Indonesia (Zamri and Md-Zain, 2022; Riyani *et al.*, 2025). The disproportionate frequency of findings of primate skeletal remains (in some cases of multiple individuals) within Meghalayan caves would imply that they are not there only by chance. It is speculated here that the steep rock in and around cave entrances might be used by these primates as a refuge from ground-based predators. Such behaviour has been reported in Assamese Macaques in Tibet (Li *et al.*, 2022). The obvious dangers of such terrain when coupled with the frequency of flooding is a plausible explanation for the common occurrence of monkey remains within caves. Supporting evidence is available in the form of a small number of observations of monkey troops frequenting various cave entrances.

Other evidence suggests that carnivorous mammals might frequent caves on a regular basis, presumably for the purpose of hunting. There are several records of animals with clawed footprints (possibly civet or mongoose) but also other records include evidence of the presence of cats. Potential sources of prey for such predators would include the fish, shrimp and crabs in the cave waters, as well as bats, and possibly the rats.

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References

- Arbenz, T, 2013. Cave pearls of Meghalaya. *A cave inventory covering the Jaintia Hills, Meghalaya, India*. Volume 1: Pala Range and Kopili River. [India: Replika Press.]
- Arbenz, T, 2016. Cave pearls of Meghalaya. *A cave inventory covering the Jaintia Hills, Meghalaya, India*. Volume 2: North Shongrim Ridge and the Liat Prah cave system. [India: Replika Press.]
- Arbenz, T, 2017. Cave pearls of Meghalaya. *A cave inventory covering the Jaintia Hills, Meghalaya, India*. Volume 3: South Shongrim and the Umthloo cave system Stelkan/Sakwa and the Pielkhlieng Pouk cave system. [India: Replika Press.]
- Barrett, L, Gaynor, D, Rendall, D, Mitchell, D, and Henzi, S P, 2004. Habitual cave use and thermoregulation in chacma baboons (*Papio hamadryas ursinus*). *Journal of Human Evolution*, Vol.46, 215–222.
- Biswas, J and Shrotriya, S, 2011. Dandak: a mammalian dominated cave ecosystem of India. *Subterranean Biology*, Vol.8, 1–7.
- Gebauer, H D, 2008. Resources on the Speleology of Meghalaya State, India. Part 1: Overview. In Laumanns, M (Ed.), Berlin Cave Research Reports 33. [Rangsdorf: Speleoclub Berlin.]
- Grueter, C and Wei, D, 2006. An observation of François' Langurs using caves at Mayanghe National Nature Reserve, Guizhou, China. *Zoological Research*, Vol.27(5), 558–560.
- Harries D B, Ware, F J, Fischer, C W, Biswas J, and Kharpran-Daly, B, 2008. A review of the biospeleology of Meghalaya, India. *Journal of Cave and Karst Studies*, Vol.70(3),163–176.
- Huang, C, Wei, F, Li, M, Li, Y, and Sun, R, 2003. Sleeping Cave Selection, Activity Pattern and Time Budget of White-Headed Langurs. *International Journal of Primatology*, Vol.24, 813–824. [https://doi.org/10.1023/A:1024628822271]
- Huang, C M, Li, Y B, Zhou, Q H, and Wei, F W, 2004. The preliminary study on behavior of cave-leaving and entering and selection of sleeping cave of François' langur in China. 137–143 in Nadler, T, Streicher, U, and Long H T (eds), *Conservation of primates in Vietnam*. [Hanoi, Vietnam: Haki Publishing.]
- Kasiwagi, K, Tsuji, Y, Yamamura, T, Takai, M, and Shimizu, M, 2018. Presence of Faeces in the Abandoned Nokado Mine, Tochigi Prefecture of Central Japan, Provides Further Evidence of Cave Use by Japanese Macaques. *Primate Research*. Vol.34(1), 79–85.
- Kemp, S, 1924. Part II. Notes on the mammals of the Siju Cave, Garo Hills, Assam. *Records of the Indian Museum*, Vol.26, 23–25.
- Kemp, S and Chopra, B, 1924. The Siju Cave, Garo Hills, Assam. Part I. *Records of the Indian Museum*, Vol.26, 3–22.
- Lamare, R E and Singh, O P, 2016. Limestone mining and its environmental implications in Meghalaya, India. *ENVIS Bulletin Himalayan Ecology*, Vol.24, 87–100.
- Latinne, A, Galan, M, Waengsothorn, S, Rojanadilok, P, Eiamampai, K, Sribuarod, K, and Michaux, J, 2014. Diet analysis of *Leopoldamys neilli*, a cave-dwelling rodent in Southeast Asia, using next-generation sequencing from feces. *Journal of Cave and Karst Studies*, Vol.76, 139–145. [https://doi.org/10.4311/2013LSC0100]
- Li, B-W, Li, W-B, Xia, D-P, Zhang, T, Yang, P-P, and Li, J-H, 2022. Sleeping sites provide new insight into multiple central place foraging strategies of Tibetan macaques (*Macaca thibetana*). *Frontiers in Ecology and Evolution*, Vol.10. 10:1067923. [https://doi.org/10.3389/fevo.2022.1067923]
- MacSwiney, M C, Vilchis, P, Clarke, F M, and Racey, P A, 2007. The importance of cenotes in conserving bat assemblages in the Yucatan, Mexico. *Biological Conservation*, Vol.136, 499–509.
- Mane, A and Manchi, S, 2018. Civets in the Limestone Caves of Andaman Islands: Notes on the Distribution and Natural History. *Ambient Science*, Vol.5(1), 6–10.
- McGrew, W C, McKee, J K, and Tutin, C E G, 2003. Primates in caves: two new reports of *Papio* spp. *Journal of Human Evolution*, Vol.44(4), 521–526. [https://doi.org/10.1016/S0047-2484(03)00042-3]
- Mittermeier, R A, Gil, P R, Hoffmann, M, Pilgrim, J D, Brooks, T M, Mittermeier, C G, and da Fonseca, G A B, 2004. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Ecoregions*. [Mexico City: CEMEX.]
- Montalvo, A E, Lopez, R L, Parker, I D, Silvy, N J, Cooper, S M, and Feagin, R A, 2021. Home range and habitat selection of cave-dwelling north American porcupines (*Erethizon dorsatum*) in central Texas. *The Texas Journal of Science*, Vol.73(1), article 4. [https://doi.org/10.32011/tjxsci_73_1_article4]
- Montalvo, A E, 2017. *Meso-mammal cave use and north American porcupine habitat use in central Texas*. PhD Dissertation, Texas A&M University.
- Pawar, S, Koo, M S, Kelley, C, Ahmed, M F, Chaudhury, S, and Sarkar, S, 2007. Conservation assessment and prioritization of areas of Northeast India: Priorities for amphibians and reptiles *Biological Conservation*, Vol.136, 346–361.
- Perry, R W, 2013. A review of factors affecting cave climates for hibernating bats in temperate North America. *Environmental Reviews*, Vol.21, 28–39.
- Prokop, P, 2014. The Meghalaya Plateau: landscapes in the abode of the clouds. 173–180 in Kale, V S (Ed.), *Landscapes and Landforms of India*. [Netherlands: Springer.]
- Redmond, I M and Shoshani, J, 1987. Mount Elgon's Elephants Are in Peril. *Elephant*, Vol.2(3), 46–66. [https://doi.org/10.22237/elephant/1521732102]
- Rishan, S T, Kline, R J, and Rahman, M S, 2023. Applications of environmental DNA (eDNA) to detect subterranean and aquatic invasive species: A critical review on the challenges and limitations of eDNA metabarcoding. *Environmental Advances*, Vol.12, 100370.
- Riyani, S R, Hernawati, D, and Chaidir, D M, 2025. Population behavior of *Macaca fascicularis*: An analysis of environmental and social interactions shaping in the Terawang Cave habitat, Central Java. *Inornatus: Biology Education Journal*, Vol.5(2), 14–28. [https://doi.org/10.30862/inornatus.v5i2.8]
- Saikia, U, Thabah, A, Chachula, O M, and Ruedi, M, 2018. The bat fauna of Meghalaya, Northeast India: Diversity and Conservation. 263–286 in Sivaperuman, C and Venkataraman, K (eds), *Indian Hotspots: Vertebrate faunal diversity, conservation and management*. Vol.2. [Singapore: Springer Nature Singapore Pvt Ltd.] 354pp.
- Saikia, U, Kharpran-Daly, B, and Ruedi, M, 2023. Caves as priority areas for the conservation of lesser known mammalian fauna in Meghalaya, North East India. *Current Science*, Vol.124(9), 1021–1022.
- Sauther, M L, Cuozzo, F, Jacky, I A, and Fish, K, 2013. Limestone cliff – face and cave use by wild ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. *Madagascar Conservation and Development*, Vol.8(2). [https://doi.org/10.4314/mcd.v8i2.5]
- Saccò, M, Guzik, M T, van der Heyde, M, Nevill, P, Cooper, S J B, Austin, A D, Coates, P J, Allentoft, M E, and White, N E, 2022. eDNA in subterranean ecosystems: Applications, technical aspects, and future prospects. *Science of the Total Environment*, Vol.820, 153223.
- Tewari, V C, 2011. Speleothems from Uttarakhand and Meghalaya indicating Holocene Monsoon and Climate. *Journal of Indian Geological Congress*, Vol.3(1), 87–104.
- Van Leeuwen, P and Michaux, J, 2023. Using eDNA for mammal inventories still needs naturalist expertise, a meta-analysis. *Ecology and Evolution*, Vol.13, e10788. [https://doi.org/10.1002/ece3.10788]
- Vernes, K and Devos, F, 2022. Use of cenotes and the cave environment by mammals on the Yucatán Peninsula, Mexico. *Biotropica*, Vol.54, 881–892. [https://doi.org/10.1111/btp.13111]
- Walker, M, Head, M J, Berkelhammer, M, Björck, S, Cheng, H, Cwynar, L, Fisher, D, Gkinis, V, Long, A, Lowe, J, Newnham, R, Rasmussen, S O, and Weiss, H, 2018. Formal ratification of the subdivision of the Holocene Series/Epoch (Quaternary System/Period): two new Global Boundary Stratotype Sections and Points (GSSPs) and three new stages/subseries. *Episodes*, Vol.41(4), 213–223. [https://doi.org/10.18814/epiugs/2018/018016]
- Wang, S, Luo, Y, and Cui, G, 2011. Sleeping site selection of François' langur (*Trachypithecus francoisi*) in two habitats in Mayanghe National Nature Reserve, Guizhou, China. *Primates*, Vol.52, 51–60. [https://doi.org/10.1007/s10329-010-0218-2]
- Denys, C, Taylor, P, and Aplin, K, 2017. Muridae. 536–884 in Wilson, D E, Mittermeier, R A, and Lacher, T E (eds), *Handbook of the Mammals of the World – Volume 7: Rodents II*. [Barcelona: Lynx.] [https://doi.org/10.5281/zenodo.6887260]
- Zamri, M A and Md-Zain, B M, 2022. Long-tailed macaques of the Batu Caves, Peninsular Malaysia: population estimate, nuisance behaviors, and human perception. *Journal of Animal and Plant Sciences*, Vol.32(4), 1150–1158.

Supplementary Material

The online instance of *Cave and Karst Science*, Volume 53, Number 1, includes supplementary material in the form of a Photographic Appendix (pp.S1-S32) comprising: 64 photographs (Supp.1 to Supp.64).