The expansion and migration of small mammals in the Makalu Barun region induced by changes of the Himalayan environment during the Quaternary

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ABSTRACT

This paper describes the course of migration and expansion of small mammals in the Makalu Barun region influenced by the orogenetic uplift of the East Nepal Himalaya and climatically conditioned changes in the extent of morphogenetic zones from the Upper Pleistocene up to the present. The results of zoological and parasitological research are compounded with the knowledge of the dynamic development of landforms, which testifies to significant changes in the high-mountain environment during the Quaternary. The migration of Palearctic species of small mammals across the gradually emerging orographical barrier during the orogenesis of the High Himalaya was completely interrupted by the glaciation in the Upper Pleistocene. This extensive glaciation also excluded occurrence and survival of small mammals in the high-mountain valleys of the Makalu Barun region. Migration routes and the extension of the territory of small mammals remained open only in the periglacial zone of the Arun and Barun Khola valleys. Following the interstadial period of warmer and humid climate conditions were changed by the Late Glacial Maximum when small mammals were again pushed away from heavily glaciated valleys to the lower altitude periglacial zone. During the Holocene interglacial, the occurrence of fauna and flora in the high-mountain valleys depended on repeated spatial changes of periglacial and glacial morphoclimatic zones. Current biogeographical hazards are accentuated due to the rapid retreat of glaciers, the expansion of the periglacial morphoclimatic zone and the increased human impact in the High Himalaya.

KEYWORDS

small mammals; the Quaternary environment; landform evolution; the Makalu Barun region; the Himalaya

Received: 26 September 2022
Accepted: 2 December 2022
Published online: 21 December 2022

Daniel, M., Kalvoda, J. (2022): The expansion and migration of small mammals in the Makalu Barun region induced by changes of the Himalayan environment during the Quaternary. AUC Geographica 57(2), 158–180
https://doi.org/10.14712/23361980.2022.13

1. Aims and methods of the study

A remarkable endeavour of pioneering mountaineering expeditions to the highest eight thousand peaks was also to gain knowledge about the natural environment of the mountains of High Asia. Half a century ago, Czechoslovak mountaineering expeditions to Makalu (8,475 m) in the East Nepal Himalaya also contributed to this effort. As a reminder of the anniversary of these Czechoslovak expeditions in 1973 and 1976, we present a regional study on a current topic that requires a systematic linking of the results of zoological, parasitological, geomorphological and geological knowledge. From a general point of view, this is a contribution to the knowledge of the exciting history of fauna expansion in the climatically harsh and variable glacial and periglacial zones of the East Nepal Himalaya from the Upper Pleistocene up to the present.

This study emphasizes the migration of small mammals and principal features of their distribution as an important biogeographic phenomenon in the Makalu Barun region (Fig. 1), which reflects the tectonic uplift, origin and oscillations of the mountain glaciation and morphoclimatic zones during the Quaternary period of collisional orogeny. The results of the zoological investigation of the present-day distribution of small mammals are integrated with the palaeogeographical and geomorphic evidence on the landform development during the Quaternary.

Fig. 1 Morphostructural and climate-morphogenetic differentiation of the Himalayan landscape between the Chomolongma and Makalu Massifs and the Barun Khola valley is conspicuous. The canyon-like valley (ca 3,000–4,000 m a.s.l.) with lateral hanging valleys is incised into crystalline rocks of the basement of the High Himalaya nappe. On the horizon, strongly glaciated mountain massifs are situated: to the left, the Peak IV (6,720 m), Nuptse (7,879 m), Lhotse (8,501 m), Lhotse Shar (8,383 m) and Sagarmatha (Mount Everest, 8,847 m; entirely in the background); to the right, Peak III (6,825 m), the southern summit (8,010 m) and the main summit of Makalu (8,475 m). Photograph by Jan Kalvoda (April, 2006).

We pursued zoological and geomorphological research in the Himalayan terrains during the years 1971, 1973, 1976, 1979, 2002 and 2006, and related laboratory works were almost completed in 2021. This long-term inquiry allowed us to make also a comprehensive interpretation of significant changes in the natural environment and human activities in the Makalu Barun region. Colonization of areas exposed by a retreat of glaciers represents a serious ecological process in high-mountain biocenoses. Because of the increasing intensity of the reduction of glacial zone owing to changes in climate during the last decades, former findings are valuable as a comparative source for the present.

The alpine fauna of the Makalu Barun region occurred in the foreland and on nunataks of the Barun glaciers. Nowadays it comprises Palearctic species as well as species of the oriental region, which, because of their wide ecological adaptability, extend up to this area from lower altitudes (Daniel et al. 1985). Typical representatives of the oriental region are birds *Tetraogallus tibetanus aquilonifer, Pyrrhocorax graculus digitatus, Corvus corax, Corvus macrorhynchos* and *Ithaginis cruentus cruentus*. In the pilot study Daniel and Kalvoda (1985) determined that the psychrophile faunal elements of Palearctic origin, for example *Alticola stoliczkanus, Ochotona roylei* and *Neodon sikimensis*, became isolated in the Barun valley by the gradually rising main crest of the High Himalaya during the Quaternary. This orographical barrier, owing to its cold climate and continuous glacial cover, has been insurmountable since the Upper Pleistocene. The southward advance of the Palearctic fauna was stopped by the bioclimatic boundary modified to the environmental adaptability of the individual species.

The presented study focused on the occurrence and migration of small terrestrial mammals tightly linked with a particular habitat in the Makalu Barun region. Their ectoparasites, which have particular zoogeographical affiliations, were also considered. Expansion of animals and their haematophagous parasites (mainly ixodid ticks; Daniel 1979) in newly exposed areas introduces the risk of vector-borne diseases caused by viral and bacterial pathogens circulating among vertebrates by means of vectors-haematophagous ectoparasites. Under particular circumstances, they are transmissible to humans and can cause severe and even fatal disease (Daniel 2015, 2017).

Our intention is also to determine changes in the altitudinal limit of risk of the vector-borne diseases occurrence based on the analysis of environmental conditions required for the survival of small terrestrial mammals and their parasites. Therefore, zoological and parasitological findings are compound with knowledge of the dynamic development of landforms, which testifies to significant changes in the high-mountain environment of the Makalu Barun region during the late Quaternary. The complex interpretation made it possible to determine the course of expansion and migration of small mammals in harmony with the orogenetic uplift of the High Himalaya and climatically conditioned changes in the extent of morphogenetic zones from the Upper Pleistocene up to the present.

Research of the Makalu Barun region was aimed especially at geology (e.g., Bordet and Latreille 1955a, b; Bordet 1961; Krummenacher 1961, 1966; Schärer 1984; Lombardo and Bortolami 1998), geomorphology and geoecology (Byers 1987a, b, 1996; Carpenter and Zomer 1996) as well as the dynamics of changes of the Himalayan environment during the late Quaternary (Chhetri and Cairs 2015; Chhetri et al. 2017; Byers et al. 2019), including natural hazards and risks. Publications concerning this environment have been evaluated by Kalvoda (1992, 2020). The largely glaciated part of the East Nepal Himalaya is an area exceeding 400 km^2 comprising complicated systems of hanging and valley glaciers, which flow from the extremely high crests. Therefore, other topics examined during the research in the Makalu Barun region have been the dynamics of glaciers and, especially, the Quaternary glacial history. Geomorphological research of landform patterns in the Chomolongma and Makalu Massifs and the Barun Khola valley regions has been undertaken by Kalvoda (1978, 1979a, b, 1982, 1984a, b, 1992, 2004, 2007 and 2020). The observation of landforms provides evidence of very dynamic landscape evolution and indicates the extraordinary features of natural hazards in the East Nepal Himalaya (Kalvoda and Emmer 2021).

In the context of environmental aspects and geoecology of the Makalu Barun region, previous articles have dealt with human disturbance (Byers 1996), forest ecology (Carpenter and Zomer 1996) and landscape analyses using satellite data (Zomer et al. 2001a, b, 2002). Zoological studies in the Barun Valley have been sporadic. Gregori and Petrov (1976) reported small terrestrial mammals collected during the Yugoslav Himalayan expedition to Makalu in 1972. Our collections of small terrestrial mammals and their ectoparasites (chigger mites and ixodid ticks) in the Makalu Barun region are discussed in papers by Daniel (2015, 2016 and 2017). Other publications concern birds (Daniel and Hanzák 1993), fleas of small mammals (Smit and Rosický 1976), chigger mites (Daniel and Stekolnikov 2009), mites (Dusbábek and Daniel 1975; Samšiňák and Daniel 1978), parasitic helminths (Baruš et al. 1975; Baruš and Daniel 1976; Moravec and Daniel 1976) and synanthropic flies (Gregor and Daniel 1976). Soil micromycetes in samples collected up to 4,900 m have also been described (Janečková et al. 1977).

The Makalu Barun National Park (1,500 km^2) with a buffer zone (830 km^2) was established in 1992. Therefore, our principal zoological data and field documents were obtained twenty years before the nature conservation in this territory. It has been designated as a *Strict Nature Reserve* (Carpenter and Zomer 1996) in order to protect natural ecosystems and processes in an undisturbed state for scientific study, environmental monitoring and the maintenance of genetic resources.

The structure of presented paper involves necessary review and original parts. The first section (2nd–4th chapter) is based on condensed survey of the high-mountain environment, recent geomorphic processes and occurrence of small mammals in the Makalu Barun region. New results of the study are presented in the 5th and 6th chapter. This original section concerns the origin, expansion and migration of small terrestrial mammals in the studied area determined by a correlation and integration of geomorphological and zoological data. Discussion takes an interest especially in current biogeographical hazards associated with rapid changes of the environment in the Himalaya.

2. A concise survey of the high-mountain environment

A comprehensive interpretation of the analysis of zoological and geomorphic materials from the Makalu Barun region assumes the use of basic knowledge about the current natural environment of the East Nepal Himalaya. The Makalu Massif represents the uppermost orographical and structural unit of the High Himalaya (Fig. 2). In the lowest part of this mountain group occur zones with geomorphic signatures of the structural unconformity overlying the lower topographic levels of the Peak III, Peak IV and Baruntse Massifs. The elevations of the Makalu crests between the Japanese Col and the Chago La are still some 1,500–1,700 m higher than these mountain groups, being comparable with the summits of the Chomolongma Massif (Odell 1925, 1948; Bordet 1961, 1970). The Makalu and Chomolongma Massifs have excellent patterns of geological structure on steep walls (see e.g. Searle et al. 2002, 2003). The great broken georelief (Fig. 3) stimulate effectiveness of cryogenic and glacial modelling. Ice masses whose bedrock dips steeply and rapidly move downhill into periglacial morphoclimatic zone where they remain stagnant and mostly abrade the earlier glacial deposits of the valley floors.

The main representatives of the High Himalayan nappes in the Makalu Barun region are the metamorphic rock complexes of the Barun nappe (Bordet and Latreille 1955a, b, c; Krummenacher 1961, 1966). Tectonically located higher is the Makalu nappe, containing rocks of both the Barun group and the Makalu Formation. These rocks form the main ridge of the High Himalaya, together with the Chomolongma nappe, in which the Chomolongma group rocks overlie the upper portion of the Makalu Formation (Kalvoda 1978, 1992). In the Makalu Massif area (Fig. 2

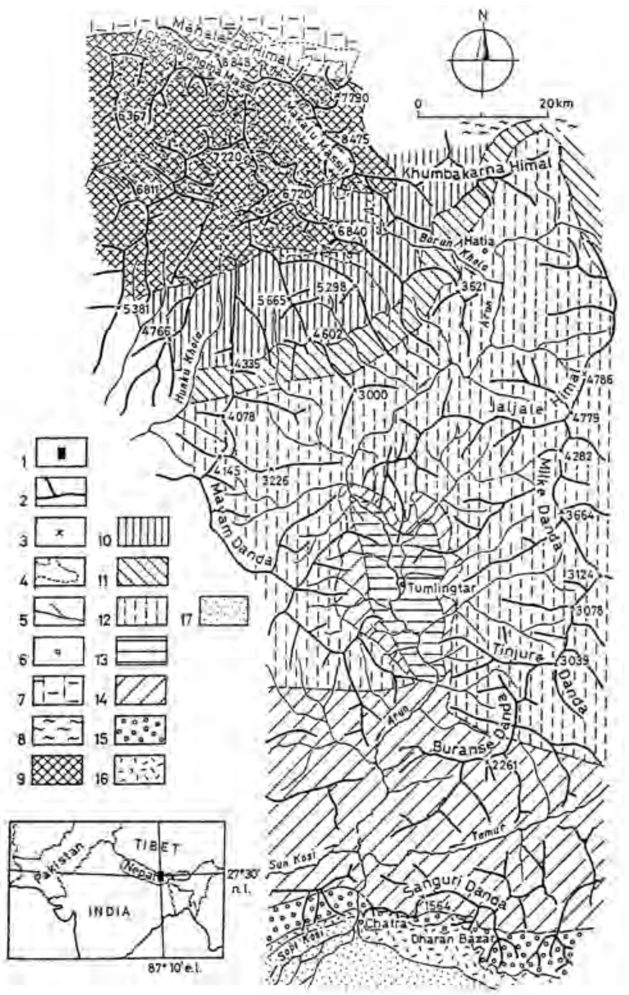

Fig. 2 Orographical patterns and geomorphological units of the East Nepal Himalaya between the Chomolongma and Makalu Massifs and Sapt Kosi lowland (Kalvoda 1992, 2020). Key: 1 – studied area, 2 – main mountain ridges, 3 – elevation points (in meters above sea level), 4 – glaciers, 5 – rivers, 6 – villages; 7–17 geomorphological units: 7–8 high-mountain relief on the sedimentary formations and crystalline rocks of the Trans-Himalaya: 7 – with alpine-type (arête) landforms, 8 – with predominance of periglacial, structural-denudation and erosion landforms in a semi-arid cold climate; 9–11 high-mountain relief on crystalline rocks of the High Himalaya: 9 – with alpine-type (arête) landforms, 10 – with predominance of periglacial, erosion and structural-denudation landforms in a humid cold climate, 11 – structural-denudation landforms of frontal parts of the High Himalayan nappe (Main Central Thrust); 12 – 14 mountainous relief on the crystalline rocks of the Lesser Himalaya: 12 – deeply eroded and highly dissected relief of the Tinjure nappe, 13 – Tumlingtar intermountain basin, 14 – dissected hilly reliefs of the Tumlingtar, Sanguri and Buranse Formations; 15 – 17 polygenetic reliefs on the Pliocene to Recent sediments of the Sub-Himalaya: 15 – dissected relief of the Siwalik hills, 16 – Late Quaternary accumulation landforms at the foot of the Siwalik, 17 – Sapt Kosi lowland.

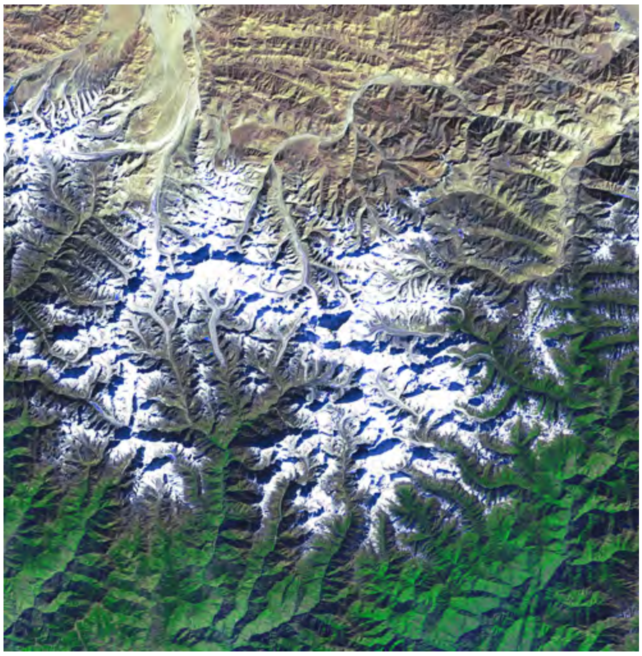

Fig. 3 Visible diversity of landscapes in the Nepal Himalaya and Trans-Himalaya recorded by satellite image on 5 January 2002 by Landsat 5. The High Himalaya range between the Cho Oyu, Chomolongma and Makalu Massifs (from the west to the east) with extensive glaciation is situated in central part of the image. Tibetan semi-arid landscape in the north and Nepalese humid monsoonal landscape in the south of the High Himalaya are striking. These landscape types are interconnected by the antecedent valley of the Arun river (situated in right part of the image) flowing from the north towards the south.

and 4), the Chomolongma Group occurs only near the unnamed peak of 7,502 m elevation, where its lower part consists of pelitic, slightly metamorphosed rocks of Palaeozoic age.

The Makalu Formation consists of a number of Miocene granite bodies (Bordet 1961, 1970; Kalvoda 1979a, b) associated with extensive contact injection zones intruded into the lower part of the Chomolongma Group and the upper part of the Barun Group. The later consists mostly of biotite gneisses, originally of Precambrian age. At lower elevations, in the Barun valley below the Shershon site towards the Main Central Thrust, the Barun Group consists of an up to 5,000 m thick formation of banded biotite gneisses (Fig. 1) with garnet, kyanite and silimanite with interlayered garnetiferous amphibolites, pyroxenite lenses and granulites. Compact bedrock relief is developed on black paragneisses along the lower parts of the eastern cliffs of Peak IV Massif, below elevation points 5,860 and 6,260 m, in the foreland of the southwestern wall of the Makalu Massif and the crests near the Col Sherpani.

The biotite-sillimanite gneisses in the upper part of the High Himalayan series were intruded by tourmaline leucogranites of the Makalu Massif in the period 24.4–21.7 Ma ago (Schärer 1984; Lombardo and Bortolami 1998; Visona and Lombardo 2002). The bedrock relief on the yellowish-white granites is developed especially on the ridges and walls of the Peak IV, Baruntse, Chago and Makalu Massifs. The largest area of this bedrock relief is occupied by the slopes and cliffs on the zones of granites injected into paragneisses. Rocky slopes are highly dissected with frequent ledges and troughs, and often-displaying block disintegration of rocks with corresponding autochthonous slope debris.

The Upper Barun glacier (Fig. 4) and its older moraines lie between 27°47′ to 27°58′ N and

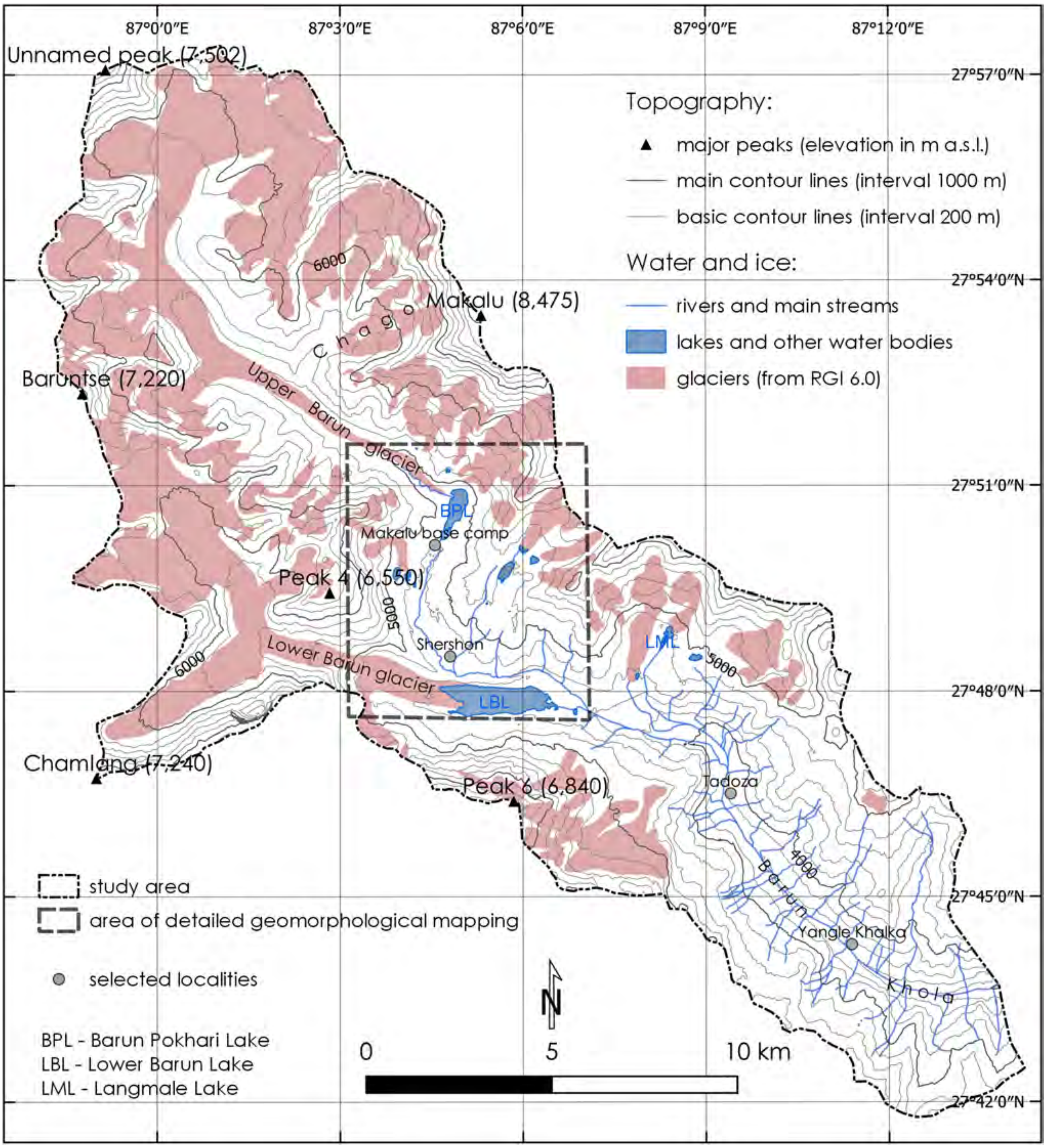

Fig. 4 Geographical position, orography and varied terrain in the central part of the Makalu Barun area (Kalvoda and Emmer 2021).

86°58′ to 87°08′ E at the western foot of the Makalu (8,475 m a.s.l.). The altitudes of the crests surrounding the Barun glacier basin are above than 6,000 m. The present-day Upper Barun glacier is 23 km long, with its´ difference in altitude being 1,370 m over this distance. The Upper Barun glacier basin adjoins the valleys of the Lower Barun glacier and the Hunku glaciers in the southwest, and the Imja and Kangshung valleys further to the northeast. In the north, the upper part of the Barun area is bounded by the unnamed peak of 7,502 m elevation which forms the eastern limit of the Chomolongma Massif. Towards the west, the Upper Barun glacier is connected with the Baruntse Massif (7,220 m) across the Cho Polu (6,734 m) by a north-south trending series of crests. Further south, three lateral glacial valleys occur. Above these the main connecting ridge adjoins the extensive Peak IV Massif (6,720 m). The opposite eastern side of the Upper Barun glacier valley is formed by crests between the Pethangtse (6,710 m) and the Chago (6,860 m), which continues to the southeast as the dominant orographic feature of the Makalu Barun region, i.e. the Makalu Massif (8,475 m). In addition to the main peak, the southeastern summit (8,010 m) of the Makalu, the

Chomo Lönzo (7,790 m) and Kangshungtse (7,640 m) also form parts of the Makalu Massif.

Continuation of the Lower Barun glacier valley represents the Barun Khola river valley, which at 1,350 m a.s.l. enters the antecedent canyon of the Arun river (Wager 1937). The total length of both joint-controlled Barun valleys from the main Himalayan ridge to the Arun river canyon exceeds 54 km. Below the confluence with the Barun Khola river, the Arun canyon is incised as deeply as 1,050 m a.s.l., and after a further 12 km, near the village of Num, it is at 850 m a.s.l. The deep dissection of the mountain relief has also been preserved in the Lesser Himalaya from the intermountain Tumlingtar basin to the structurally controlled denudational slopes of the Main Boundary Fault at the southern margin of the mountain range (Kalvoda 1978; Brunsden et al. 1981).

Described orographical section across the East Nepal Himalaya encompasses a series of altitudinal-controlled climatic zones each characterised by corresponding types of geomorphic exogenous processes and vegetation conditions. The georelief configuration and altitudinal pecularities of the mountain belts are responsible for the remarkable variations of climate within the Himalayan regions (Fig. 2).

The altitude-dependent distribution of temperature in the East Nepal Himalaya may be characterised by the following average temperatures of the warmest month (July or August) in the main climatic zones of the region (Troll 1967; Daniel et al. 1985; Pratt-Sitaula 2004): very cold (above 5,200 m a.s.l.) less than 0 °C, cold (5,200–4,100 m) 0–10 °C, moderately cold (4,100–3,100 m) 10–18 °C, moderate (3,100–1,800 m) 18–25 °C, moderately warm (1,800–1,200 m) 25–30 °C and subtropical (below 1,200 m a.s.l.) more than 30 °C. These climatic zones vary somewhat with the boundaries increasing from west to east, as well as from south to north.

The perpetual snowline rises from altitudes of 5,400–5,500 m in the southern Khumbu Himal area to 5,600–5,700 m at the foot of the Chomolongma Massif and further to the north of the main crest up to 5,900 m a.s.l. (Odell 1925; Kalvoda 1978; Fushimi 1977, 1978). From recent observations, it follows that the perpetual snowline on the southern slopes of the Makalu, Lhotse, Khumbutse and Cho Oyu Massifs oscillates between 5,400 and 5,600 m, and on the northern slopes of the Sagarmatha and the Cho Oyu between 5,800 and 5,900 m a.s.l.

In the periglacial area south of the Chomolongma and Makalu Massifs alpine meadows with *Juniperus squamata* and *Rhododendron nivalis* occur. This biogeographical zone is separated from the treeline (Fig. 3), which south of the main ridge of the High Himalaya represents the treeline of the semi-arid continental zone (Chhetri and Cairns 2015), by a zone of humid alpine meadows with *Rhododendron spp.*, *Lonicera spp.* and *Juniperus recurva*. Alpine shrubs and meadows occur abundantly at 4,100–5,200 m (Troll 1967; Chhetri and Cairns 2015), the continuous vegetation cover ending at 5,200 m a.s.l. In the Barun Khola valley (Fig. 4), the treeline runs on the sheltered slopes at 3,800 m a.s.l., and on the more humid shaded slopes at 4,200 m a.s.l., which are roughly 1,500–1,700 m below the snowline. The vicinity of the treeline represents a habitat characterised by *Betula utilis*, *Abies spectabilis* and shrubs of *Rhododendron campanulatum*; in drier places, *Abies* is replaced by *Juniperus recurva*. A sub-alpine forest between 3,100–4,100 m a.s.l. is occupied by *Betula utilis*, *Abies densa*, *Rhododendron arboreum* and other rhododendron species. In the range of 1,800–3,100 m a.s.l. is remarkable a subtropical evergreen mountain mist forest with *Pinus khasya*, *Quercus lamellosa* and other oak species, *Tsuga dumosa* and *Abies densa*. Between 800 m and 1,800 m a.s.l., a tropical evergreen forest predominates with *Betula alnoides*, *Lyonia ovalifolia*, *Toona ciliata* and *Phoebe lanceolata*. At altitudes below 800 m a.s.l., the hills are covered by a near-tropical deciduous forest dominated by the species *Shorea robusta* and *Terminalia tomentosa*.

The East Nepal forests abound in a wide variety of animals of which the most famous are snow leopard (*Panthera uncia*), black bear (*Selenarctos tibetanus*), musk deer (*Moschus moschiferus*) and Himalayan tahr (*Hemitragus jemlahicus*) in the higher mountain zones. In the middle mountains are found bharal (*Pseudois nayaur*), ghural (*Nemorhaedus goral goral*) and kankar (*Muntiacus muntjak vaginalis*), whilst the Siwalik Hills are colonised by elephants, tigers, panthers and rhinoceros. All the Himalayan regions are also remarkable for their hundreds of species of birds (Mehta and Kellert 1998; Khanal et al. 2014).

3. Recent geomorphic processes and phenomena

Landforms in the East Nepal Himalaya and neighbouring regions provide evidence for the nature of very dynamic landscape evolution, including extensive tectonic movements, extremely high rates of denudation, sediment transfer and deposition (Kalvoda 1978, 1992). We present our observation of recent geomorphic processes in the Makalu Barun region in four main morphoclimatic areas (Fig. 5 and 6): 1) Extreme glacial zone; 2) Glacial zone; 3) Periglacial zone; and 4) Seasonally cold / warm humid zone. We have been dealing this current topic since 1971 (Kalvoda 1976; Daniel and Kalvoda 1978), while we emphasized the significant changes of the high-mountain environment particularly in recent works by Kalvoda (2020) and Kalvoda and Emmer (2021). Recent geomorphic processes and related phenomena represent key features of the environment, which control current expansion and migration of small mammals in the Himalaya.

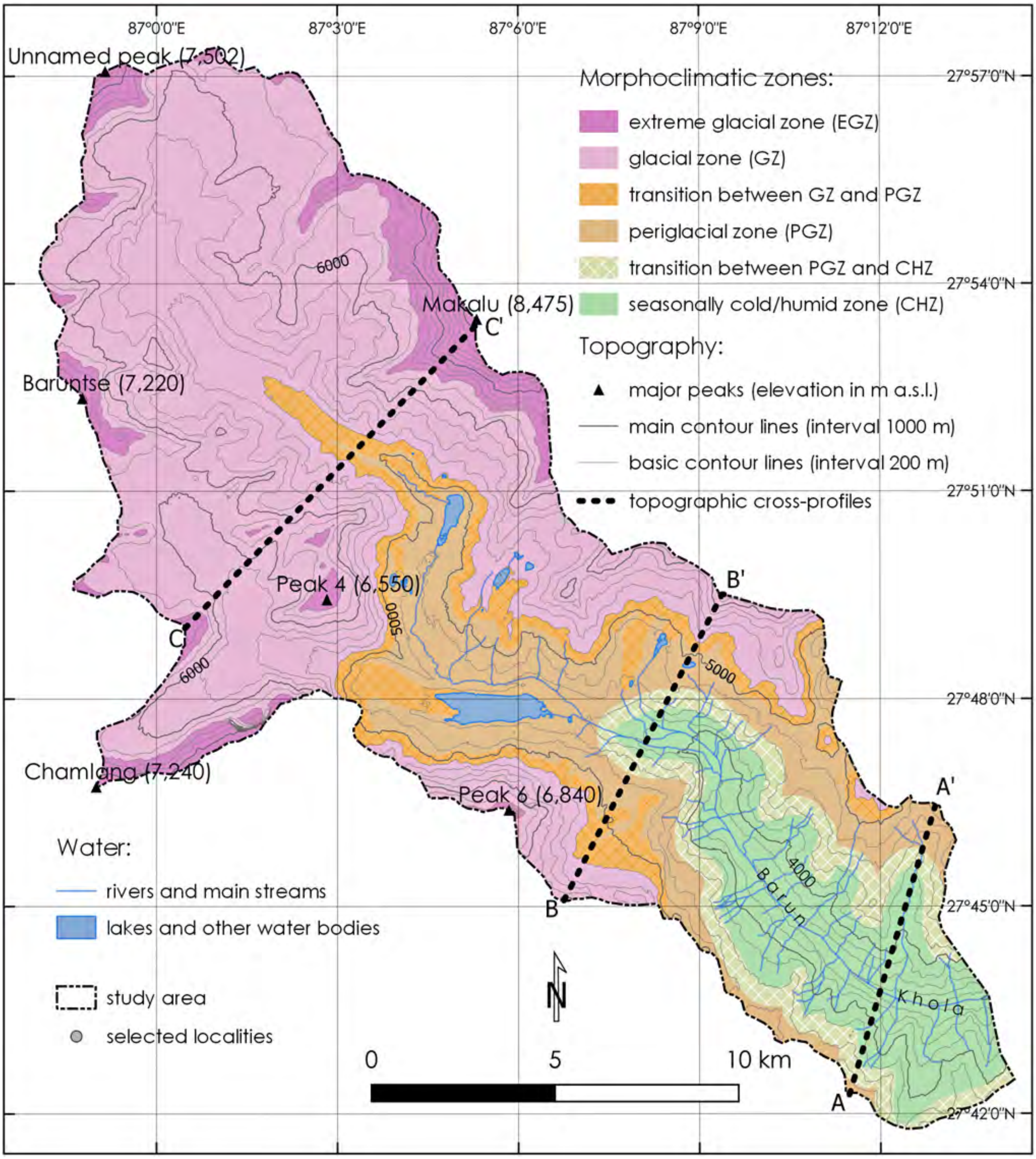

Fig. 5 Delimitation of studied morphoclimatic zones in the Makalu Barun region of the East Nepal Himalaya. Cross-profiles A–A', B–B', C–C' are presented at Figure 6. Definition of four morphoclimatic zones and two transitional zones (modified after Kalvoda and Emmer 2021):

Morphoclimatic zone	Definition
Seasonally cold/humid zone (CHZ)	delimited on a basis of the presence of compact vegetation cover (trees and rhododendron shrubs)
Transition zone between CHZ and PGZ	500 m upstream distance buffer from the limit of the Seasonally cold/humid area
Periglacial zone (PGZ)	located between transition buffer area of CHZ and transition area between PGZ and glacial zone (GZ)
Transition zone between PGZ and GZ	250 m downstream distance buffer from the 5,200 m a.s.l. overlaid and combined with glacial tongues reaching downstream this buffer
Glacial zone (GZ)	between 5,200 m a.s.l. and 6,400 m a.s.l.
Extreme glacial zone (EGZ)	above 6,400 m a.s.l.

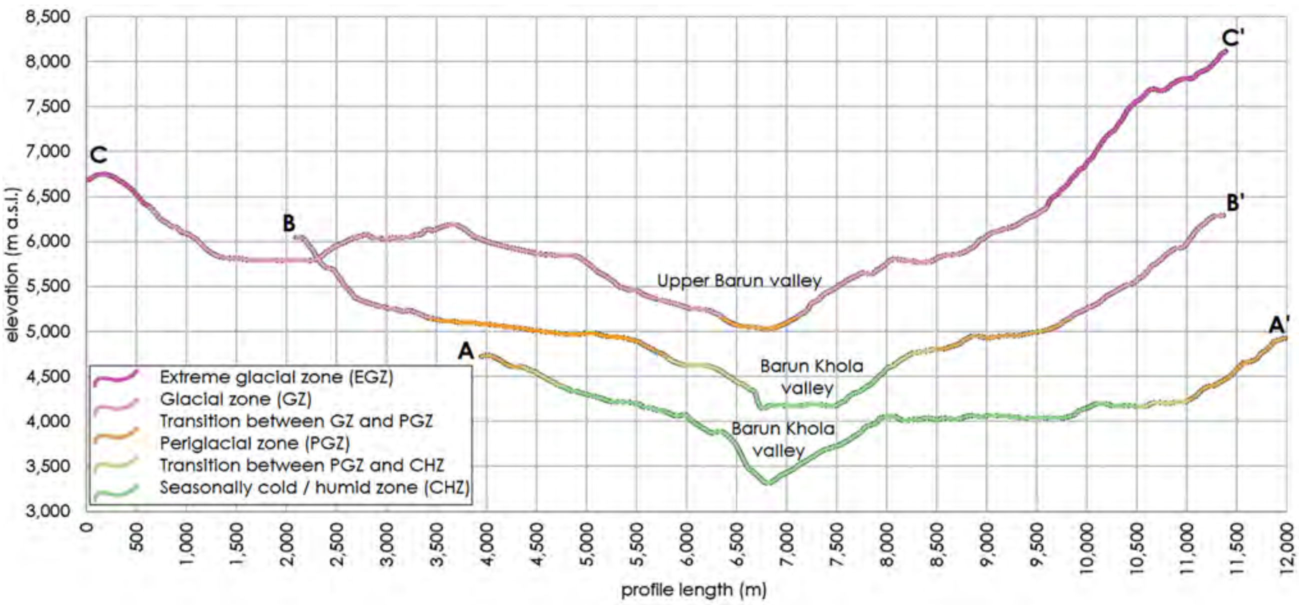

Fig. 6 Extension of morphoclimatic zones in the three cross-profiles throughout the Makalu Barun area (for the location of cross-profiles see Figure 5; after Kalvoda and Emmer 2021).

Fig. 7 Southeastern area of the Chomolongma Massif near the head of Upper Barun valley. The steep cliffs behind the Cho Polu ice dome (6,734 m) rise up to the Lhotse (8,501 m) and Lhotse Shar (8,383 m) and pass into the crest of unnamed peaks with heights 7,596 and 7,502 m. Clouds and snow hide the catchment area of the Kangshung glacier situated below the eastern face of the Sagarmatha (8,847 m). Photograph by Jan Kalvoda (May, 1973).

3.1 Extreme glacial zone

The extreme glacial area with a remarkable landscape of alpine-type (arête) ridges displays an effective combination of deep cryogenic weathering with a complex of glacial and nival morphogenetic processes in the very cold and semi-arid environment (Fig. 7). The intensity and duration of temperatures below freezing point have led to deep rock disintegration and macrogelivation (Kalvoda 2007). The largest areas of glaciation are concentrated in the upper end of the Upper Barun glacier valley, which cuts between the Chomolongma and Makalu Massifs into the main ridge of the High Himalaya. The steep cliffs lacking permanent snow and ice cover, underwent deep cryogenic disintegration, and were subjected to aeolian corrasion; the harder rocks and dykes being selectively carved out. Field observations during the period 1971–2006 as well as later, together with present remote sensing data (Kalvoda and Emmer 2021), have shown that conspicuous recent changes in the rock slope patterns and volume of ice masses accompanied by a recession of the frontal parts of hanging glaciers, are only in the lower parts of the mountain walls.

3.2 Glacial zone

The present-day glaciation of the Makalu Barun region displays regression signatures due to the small amount of precipitation and the expansion of the periglacial zone by recent warming of monsoonal climatic conditions. The perpetual snowline oscillates on the southern slopes between 5,400–5,600 m, and on the northern slopes between 5,700–5,800 m. The spreading of the periglacial zone to the detriment of lower areas of the cold glacial zone is striking (Kalvoda 1992, 2020; Kalvoda and Emmer 2021). The valleys and ridges are fully filled with glacier masses at high altitudes above ca 6,000 m. A remarkable phenomenon is also the occurrence of the relics of glacial and related sediments of Upper Pleistocene and Holocene age.

The valley glaciers in the Makalu Barun region arose by the retreat of a large glacier (Fig. 8) and it is splitting up into smaller flows. The largest slope glaciers are developed on broad ridges in the vicinity of the 6,250 m and 6,170 m peaks and below the southern Makalu face. Here hanging glaciers form the main feeding source for the lower-lying slope and

Fig. 8 Landforms in the foreland of the Upper Barun glacier situated between 4,900 and 4,700 m a.s.l. and the Barun Pokhari lake. Relics of Upper Pleistocene to modern moraines as well as Holocene to Sub-recent lacustrine sediments and outwash fan deposits have been preserved (see also Figure 9). The oldest conserved glacial sediments of the Upper Barun glacier originated during the Late Glacial Maximum. Rock glaciers and recent landslide deposits are also remarkable. Photograph by Jan Kalvoda (April, 1973).

valley glaciers and avalanche masses (Kalvoda 1978, 1979a, b). Remarkable geomorphic signatures of substantial loss in the volume of glaciers during the late Holocene are expressed by a variety of landforms (Fig. 7 and 8). Gravitational landforms include active talus fans developed at the foot of huge rock faces as well as older talus fans of great areal extent, and accumulation piles resulting from avalanches, rockfalls and landslides.

3.3 Periglacial zone

High rates of erosion and denudation have been observed in the periglacial environment around the lower part of glaciated area (Fig. 5 and 6). Intense freeze-thaw activity of water is the basis of periglacial processes and related landforms. A remarkable enlargement of the active periglacial zone increases the volume of transported products of erosion and denudation and the level of geomorphological hazards, including frequent mass movements (triggered also by earthquakes; compare e.g. Fort 2000; Avauac 2003; Bilham 2019), avalanches, landslides and flash as well as outburst floods (Byers et al. 2019; Kalvoda and Emmer 2021). The current decrease in the distribution of permafrost has implications for landscape stability, which is reflected in solifluction movements, rock-glacier evolution and sediment release into streams and rivers.

In the foreland of glaciers in the Barun valley a system of slope, glaciofluvial, lacustrine and fluvial accumulation landforms have developed (e.g. Fig. 8). The Late Holocene to modern terraces and cones of outwash sediments represent the earlier of two generations of glaciofluvial landforms which occur in the depressions between individual moraine ridges. They occur on the floor of the valley between the Holocene frontal moraines of the Upper Barun glacier and the left lateral sub-recent moraine of the Lower Barun glacier near the Shershon site (Fig. 9). From the Lower Barun icefall south of the Peak IV Massif to the Tadosa site, the valley floor is filled with ridges of fossilised oscillation moraines, rockfalls, talus fans and the retreating glacier tongue.

In the periglacial area of the Barun Khola valley between the present-day end of the Lower Barun glacier and Yanle Khalka locality are conspicuous features of rapid nival and fluvial erosion, active exfoliation sculptures on the rock walls and varied slope processes (Fig. 10). Remarkable are products of recent flash floods, landslides and related mass movements. Mass-wasting processes are intensified and slopes are deeply denuded (Kalvoda and Emmer 2021). Very marked periglacial landforms are rock glaciers that have been situated on steep slopes above glacier basins and in zones from which glaciers have retreated but a cold climate still persists.

The presence of recent and former lakes of glacial origin on the Barun valley floors is indicated by three terraces of lacustrine sediment up to 6 m thick, lying between the fronts of the tongues of the Upper Barun glacier and the Shershon site, surrounded throughout by fossil moraines. The middle of these is the largest, situated at 4,850 m a.s.l. between the sub-recent frontal moraines of the Upper Barun glacier and the glacier of the eastern faced of Peak IV. Minor relicts of lacustrine terraces lie on the banks of the Barun Pokhari lakes at two levels; the higher of the terraces corresponds to the level of the filled lake before the collapse of the morainic dam.

In the periglacial morphoclimatic zone extends a vegetation belt of alpine shrubs and meadows with typical representatives of *Rhododendron* species, *Juniperus* and *Lonicera*. Sporadic flowering plants appear in protected places on steep scree-covered slopes even in the vicinity of the snowline. The upper boundary of the alpine steppe is in some places modified by rock outcrops. At altitudes of 4,500–5,000 m, the granular character and occasional movements of sub-recent to modern lacustrine and glaciofluvial sediments hinder and retard the establishment of vegetation over large areas.

The contact of the sub-recent moraines of the Upper Barun and Chago glaciers at 5,450 m a.s.l. (Fig. 11), covered relatively continuously with grass and moss, is the uppermost locality at which plants occur. Above 5,200 m, the zone of alpine shrubs and meadows passes into an extremely cold semi-arid zone with moss and lichen assemblages. Organic landforms include rocky outcrop surfaces and detritus affected by

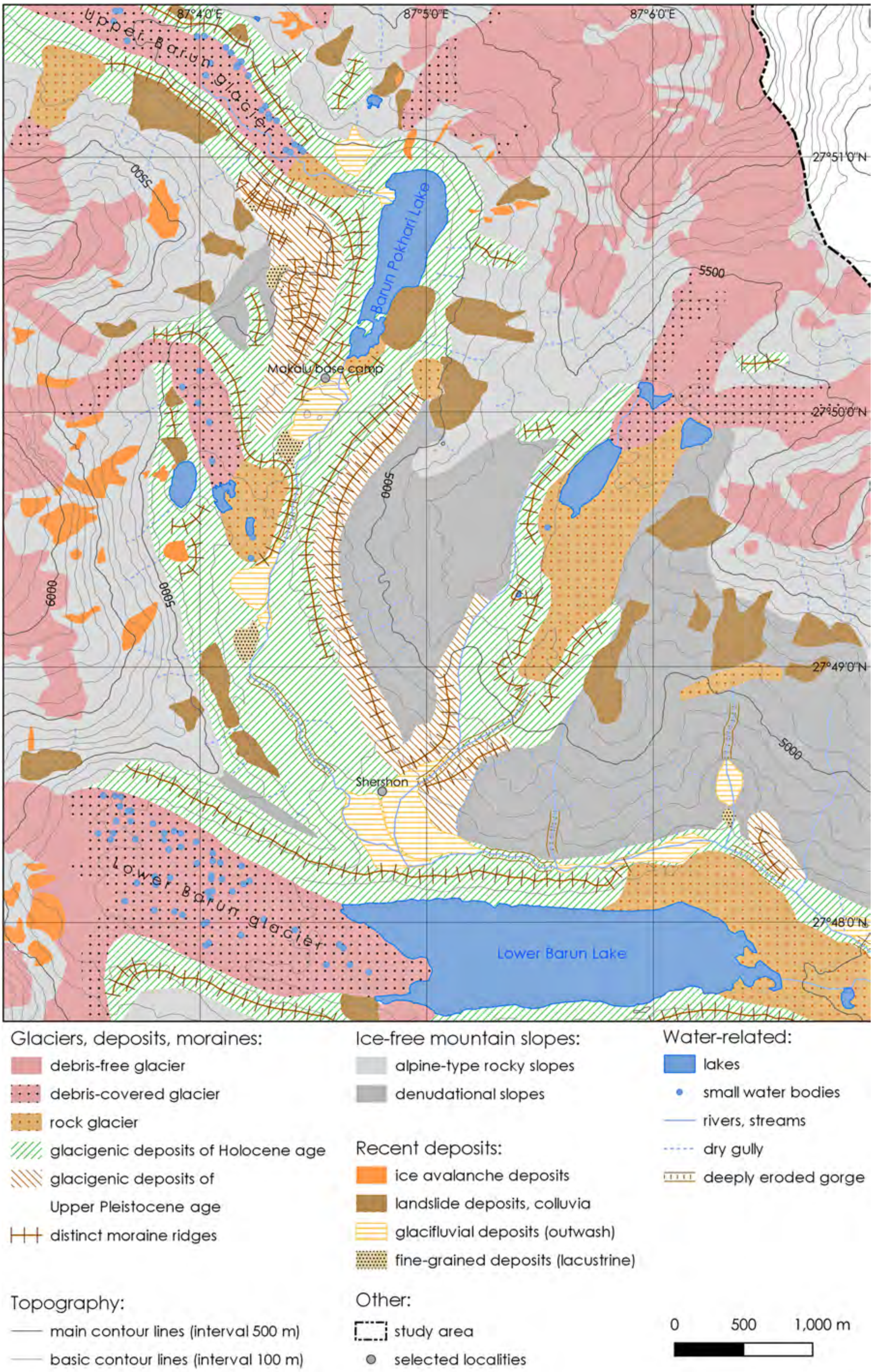

Fig. 9 Geomorphological map of the area between the southern face of the Makalu Massif and the Lower Barun glacier (Kalvoda and Emmer 2021).

Fig. 10 Landscape around the Lower Barun glacier between the icefall above Shershon site (4,752 m a.s.l., in the background) and Phematan (3,483 m) in the Barun Khola valley developed in the paragneisses of High Himalaya nappe. Remarkable are detachment planes of rockfalls, glacial and glacifluvial deposits as well as accumulation landforms of landslides and related mass movements. Photograph by Jan Kalvoda (May, 1971).

Fig. 11 High-mountain landscape above the permanent snow line (5,500–5,600 m a.s.l.) west of the Makalu Massif gives remarkable evidence for retreating of glaciers, extremely high intensity of weathering processes and varied mass movements in very cold and semi-arid climatic conditions. The hill of glacigenic and slope deposits (5,450 m a.s.l.) in the central part of figure was the highest site where *Alticola stoliczkanus* was found. Photograph by Jan Kalvoda (April, 2006).

biogenic weathering above the upper boundary of the alpine steppe (at 4,950–5,100 m a.s.l.), which is irregularly covered with mosses and especially lichens.

3.4 Seasonally cold/warm humid zone

The Barun Khola canyon-like valley has a strongly U-shaped form and it is primarily of glacial origin with the main stages of its landform evolution during the Middle and Late Pleistocene. The periglacial

Fig. 12 Vegetation zone of the subtropical evergreen mountain mist forest occurs in the lower part of the Barun Khola valley up to 3,100 m a.s.l. Epiphytic plants, receiving water from air humidity, cover the trunks and branches of trees and shrubs. Photograph by Milan Daniel (March, 1973).

weathering features of the marginal ridges of the Barun Khola valley disappear even before this valley enters the rocky cliffs of the High Himalayan nappe in the evergreen monsoon mountain forest zone. The Barun Khola valley floor, at up to 2,800 m a.s.l., is covered by thick deposits of glaciofluvial and slope sediments of Holocene age cut by vertical erosion from the Phematan site to as low as the paragneisses and granulites bedrock of the lower part of the High Himalayan nappe. At altitudes in the range of 1,800–3,100 m is remarkable a subtropical evergreen mountain mist forest (Fig. 12) with *Pinus khasya*, *Quercus lamellosa* and other oak species, *Tsuga dumosa* and *Abies densa*.

The Barun Khola and Arun canyon-like valleys are areas of frequent natural disasters with high risks involved to all types of human activities (Kalvoda 1984a, b, 2007; Byers 1996; Chhetri et al. 2017). A large number of rockfall accumulations has been found in the lower part of the Barun Khola valley. The erosion and denudation of rock massifs is driven by tectonic activity and the humidity of the summer monsoons. Makalu Barun National Park and Conservation area protects a broad range of Himalayan forest types, ranging from near-tropical dipterocarp monsoon forest (up to 400 m a.s.l.) to subalpine conifer stands (4,000 m a.s.l.). Below ca 2,000 m a.s.l. forests are strongly affected by subsistence agricultures (Carpenter and Zomer 1996) and above 2,000 m a.s.l., a cool, humid climate suppresses agricultural activity.

4. The occurrence of small terrestrial mammals in the Makalu Barun region

Small terrestrial mammals and birds were collected by Milan Daniel in the complex of Barun valleys (Fig. 9), which are formed by the Upper Barun and Lower Barun glaciers from which the Barun Khola river is rising as the right tributary of the Arun river. There were selected seven main localities (in a span of 3,450–5,950 m a.s.l.) of differing landform patterns, the current environmental conditions, and geomorphological history. At these sites the collection was carried out in all habitats (biotopes) allowing the occurrence of small terrestrial mammals (Tab. 1).

Landscape patterns of the zoological sample sites were as follows:

1. Phematan (27°44′20.86″N, 87°11′15.04″E; 3,483 m a.s.l.): 1A – Glacio-fluvial deposits on the valley floor, on the right bank of the Barun Khola river (running from NWW to SEE), comprised coarse sandy or gravel material overgrown with turf. These deposits were bordered by a humid coniferous forest mixed with rhododendrons. In summer, the glacio-fluvial terrace serves as pasture and an occasional camping site for shepherds. 1B – Fluvio-glacial deposits on the left bank of the Barun Khola river, densely overgrown with low creeping shrubs and partly covered with large rock fragments, devoid of any traces of human activity. 1C – Accumulation of a rockfall with coarse sandy material, covered with turf and moss, on the left bank of river. 1D – Forest margin near the preceding biotope with numerous uprooted trees situated on the left bank of river.

2. Yanle Khalka (27°46′21.31″N, 87°09′15.72″E; 3,743 m a.s.l.): 2A – Upper Holocene river accumulation terrace is composed of coarse sand, gravel and boulders, with the vegetation strongly modified by grazing, when shepherds inhabit the surface of river terrace. 2B – Edge of fir-tree forest (*Abies spectabilis* and rhododendrons) situated on glacio-fluvial deposits. 2C – Fluvio-glacial terrace with chaotic piles of rocky blocks, covered with boulders and scattered areas of turf. The uneven surface of the terrace is a result of intensive periglacial processes. 2D – Fir-tree forest on the end of a large talus slope. 2E – Edge of a fir-tree forest with numerous uprooted trees located on slope deposits.

3. Tadosa (27°47′59.25″N, 87°06′26.43″E; 4,555 m a.s.l.): 3A – Loamy screes under walls built by crystalline rocks exposed at the eastern side of the valley. The slope material consists of a sandy deposits accumulated by perennial melt water from snow fields, and is overgrown with *Lonicera* sp. 3B – recent aluvium of the river and moraines with willow shrubs in front of the Lower Barun glacier. 3C – Sandy-debris talus fixed by vegetation (rhododendrons, tsuga, willows, developed herb layer) serving as a summer pasture.

4. Shershon (27°48′29.00″N, 87°04′40.07′′E; 4,752 m a.s.l.): 4A – Paraglacial depression situated between the Upper Holocene moraine of the Lower Barun glacier and the right side of valley covered with debris and sandy material. Turfs and creeping rhododendrons are present. 4B – Dissected surface of the washed out fluvio-glacial cone on the valley floor where a stone enclosure for round up of sheep and goats had been built at the highest level of the valley which was utilized as pasture. 4C – Southern edge of the recent frontal moraine of a slope glacier situated below the eastern face of Peak IV near the plateau of lacustrine deposits.

5. Front of the Upper Barun glacier (27°50′40.01″N, 87°05′16.08″E; 4,930 m a.s.l.): 5A – The base camp of the expedition at the base of Upper Pleistocene moraine. 5B – Boulders scattered at the base of a large Holocene moraine. 5C – Recent moraine of a slope glacier of the eastern face of Peak IV. 5D – The hill part of a side Holocene moraine of the Upper Barun glacier. The moraine surface is remodelled by periglacial processes and is covered with initial polygonal soils. 5E – the Holocene moraine situated along the left side of the Upper Barun glacier.

6. Junction of the Upper Barun and Chago glaciers (27°52′49.80″N, 87°02′14.32″E; 5,490 m a.s.l.): 6A – Rampart of the Upper Holocene moraine above the junction of the glaciers, formed by chaotic block accumulations. In this site, Camp 1 of the French climbing expeditions was situated in 1954, 1955 and 1971. 6B – NW of the preceding biotope, about 500 m away, there are large rocky slopes covered by strongly weathered blocks and scree of paragneises and granites.

7. The top of the rock tower in the lower part of the SW face of Makalu (27°51′47.50″N, 87°05′16.08″E; 5,950 m a.s.l.): It is situated at the end of a rocky ridge between hanging glaciers. Camp 1 of the Czechoslovak climbing expedition was situated at a small platform of cryogenically weathered black gneisses with dykes of granites. The only ice-free way leading to this site is crossing precipitous rocky outcrops and steep slopes covered by debris of crystalline rocks.

Altogether 139 small terrestrial mammals were collected and evaluated taxonomically (Daniel and Hanzák 1985). They comprised 11 *Soriculus nigrescens centralis* (Hinton 1922), 8 *Episoriculus caudatus soluensis* (Gruber 1969) (Soricomorpha, Soricidae), 10 *Ochotona roylei roylei* (Ogilby 1839) (Lagomorpha, Ochotonidae), 98 *Neodon sikimensis sikimensis* (Hodgson 1849), 10 *Alticola stoliczkanus* (Blanford 1875) (Rodentia, Cricetidae), and 2 *Niviventer eha* (Wroughton 1916) (Rodentia, Muridae); see Table 1. Birds were collected in the same localities as small mammals. Most of them were shot by gun and

Tab. 1 Distribution of small terrestrial mammals by locality found in the Barun valley during the year 1973 (Daniel 2015, 2017).

	Date	Species	Number
Phematan 3,450 m a.s.l.	25/03–4/04	*Episoriculus caudatus soluensis*	4
		Soriculus nigrescens centralis	7
		Neodon sikimensis sikimensis	44
		Niviventer eha	2
		Ochotona roylei roylei	7
Yanle Khalka 3,600 m a.s.l.	4–9/04	*Episoriculus caudatus soluensis*	3
		Soriculus nigrescens centralis	4
		Neodon sikimensis sikimensis	35
		Ochotona roylei roylei	1
Tadosa 3,900–4,000 m a.s.l.	12–19/04	*Neodon sikimensis sikimensis*	17
Shershon 4,600 m a.s.l.	26/04–2/05	*Neodon sikimensis sikimensis*	3
Front of the Barun Glacier 4,900 m a.s.l.	21/04–14/05	*Alticola stoliczkanus*	9
		Ochotona roylei roylei	1
Junction of Barun and Chago glaciers 5,450 m a.s.l.	8/05	*Alticola stoliczkanus*	1
Top of the rock tower SW face of Makalu 5,950 m a.s.l.	8/05	*Ochotona roylei roylei*	1
Total			139

only a few were caught in nets. A total of 94 birds of 28 species were collected (Daniel and Hanzák 1993): Galliformes (three species), Charadriiformes (one), Columbiformes (one), Coraciiformes (one) and Passeriformes (22 species).

Representatives of the Soricidae (*Soriculus nigrescens* and *Episoriculus caudatus*) were found only in the first two valley zones described (Phematan and Yanle Khalka). Soricidae have not extended their range to higher altitudes, although suitable biotopes (primarily the forest composed of *Abies spectabilis*, drained by rivulets and with humid sparsely overgrown places) exist at Tadosa locality. Similar observations apply to *Niviventer eha.*

Neodon sikimensis is the most abundant small terrestrial mammal in the Barun valley penetrating (Table 1), ranging from the lowest zone to the level of the lacustrine terrace in the front of recent moraine of the Barun glacier. The great ecological adaptability of this species enables it to occupy all biotopes with favorable vegetation cover in the lower part of the valley, irrespective of their ages and origins. In the higher part of the valley, this species inhabits the fossil moraines stabilized by present-day vegetation, which are primarily rhododendrons. The upper boundary line of its observed distribution represents the Holocene moraine of a hanging glacier tongue at foot of the eastern face of Peak IV, which formerly also participated as a dike of the middle glacial lake.

The occurrence of *Alticola stoliczkanus* follows the upper range of *N. sikimensis* (Table 1). The glacigenous landforms designated as the upper limit of the distribution of *N. sikimensis*, demarcate the lower limit of the distribution of *A. stoliczkanus*. This species is a distinct hypsobiont in a landscape otherwise devoid of small terrestrial mammals. Despite the fact that Ochotona roylei was found at the highest altitude, its distribution is concentrated in much lower elevations, primarily in the section between Yanle Khalka and Tadosa sites (Fig. 10). This is in line with the overall distribution of O. roylei in Nepal, published by Thapa et al. (2018). These authors consider the occurrence of this species at an altitude above 5000 m a.s.l. to be rather exceptional and cite our find as the highest in Nepal so far. It is evidence of the high potential of adaptability of this pika to the environment of the high mountains. In doing so, an important factor in this herbivorous species is the consumption of fresh and dry plant material of a wide species spectrum, including mosses and lichens. Cercophagy (eating one's own droppings) is a supplement to the ability to make maximum use of the food.

Neodon sikimensis showed a clear preference for open spaces, but also readily inhabits both the forest edges (locality 1D; 2B, 2E) and the interior of dense forest (1B; 2D), where it was always the most abundant small terrestrial mammal. N. sikimensis is the only species among the small terrestrial mammals, which ranges from the lowest altitudinal zone of the Barun Khola valley into places high above the 4,900 m a.s.l., confirming the striking ecological adaptability of this species. Grassy open spaces inhabited by *N. sikimensis* (localities 1A, 1B; 2A, 2C; 3C) display characteristic piles of displaced soil and traces of burrowing. The greatest concentration of such signs of vole activity was observed in spaces, which serve

Fig. 13 Conifers grade of mountain forest with rhododendrons and *Abies spectabilis* fir is substantially destroyed above Phematan site in the Barun Khola valley (at 3,500 m a.s.l.) by human activities especially at summer pasturelands near the treeline. Photograph by Milan Daniel (May, 1973).

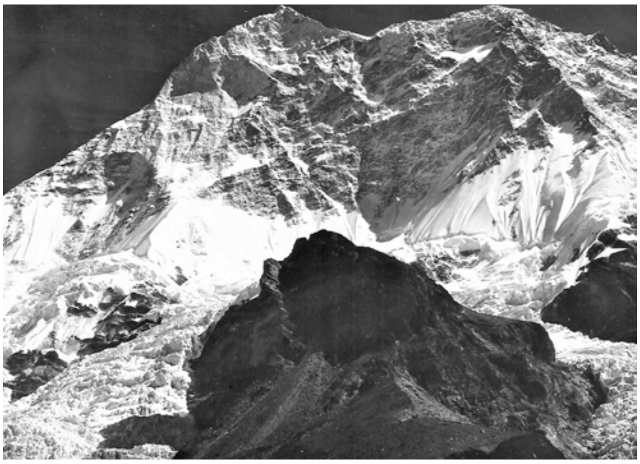

Fig. 14 Beyond the top of black gneisses tower (5,950 m a.s.l.) in the lower part of the south-western Makalu wall originated blocky fields of cryogenically weathered crystalline rocks. It was the highest site where *Ochotona roylei roylei* was found. Photograph by Milan Daniel (May, 1973).

as temporary round-up areas for pastured animals (Fig. 13).

Comparison of the results obtained in all localities where *N. sikimensis* occurred reveals how the presence of humans and pastured sheep flocks as well as economic activities producing heaps of organic waste in otherwise sterile landscape, can affect the occurrence of this species, which is showing a tendency towards synanthropy. Association of *A. stoliczkanus* was also influenced by human activities. The base camp of mountaineering expeditions, with stored foodstuffs and concentrated garbage, attracts *A. stoliczkanus.* The animals concentrated in locality 5A within three weeks of the base camp being established. The highest altitude at which *A. stoliczkanus* was found (5,450 m; locality 6A; Fig. 11) topographically coincides with an islet of Alpine tundra vegetation. Even in this case, however, the survival of local population may have been affected by human activities because in this locality the camps of French expeditions were pitched in 1954, 1955 and 1971. A considerable amount of garbage (primarily tin cans and other packaging) suggests that in those years there was an unusual supply of food for small terrestrial mammals.

Our finding of the pika *Ochotona roylei* at 5,950 m a.s.l. (Table 1) is also evidence of human influence on the Alpine fauna. This pika was found at the site of camp 1 of the Czechoslovak mountaineering expedition (Fig. 14), and in the previous year (in the autumn post-monsoon period 1972) a camp of the Yugoslav expedition to Makalu was pitched there. It is situated above the permanent snowline and is devoid of any vegetation except for lichens on rocks. The animal, in order to reach this place, had to overcome rocky slopes and of unconsolidated debris. This camp 1 was supplied with foodstuffs, which attracted the animal. Tracks in the fresh snow indicated that the pika first sought garbage outside the tents, later entering the tents and finally accessing the boxes containing food supplies, chocolate being the most attractive to the animal.

5. The origin of small terrestrial mammals

The High Himalaya functions as an almost impenetrable divide between the Palearctic (Tibetan) and Oriental (Indo-Malayan) biogeographical regions. At least since the Upper Pleistocene, life has been maintained at the forefront of the Himalayan glaciers, pushed back by them into lower elevations during repeated advances only to migrate again closer to the ridges during retreat of glaciation. These environmental processes took place during long-term orogenic uplift of mountain ranges by about 4,000–5,000 m in the East Nepal Himalaya during the Quaternary. The dynamics of landform evolution of the High Himalaya in the Quaternary have become a decisive factor in species distribution and in the direction of migratory routes of small terrestrial mammals.

The present state of the distribution and living conditions of small terrestrial mammals in the Barun region is controlled by the processes causing the colonization of these high-mountain areas. Two aspects are particular here in comparison and linking of biological and geomorphic data. All detected representatives of the Barun fauna are of Palearctic origin, while the only open contemporary aspect of the Barun valley is southwards in the direction of the Oriental biogeographic region. Weigel (1969) designates the species *Soriculus nigrescens, Episoriculus caudatus* and *Niviventer eha* as faunistic elements with Palearctic-arboreal Nepalese distribution (sensu De Lattin 1967); *Neodon sikimensis* as Palearctic-arboreal (Sino-Tibetan) element and *Alticola stoliczkanus* as Palearctic (Tibetan-eremic) species.

The Barun Khola river empties at 1,350 m a.s.l. into the canyon-like valley of the Arun river (Fig. 3),

Fig. 15 The deforested structural denudational slopes above the Barun Khola and Arun river valleys around the Sedoa village (27°35′N, 87°16′E; ca 3,400 m a.s.l.) are affected by strong precipitation and associated erosion processes of soils. The broken slopes are reshaped by forest burning, clearing and agricultural terrace fields up to altitudes of 3,200 m. Photograph by Jan Kalvoda (April, 2006).

Fig. 16 Pika *Ochotona roylei roylei* was found in the Barun valley at the altitudes of 3,450–5,950 m (after Daniel 1973; see also Figure 14). Photograph by Milan Daniel (April, 1973).

which rise from the glaciers of the northern slopes of the main Himalayan ridge and join the semi-arid cold zone of the Trans-Himalaya. It is remarkable difference between the semi-arid cold climate of Tibetan region in the north and Nepalese humid monsoonal climatic conditions in the south (e.g., Wager 1937; Bordet 1961; Kalvoda 1978, 2021; Chowdhury et al. 2022). The Arun river valley transects antecedently the rock assemblages of the High Himalaya, Lower Himalaya and Siwalik in the meridian direction, and opens into the Ganges Plain. This transverse suture through the High Himalaya, representing one of the most ancient relicts of the pre-Quaternary drainage pattern, might have been a corridor for the exchange of faunistic elements between the northern Tibetan Plateau and southern Indian sub-continent during the Quaternary. Today the confluence area of the Arun and Barun Khola rivers occurs in the zone of the warm and humid montane climate of the sub-tropical evergreen forest (Fig. 12). Extensive steep erosion and denudation slopes above the confluence of both rivers are situated in the seasonally cold/warm humid morphoclimatic zone (Fig. 15). Expansion of small mammals into the Barun valley is possible for species that can survive in these environments.

Climate change affects all Earth surface systems but with the greatest impact in high-altitude cold environments, especially through its impact on frost penetration and duration within the ground surface layers and by altering vegetation cover. We take into account the rapid uplift of the High Himalaya (Fig. 3) and substantial changes of its glaciation during the Quaternary. It is the period when small terrestrial mammals might have been differentiated to the level of today genera. The most interesting are the representatives of species and genera currently found at the highest elevations: *Alticola stoliczkanus*, representing the genus known in the Asian region since the Pleistocene, and *Ochotona roylei* (Fig. 16), belonging to the genus known (after Simpson 1945) also since the Pleistocene.

Analysis of the results obtained in our collecting sites (Table 1) shows that even the present state of georelief, climatic and vegetational conditions in the bottom part of the Barun valley would not prevent colonization by *Neodon sikimensis*, *Niviventer eha* and the two shrew species. Of these, only *N. sikimensis* is found above the timberline. The occurrence of pikas in the lowest zones of the Barun valley is not confirmed. Their presence in the Shipton Pass (27°41′01″N, 87°12′16″E; 4,216 m a.s.l.) indicates that their migration might have taken place through tributary hanging valleys. In contrast, the present distribution of *A. stoliczkanus*, which forms sharply limited and isolated population, has the upper occurrence close to the forefront and glaciated area of the Upper Barun glacier as high as the permanent snow line.

The High Himalayan ranges, preventing the migration of fauna and flora, were not an invincible barrier up to the Middle Pleistocene. There were favourable conditions for the southward spread of psychrophilic fauna, including representatives of the genus *Alticola*. During the Pleistocene, in the period of culminated collision orogeny, the Chomolongma, Makalu and Chamlang Massifs were uplifted. The faunistic connection between the deeply continental Tibetan Plateau and the Indian sub-continent was consequently interrupted both by the rising mountain vault and the beginning of its continuous glaciation. Only transverse morphotectonic sutures of the antecedent valleys in the High Himalaya, e.g. of the Arun river, remained open to the penetration of faunistic elements, namely during interglacial periods.

Small terrestrial mammals had to immigrated exclusively through the Arun river valley either from the area of contemporary Sibrung (27°41′31″N, 87°22′31″E; 1,800 m a.s.l.) at the mountain stream

Barun Khola mouth of the river Arun directly upward into the Barun valley, or indirectly through the Shipton Pass (27°41′01″N, 87°12′16″E; 4,216 m a.s.l.) continuing along the crest of the contemporary pasture-settlement Mumbuk (27°42′58″N, 87°12′38″E; 3,700 m a.s.l.). Migration through the Shipton Pass could have been a) through the Kasuwa Khola valley (Fig. 15) flowing into the Arun river near the contemporary settlement Num (27°32′25″N, 87°17′29″E; 1,340 m a.s.l.) continuing northward directly to the Shipton Pass, or a parallel way b) through the Isuwa Khola valley situated further west. These migration paths followed the changes and vegetation ascent of Rhododendron-coniferous forest (the upper belt of tropical evergreen montane forest) and moist alpine scrub and meadows. Any alternative migration route for small terrestrial mammals from the north was excluded owing to the inconvenient orographic and glacial conditions (Daniel and Kalvoda 1978; Daniel et al. 1985; Kuhle 1991, 2006a, b).

The psychrophilic fauna of northern origin in the southern Nepalese valleys of the Himalaya are consequently restricted by two boundaries: in the north by an orographic barrier with a strictly unsurpassable zone of continuous glaciation effective since the Upper Pleistocene, and in the south by a bioclimatic boundary. Representatives of the genus *Alticola* found on the late Quaternary moraines of the Barun glacier and in its close foreland are the remains of the population separated from the northern Tibetan populations during the Upper Pleistocene by extensive glaciation of the highest ranges of the High Himalaya. The initial migration route of *Alticola* spp. was most probably from the north directly through the gradually rising mountain ranges and not through the Arun river valley and then along the Barun Khola valley. This interpretation agrees with the systematic classification of the east-Nepalese representatives of the genus *Alticola,* which were listed by Biswas and Khajuria (1955). These authors were the first to describe *Alticola bhatnagari* based on specimens from the Khumbu Himal region. Gregori and Petrov (1976) consider this taxon to be a subspecies of *Alticola stoliczkanus bhatnagari*. They point out that the representatives of the *A. stoliczkanus* populations from the southern slopes of the Himalaya are distinctly smaller than those from the northern Tibetan elevations as already reported by Hinton (1926).

A similar history of migration also may account for the distribution of pikas (Table 1), which extended as high as the forest zone owing to their greater ecological adaptability. For *N. sikimensis*, initial colonization of the Barun valley may have been by offspring of the original migrants penetrating directly from the north together with representatives of the genus *Alticola.* These species can migrate since the Upper Pleistocene along slopes near the mouth of the Barun Khola from the Trans-Himalayan and High Himalayan part of the Arun river valley.

6. Colonization of the Makalu Barun region by small terrestrial mammals

Comparison of the present occurrence of fauna and flora and geomorphological patterns of the Makalu Barun area, primarily in the key sector between the southern part of the Makalu Massif and the tongue of the Lower Barun glacier near Shershon (Fig. 9), facilitates a reconstruction of relations between advance and retreat of mountain glaciation and the spread of small terrestrial mammals since the Late Glacial Maximum in the Upper Pleistocene up to the present time.

Natural features significant for the spread of small terrestrial mammals in the Barun glacier area are characterised by landform patterns as abiotic elements of the environment. The alpine-type (arête) relief of predominantly gneiss and granite rocks, characteristic of highly rugged ridges, peaks and cols and precipitous walls (Fig. 1 and 14), is inaccessible to migrating fauna both in the glacial zone above the permanent snow line (at present ca 5,600–5,700 m a.s.l.) and in the foreland of the glaciers. Denudational slopes with block debris deluvium form extensive areas above the contact between the Upper Barun and Chago glaciers in the Pethangtse Mt. direction (Fig. 11) and in some places also form the foot of faces of Peak IV and Makalu Massifs. The glacier bulks and permanent snowfields furrowed by systems of crevasses and avalanche scars represent extremely unfavourable ecological conditions.

Relatively favourable environment for small mammals are late Quaternary deposits of glacigenous, glacio-fluvial, lacustrine and eolian origin, together with current slope debris and talus cones. Some of these accumulation landforms in the periglacial morphoclimatic zone of the Makalu Barun region are covered with vegetation of Alpine tundra. The thickness and position of glacier tongues during the Late Glacial Maximum as well as their retreats and advances in the Holocene created a barrier against the spread of fauna. The course of expansion of fauna also depends on local landforms and microclimatic conditions, including glaciological and hydrological features. In the periglacial zone (Fig. 5 and 6) are in progress intensive regelation processes of repeated freezing and thawing of water in weathered deposits, solifluction and related phenomena of mass movements.

In some places the continuous sheet of ice tongues through the debris of surface moraines indicates the possible direction of migration of psychrophilic species of small terrestrial mammals across the ice-covered valley. The still preserved as well as extinct lake surfaces, together with the rapid glacier torrents represent unsurpassable obstacles. The great distance between the individual sites suggests the possible spread of small terrestrial mammals, as described above. Apart from direct evidence of small mammals, indirect evidence was provided by the long lasting,

Tab. 2 The expansion of small terrestrial mammals associated with essential changes of glacial and periglacial morphoclimatic processes in the Makalu Barun region from the Upper Pleistocene up to the present day.

Stratigraphical divisions of the Quaternary *(MIS = Marine isotope stages*	Main glacial stages in the East Nepal Himalaya and their approximate dating (Kalvoda 2007, 2020)	Extension and migration of small terrestrial mammals in the Makalu Barun region and its neighbouring Himalayan areas
-------- 0.00 Ma Holocene Epoch *~MIS 1 (warm period)* -------- 0.0117 Ma	Rapid retreat of glaciers and increasing human influence on the high-mountain environment. Little Ice Age (Historical, Recent, ca 1,000–850 years ago) Lobuche (2,000–1,000 years ago; Lingten-type moraines) Retreat of glaciers (3,000–2,000 years ago) Thukhla (Mid-Holocene, ca 4,900–3,600 years ago; Khumbu-type moraines) Retreat of glaciers (8,000–4,000 years ago) Chhukung (Early Holocene, 10,000–8,000 years ago; Changri-type moraines)	Opening of migration routes of *Alticola stoliczkanus* and *Ochotona roylei* to the ice-free sites above 5,000 m a.s.l. Small mammals survived during the colder periods in the periglacial zone (pushed down) and/or on the higher situated former moraines and other types of deposits with isolated thawing surface layers of permafrost up to the altitudes of ca 4,600 m. The extension of small mammals depends during the Holocene on spatial changes of periglacial and glacial climate-morphogenetic zones. The occurrence of fauna and flora in the high-mountain valleys is proportional to changes in the extent of seasonally thawing surface layers of permafrost on glacial, glacio-fluvial, slope, lacustrine and aeolian deposits.
Pleistocene Epoch: Upper Pleistocene *(MIS 2 – maximum of cold period)* *(MIS 3 – cold period)* *(MIS 4 – cold period)* -------- 0.126 Ma	Retreat of glaciers (13,000–10,000 years ago) Pheriche II (13,600 years ago) Pheriche I (Late Glacial Maximum, 25,000–16,000 years ago; Dusa-type moraines) Thyangboche II (36,000–25,000 years ago; the development of well-preserved glacial valleys) Thyangboche I (Late MIS4-Early MIS3, 74,000–(top 57,600)–36,000 years ago; it is the maximum extent of glaciation in the Upper Pleistocene during which the oldest U-shaped valleys and high situated flat glacial valleys originated.	Gradual return of small mammals to the Barun and related valleys by their migration on glacial and slope deposits was enabled by the expansion of periglacial zone. Small mammals were again pushed away from heavily glaciated valleys to the lower situated periglacial zone. Migration route and extension territory of small mammals remains open in the periglacial zone of the Arun valley. The extensive glaciation excluded occurrence and survival of small mammals in the mountain valleys. The migration of Palearctic species of small mammals across the gradually emerging orographical barrier during the orogenesis of the High Himalaya was completely interrupted by the development of glaciation in the Thyangboche stages (relics of related glacial deposits are not preserved).
Middle Pleistocene *(MIS 5, warm oscillation)* -------- 0.781 Ma *(MIS 19, warm oscillation)*	Later morphogenetic processes could destroy landforms of glacial origin, which would be evidence of the Middle Pleistocene glaciations.	Palearctic fauna and flora were widespread throughout the gradually evolving Himalayan mountain ranges until the early period of the Upper Pleistocene.

repeated flights of a pair of eagles above denuded debris slopes in the Barun valley head. These raptors prey upon small mammals.

Preceding particular considerations about the origin of the mammalian fauna in the varied environment of the Makalu Barun region are componed with knowledge of landform evolution since the Upper Pleistocene (see Table 2). During the Late Glacial Maximum (25,000–16,000 years ago), proved by the considerable advance of glaciers, the fauna of the upper part of the Barun valley was pushed by ice masses at minimum to the Yanle Khalka locality, that is to altitudes below 3,600 m. Advanced tongues of the Upper Barun and Lower Barun glaciers were joined together and they also developed conspicuous Dusa-type moraines. The upper part of the Barun valley was lifeless during the Late Glacial Maximum (Table 2). This extremely cold environment was characterised by strong action of cryogenic, nival and glacigenous processes.

During the Late Glacial Maximum, the width, position and thickness of glaciers and the abrasive action of their ice masses in the Makalu Barun region were influenced by changes of climatic conditions as well as morphotectonic activity with developing extreme dissection of mountain massifs. The largest areas of glaciation in the Upper Pleistocene were concentrated in the upper end of the Upper Barun glacier valley, which cuts between the Chomolongma and Makalu Massifs into the main ridge of the High Himalaya. This strongly glaciated area passes with a wide transfluence of ice masses into the Kangshung valley to the east of Sagarmatha. The glacial polish on the groups of roches moutonées, exposed 1.5 km from the peak of elevation point 6,260 m, in the vicinity of the 6,540 m peak below the northwestern face of the Makalu and above the Barun Pokhari lake towards the Japanese Col, provide evidence of the considerable extent of the Upper Pleistocene period of glaciation.

In the Late Glacial Maximum, the tongues of both Barun glaciers joined, but during the later glacier regression, they already became separated. The lateral glacial valleys and crests protruding from the Peak III Massif constitute a remarkable denudation level with alpine-type modelling in a progressive stage of destruction. The relatively considerable width of the Lower Barun valley is striking, being preserved to the southern foot of the Makalu Massif and to the south up to the prism-shaped Peak VI Massif. The western crest of the Peak VI (6,840 m) passes into the strongly glaciated group of peaks in the Chamlang Massif (7,290 m) with a huge system of hanging glaciers.

Beginning of the interglacial period at the end of the Pleistocene and early Holocene (Table 2) was the main cause that the valley glaciers lost almost half of their volume and retreated by several kilometres. The front of the Upper Barun glacier tongue retreated as far as below the southern face of Makalu. Extensive areas of the periglacial morphoclimatic zone were thus uncovered for the upward migration of fauna and flora not only along the valley floor, but also on the late Quaternary deposits free from ice. The exposed virginal space was gradually colonized up to the front of valley glaciers, where presumably a biocenosis very similar to the present one was created. Together with other hypsobionts these periglacial areas elevations were also colonized by representatives of the genera *Ochotona* and *Alticola.* Likewise the genus *Neodon* most likely migrated to higher localities, possibly as far as the close vicinity of the front of retreated glaciers.

The earliest Holocene advance of glaciers in the Makalu Barun region dates back to 10,000–8,000 years ago (Table 2). Preserved Changri-type moraines indicate that the ice masses at that time filled the main valley almost to the Shershon site. This advance of glaciers pushed again the vegetation and animal communities down to lower parts of the Barun valley. However, the valley glaciers did not reached the dimensions of the preceding advance, so that the huge right-sided Upper Pleistocene lateral moraine below the eastern face of Peak IV was laid bare. Its considerable extent (the biotopes described in preceding chapter as 5B, C, D) facilitated the survival of those communities which can endure the environmental conditions at the boundary between glacial and periglacial morphoclimatic zones. The possibility of an “island” survival of small mammals at this boundary can be indicated, for example, by the seasonal melting of the upper layer of permafrost and the degradation of the ice fill in weathered deposits of glacigenic and slope origin. On the basis of data on the present environmental requirements, these conditions were agreeable to pikas (Fig. 16) and species of the genus *Alticola.* If these moraines and slope sediments were ever inhabited by *Neodon* in the previous interstadial period, they must have descended at that colder time to periglacial morphoclimatic zone below the front of advancing glaciers.

The subsequent warming up and rise of humidity in the Early Holocene ca 8,000–4,000 years ago (Table 2) forced again the front of the valley glacier to retreat below the southern face of Makalu. Conditions in the ice-free space were restored to those similar to the preceding period of glacier retreat. Colonization of repeatedly exposed areas continued faster than in the preceding interstadial period. Namely, the first migrants of small mammals comprised members of surviving populations that had been isolated on relics of the Upper Pleistocene moraines below the eastern face of Peak IV. On the contrary, during this regression the lateral valley and hanging glaciers in the upper part of the Barun valley still reached as far as the main glacier tongue, so that the migration routes of small mammals in these areas continued to be blocked.

During the following Middle Holocene advance of glaciers, evidenced by the development of Khumbu-type moraines, the fauna and flora retreated again to lower zones of periglacial conditions, but some isolated populations can survived on the exposed fossil moraines. Not only the Upper and Lowers Barun glaciers, but also the hanging glaciers descending from the Japanese Col of the Makalu Massif as well as the eastern faces of Peak IV advanced considerably. A terminal moraine was created which later blocked the present-day Barun Pokhari lake and push moraines of short tongues hanging glaciers (Fig. 8 and 9). The later retreat of glaciers ca 3,000–2,000 years ago (Table 2) produced development of (at least) three lakes from the thawing waters beyond above mentioned dams. These lakes blocked the migration routes of small mammals leading through the valley floor upwards in the wake of a retreating glacier. The newly created biotopes suitable for the existence of small terrestrial mammals near the present front of a glacier were therefore colonized mainly by pikas and mice from autochthonous populations surviving the Holocene advances of glaciers on fossil moraines and slope deposits.

The advancement of small terrestrial mammals from lower elevations was partly blocked by existence of lakes which prolonged during the Upper Holocene the isolation of populations living higher above them. The two lower lakes were later emptied after the terminal moraine of the hanging glacier and the chaotic moraine ramparts above Shershon site had been broken through by erosion, leaving several striking plateaus with prevailingly lacustrine sediments. The discontinuity in distribution of mammalian fauna caused by long-term existence of these Upper Holocene glacial lakes and related landform patterns is apparent up to the present day. The moraine of the hanging glacier of the Peak IV eastern face, contacting the left lateral moraine on the opposite side of the valley, remains as a marked dividing line between the distribution of *Neodon sikimensis* extending to it from the south and of *Alticola stoliczkanus* which colonized the moraine from the north.

The recent retreat of valley glaciers has brought about significant changes in higher parts of their tongues and also in their catchment areas (Table 2). For example, above the confluence of the Upper Barun and Chago glaciers, the structural denudational slopes with block debris were laid bare and some lateral glacial trains were separated from the main tongue of the Upper Barun glacier. Volume of ice masses around the Hillary's Nunatak (27°55′43″N, 87°01′23″E; 6,140 m a.s.l.) is reduced which is connected above all with the onset of a significant increase of aridity in the extremely cold climatic conditions northwest of the Peak IV – Makalu line. By this means, new areas were created suitable for the colonization by small terrestrial mammals and new migratory routes appeared facilitating the colonization of these islet-like sites. The pronounced increase in aridity of the extremely cold climate northwest of the Peak IV and Makalu Massifs and the substantial decrease in the volume of the glaciers and the lengths of the glacier tongues have persisted up to the present day (Fig. 7 and 11).

The periglacial zone and varied accumulation landforms which facilitate the spread of small terrestrial mammals are rapidly expanding. The areal extent and volume of the glacial, glacio-fluvial and fluvial deposits appear to be remarkably limited when compared to the huge cliffs and slopes being eroded. Slope sediments, especially block eluvia and deluvia, talus cones and foot-of-slope debris are most frequent. On the denudational slopes of gneisses and migmatites and their connecting ridges, block deluvia form continuous fields rimming the foot of isolated rocky outcrops. They also form the substantial part of rockfalls and ice-stone avalanches.

7. Discussion

The mode by which small terrestrial mammals spread is specific for the Makalu Barun region. It probably applies to the entire periglacial zone of the Nepal Himalaya. Large areas of the permafrost domain are ice-rich terrains affected by thermokarst processes. Permafrost is a major factor influencing cold-region hydrology, soil carbon storage and ecosystems. Key feedbacks from permafrost degradation in the context of climate change include transformation in geomorphic and ecosystem processes.

Predictions can be made about the future spread of small terrestrial mammals in the Makalu Barun region. It is most likely that *N. sikimensis* will advance to places close to the present fronts of valley glaciers. For this, there are sufficient biocenotic as well as morphoclimatic conditions in the substantially enlarged periglacial zone. The extensive summer pasturing of sheep as high as these elevations may further accelerate this process. We can observe by the increased burrowing activity of *N. sikimensis* how the presence of man and pastured animals affect the occurrence of this vole species. Anthropogenic disturbances in a dynamic environment, including the possibility of regular burning in a presumed attempt to increase pasture area (Byers 1996), could have significant roles in modifying the Barun valley landscapes. Corridors of disturbance related to contemporary indigenous and turist use, e.g. tree harvesting, burning and grazing, was observed along the main valley trial, and impacts appeared to be growing in frequency and magnitude.

The substantial changes in the colonization of landscape by small mammals may be anticipated in the highest part of the Barun valley. In newly exposed places near the permanent snow line, the semi-arid climate is more severe than more humid climatic conditions along the front of valley glaciers. It can be endured only by representatives of distinct psychrophilic hypsobionts, such as are *A. stoliczkanus* and *O. roylei* (Fig. 16). Their population will gradually increase and the islet-like character of their distribution will be preserved according to local climatic and geomorphic conditions. Increasing human activities may play a relevant role. This is indicated by the concentration of *A. stoliczkanus* in and around the Makalu base camps at 4,800–4,900 m a.s.l. and by the penetration of O. roylei even into much higher located camp I (5,900 m a.s.l.) in the lower part of the southwestern face of the Makalu Massif.

All the trapped animals were examined for the presence of ecto- and endoparasitic infestation (Daniel 1974). This work was carried out while respecting the safety conditions for working with potentially infectious material, which in itself was a problem to carry out in a tent in the harsh Himalayan climate. Such a set has not been (and still is not) collected, analyzed and evaluated in the Himalaya before. Some of the results provided important information supplementing knowledge of the migratory routes of small mammals in the Barun valley during retreat of glaciers and of the role of human activity. Among the parasites that can be bioindicators of change are two groups of external parasitic mites (chigger mites and ticks), which undergo an important part of their life cycle exposed to environmental conditions during their non-parasitic phases of development. Infestations of Ixodid ticks, Trombiculid chigger mites and fleas were tightly linked to the local habitat where these ectoparasites must survive during their non-parasitic phase. An indicator of anthropogenic impact was the occurrence of synantropic flies. Results of parasitological research in the studied area are presented in detail by Daniel (2015, 2016 and 2017). In view of the Palearctic origin of small mammals in higher areas of the Makalu Barun region, one can assume the primary possibility of occurrence of pathogens circulating to the north of the High Himalayan ridge. It is possible to assume an occurrence of arboviruses transmitted by ticks and also rickettsioses transmitted by ticks and chigger mites. Bacteriological infections including plague could be occurred.

Human activity can influence secondary formation of natural foci of vector-borne diseases in several respects. An extensive form of pasturage provides a blood source for adult ticks necessary for the existence of local populations. Arrival of pastured cattle in summer alpine pasturelands (Fig. 13) can repeatedly introduce ticks, give rise to local populations and thus increase the species spectrum of local fauna. The introduction of an infected tick can, by means of transovarial and transstadial transmission, form a local infected filial generation; in this respect, *Haemaphysalis aponommoides* (Warburton 1913) is potentially dangerous. In addition, the arrival of infected domestic animals can infect local tick populations. Accumulation of organic rubbish positively influences the local population density of small mammals, concentrates them and thus increases their mutual contact and the transmission of infections and of vectors.

The zoological and parasitological research was carried out 20 years before the designation of the Barun-Makalu National Park, i.e. before the application of regulatory measures of nature conservation. It is thus an important comparative material for the evaluation of changes in the biosphere that took place in the next three decades under the influence of observed changes in climate and human activities, as well as for the prediction of the further possible course of these processes. This also fully applies to the spread of diseases transmissible from the wild to humans and possible changes in landscape epidemiology caused by climate change and human activities not only in the Himalaya, but more broadly also in other mountain systems of the Palearctic.

8. Conclusions

Principal regularities of expansion and migration of small mammals caused by the late Quaternary geomorphological history of the Makalu Barun region are explored. The study is based on collection of 139 small terrestrial mammals (Table 1) and 94 birds collected in the Makalu Barun region at altitudes of 3,450–5,950 m a.s.l. in the pre-monsoon period of 1973. Further author's primary data are earlier published results of geomorphological analysis, including a set of geomorphic maps and collection of rocks, and physical-geographical observations from the years 1971–2006. Zoological and parasitological findings are correlated with the landform patterns and their evolution. The correlation testifies to significant changes in the high-mountain environment of the Makalu Barun region during the late Quaternary. It was determined the course of expansion and migration of small mammals related both to the orogenetic uplift of the East Nepal Himalaya and climatically conditioned changes in the extent of mountain glaciation and periglacial morphoclimatic zone from the Upper Pleistocene up to the present day.

Palearctic fauna and flora were widespread throughout the evolving Himalayan mountain ranges until the early period of the Upper Pleistocene (Table 2). The migration of Palearctic species of small mammals across the gradually emerging orographical barrier during the orogenesis of the High Himalaya was completely interrupted by the Thyangboche stages of glaciation in the Upper Pleistocene. This extensive glaciation also excluded occurrence and survival of small mammals in the high-mountain valleys of the Makalu Barun region. Migration routes and the extension of the territory of small mammals remained open only in the periglacial zone of the Arun and Barun Khola valleys. Following the interstadial period of warmer and humid climatic conditions were changed by the Late Glacial Maximum (25,000–16,000 years ago) when small mammals were again pushed away from heavily glaciated valleys to the lower altitude periglacial zone.

During the Holocene interglacial (Table 2), the occurrence of fauna and flora in the high-mountain valleys depended on repeated spatial changes of periglacial and glacial morphoclimatic zones. Gradual return of small mammals to the Barun and neighbouring valleys by their migration on former glacial and slope deposits was enabled by the expansion of periglacial zone. They retreated to lower zones of periglacial conditions during colder periods. In the Upper Holocene, isolated populations of small mammals could survive on the exposed former moraines and other types of weathered and/or transported deposits with seasonally thawing layers of permafrost. Conspicuous reduction of the volume and length of glaciers observed in the last hundred years opened migration routes of *Alticola stoliczkanus* and *Ochotona roylei* to ice-free sites situated even at the altitudes above 5,000 m a.s.l.

Current biogeographical hazards in the Nepal Himalaya are associated with rapid retreat of glaciers, the expansion of the periglacial morphoclimatic zone and the increased human impact in the High Himalaya. The cause-and-effect relationship between active morphotectonic processes, landform evolution, climate changes and faunal/vegetation patterns of the biosphere could result cumulatively from the responses of individual species, affecting the dynamics of communities to the extent and mode of dispersion of mankind.

Acknowledgements

This work is dedicated to all members of the Czechoslovak mountaineering expeditions to Makalu in the Nepal Himalaya, which were carried out half a century ago, i.e. in the years 1973 and 1976. The presented study was prepared in the framework of the Charles University project "Cooperatio Geography".

References

Avouac, J. P. (2003): Mountain building, erosion, and the seismic cycle in the Nepal Himalaya. Advances in Geophysics 46, 1–80, https://doi.org/10.1016/S0065-2687(03)46001-9.

Baruš, V., Daniel, M. (1976): Capillariids from passeriform birds of Nepal. Folia Parasitologica 23(2), 105–110.
Baruš, V., Ryšavý, B., Daniel, M. (1975): Some Cestodes and Nematodes parasitizing gallinaceous and columbiform birds in Nepal. Folia Parasitologica 22(4), 327–335.
Bilham, R. (2019): Himalayan earthquakes: a review of historical seismicity and early 21st century slip potential. In: Treolar, P. J., Searle, M. P. (Eds.): Himalayan Tectonics: A Modern Synthesis. The Geological Society of London, Special Publications 483(1), 423–482, https://doi.org/10.1144/SP483.16.
Biswas, B., Khajuria, H. (1955): Zoological results of the "Daily Mail" Himalayan Expedition 1954. Four new mammals from Khumbu, eastern Nepal. Proceedings of Zoological Society (Calcutta) 8, 25–30.
Bordet, P. (1961): Recherches géologiques dans l'Himalaya du Népal, région du Makalu. C. N. R. S., Paris.
Bordet, P. (1970): La structure de l'Himalaya. Bulletin de l'Association de géographes français 379–380, 59–66, https://doi.org/10.3406/bagf.1970.5946.
Bordet, P., Latreille, M. (1955a): La géologie de l'Himalaya de l'Arun. Bulletin de la Société géologique de France 5, 529–542, https://doi.org/10.2113/gssgfbull.S6-V.7-9.529.
Bordet, P., Latreille, M. (1955b): Précisions sur la stratigraphie de l'Himalaya de l'Arun. Comptes rendus Hebdomadaires des Scéances de l'Académie des Sciences de France 241(20), 1400–1402.
Bordet, P., Latreille, M. (1955c): Précisions sur la tectonique de l'Himalaya de l´Arun. Comptes rendus Hebdomadaires des Scéances de l'Académie des Sciences de France, 241(22), 1594–1597.
Brunsden, D., Jones, D. K. C., Martin, R. P., Doornskampf, J. C. (1981): The geomorphology of part of the Low Himalaya of Eastern Nepal. Zeitschrift für Geomorfologie, Supplementband 37, 25–72.
Byers, A. C. (1987a): An assessment of landscape change in the Khumbu region of Nepal using repeat photography. Mountain Research and Development 7(1), 77–81, https://doi.org/10.2307/3673327.
Byers, A. C. (1987b): Landscape change and man-accelerated soil loss – the case of the Sagarmatha (Mt. Everest) National Park, Khumbu, Nepal. Mountain Research and Development 7(3), 209–216. https://doi.org/10.2307/3673195.
Byers, A. C. (1996): Historical and contemporary human disturbance in the upper Barun Valley, Makalu–Barun National Park and Conservation Area, East Nepal. Mountain Research and Development 16(3), 235–247.
Byers, A. C., Rounce, D. R., Shugar, D. H., Lala, J. M., Byers, E. A., Regmi, D. (2019): A rockfall-induced glacial lake outburst flood, Upper Barun valley, Nepal. Landslides 16, 533–549, https://doi.org/10.1007/s10346-018-1079-9.
Carpenter, C., Zomer, R. (1996): Forest ecology of the Makalu–Barun National Park and Conservation Area, Nepal. Mountain Research and Development 16(2), 135–148, https://doi.org/10.2307/3674007.
Chhetri, P. K., Cairns, D. M. (2015): Contemporary and historic population structure of Abies spectabilis at treeline in Barun valley, eastern Nepal Himalaya. Journal of Mountain Science 12(3), 558–570.
Chhetri, P. K., Shresta, K. B., Cairns, D. M. (2017): Topography and human disturbances are major controlling factors in treeline pattern at Barun and Manang area in the Nepal Himalaya. Journal of Mountain Science 14(1), 119–127.
Chowdhury, A., De, S. K., Sharma, M. C., Debnath, M. (2022): Potential glacial lake outburst flood assessment in a changing environment, Chhombo Chhu Watershed, Sikkim Himalaya, India. Geocartography International 1, 1–29, https://doi.org/10.1080/10106049.2022.2102219.
Daniel, M. (1974): Parasitological studies within the Czechoslovak expedition to the Himalaya 1973. Folia Parasitologica 21, 187–188.
Daniel, M. (1979): Ixodid ticks of Barun Glacier region (the Nepal Himalaya). Folia Parasitologica 26(4), 337–341.
Daniel, M. (2015): Expansion of small terrestrial mammals and their parasites into the Barun valley (Makalu Mt. region, Nepal Himalaya) linked with changes in glaciation and human activities. Journal of Mountain Science 12(1), 14–29, https://doi.org/10.1007/s11629-013-2936-6.
Daniel, M. (2016): Little terrestrial mammals and birds dataset in Barun Valley, eastern Nepal (1973). Global Change Research Data Publishing & Repository, https://doi.org/10.3974/geodp.2017.04.02.
Daniel, M. (2017): Dataset of little terrestrial mammals and birds in Barun valley, Himalaya, Nepal (1973). Journal of Global Change Data and Discovery 1(4), 391–401, https://doi.org/10.3974/geodp.2017.04.02.
Daniel, M., Hanzák, J. (1985): Small mammals in eastern part of Nepal Himalaya. Transactions of the Czechoslovak Academy of Sciences, Series of Mathematical and Natural Sciences 95, 1–59.
Daniel, M., Hanzák, J. (1993): Birds in the Barun valley (the High Himalaya, East Nepal). Časopis Národního Musea (Praha), Řada přírodovědná (Journal of the National Museum, Prague, Czech Republic, Series of Natural Science), 161, 71–83.
Daniel, M., Kalvoda, J. (1978): Himálaj. Academia, Praha. (In Czech.)
Daniel, M., Kalvoda, J., Hanzák, J. (1985): Zoological part: The origin of fauna of small terrestrial mammals in the Barun region. In: Daniel, M., Hanzák, J.: Small mammals in eastern part of Nepal Himalayas. Rozpravy Československé akademie věd, Řada matematických a přírodních věd 95(8), 42–51.
Daniel, M., Stekolnikov, A. A. (2009): Chigger mites (Acari: Trombiculidae) from Makalu region in Nepal Himalaya, with a description of three new species. Journal of Medical Entomology 46, 753–765.
De Lattin, G. (1967): Grundriss der Zoogeographie. Fischer Verlag, Stuttgart. (In German.)
Dusbábek, F., Daniel, M. (1975): Two myobiid mites (Myobiidae: Trombidiformes) from the Great Himalaya Mountains. Folia Parasitologica 22(4), 327–335.
Fort, M. (2000): Glaciers and mass wasting processes: their influence on the shaping of Kali Gandaki valley, Nepal. Quaternary International 65–66, 101–119, https://doi.org/10.1016/S1040-6182(99)00039-7.
Fushimi, H. (1977): Glaciations in the Khumbu Himal. Journal of the Japanese Society of Snow and Ice 39, 60–76, https://doi.org/10.5331/seppyo.39.Special_60.
Fushimi, H. (1978): Glaciations in the Khumbu Himal (2). Journal of the Japanese Society of Snow and Ice 40, 71–77, https://doi.org/10.5331/seppyo.40.Special_71.

Gregor, F., Daniel, M. (1976): To the knowledge of fauna of synanthropic flies of the Nepal Himalaya. Folia Parasitologica 23, 61–68.
Gregori, J., Petrov, B. (1976): Scientific results of the Yugoslav 1972 Himalaya Expedition – Mammalia. Razprave, Slovenska Akademija Znanosti in Umetnosti, Razred IV (Transactions of the Slovenian Academy of Sciences and Arts, Series IV) 19, 1–20.
Hinton, M. A. C. (1926): Monograph of the voles and lemmings (Microtinae) living and extinct. Bitish Museum (Museum Natural History), London. Volume I, https://doi.org/10.5962/bhl.title.8319.
Janečková, V., Fassatiová, O., Daniel, M., et al. (1977): Nález půdních mikromycetů ve Vysokém Himálaji (Nepál). (Findings of the soil microscopic fungi in the Himalaya Mountains (Nepal). Czech Mycology 31(4), 206–213. (In Czech.)
Kalvoda, J. (1976): The relief of the Himalayas and its recent modellation. Rozpravy ČSAV, Ř. mat. přír. Věd 86(1), 1–52.
Kalvoda, J. (1978): Genesis of the Mount Everest (Sagarmatha). Rozpravy Československé akademie věd, Řada matematických a přírodních věd 88(2).
Kalvoda, J. (1979a): The Quaternary history of the Barun glacier, Nepal Himalayas. Věstník Ústředního ústavu geologického 54(1), 11–23.
Kalvoda, J. (1979b): Geomorphological map of the Barun glacier region, Khumbakarna Himal. Acta Universitatis Carolinae Geographica 14(1), 3–38.
Kalvoda, J. (1982): An outline of the Quaternary morphogenetic processes in the East Nepal Himalaya. In: Verma, V. K. (Ed.): Himalaya, landforms and processes. Today and Tomorrow Printer and Publishers (New Delhi), 87–113.
Kalvoda, J. (1984a): The nature of geomorphic processes in the Himalayas and Karakoram. Studia Geomorphologica Carpatho-Balcanica 18, 45–64.
Kalvoda, J. (1984b): The landforms design in the East Nepal Himalayas. Rozpravy Československé akademie věd, Řada matematických a přírodních věd 94(1).
Kalvoda, J. (1992): Geomorphological Record of the Quaternary Orogeny in the Himalaya and the Karakoram. In: Development in Earth Surface Processes, 3, Elsevier, Amsterdam.
Kalvoda, J. (2004): Glacial and periglacial landforms and processes. In: Cílek, V. (Ed.): Earth System: History and Natural Variability. Encyclopedia of Life Support Systems, UNESCO, EOLSS Publishers, Oxford (http://www.eolss.net).
Kalvoda, J. (2007): Dynamics of landform evolution in the Makalu – Barun region, Nepal Himalaya. Geografický časopis 52(2), 85–106.
Kalvoda J. (2020): The Dynamics of Geomorphic Evolution in the Makalu Barun Area of the Nepal Himalaya. P3K publishers, Prague.
Kalvoda, J., Emmer, A. (2021): Mass wasting and erosion in different morphoclimatic zones of the Makalu Barun region, Nepal Himalaya. Geografiska Annaler: Series A, Physical Geography 103(4), 368–396, https://doi.org/10.1080/04353676.2021.2000816.
Khanal, S. N., Hogland, W., Bhatt, R. P., Manandhar, D., Kafle, K. (2014): Implications of Climate Change and Tourism in the Mt. Everest Region in Nepal. Impact of Climate Change on Water and Health, 377–399.
Krummenacher, D. (1961): Détermination d'âge isotopique faite sur quelques roches de l'Himalaya du Népal par la méthode potassium-argon. Bulletin Suisse de la minéralogie et pétrographie 41(2), 273–283.
Krummenacher, D. (1966): Népal Central: Géochronometrie des séries de l'Himalaya. Bulletin Suisse de la minéralogie et pétrographie 42(1), 43–53.
Kuhle, M. (1991): Observations Supporting the Pleistocene Inland Glaciation of High Asia. GeoJournal 25(2–3), 33–233, https://doi.org/10.1007/BF02682191.
Kuhle, M. (2006a): Reconstruction of the ice age glaciation in the southern slopes of Mt. Everest, Cho Oyu, Lhotce and Makalu (Himalaya). Part 1. Journal of Mountain Science 3, 91–124, https://doi.org/10.1007/s11629-006-0191-9.
Kuhle, M. (2006b): Reconstruction of the ice age glaciation in the southern slopes of Mt. Everest, Cho Oyu, Lhotce and Makalu (Himalaya). Part 2. Journal of Mountain Science 3, 191–227, https://doi.org/10.1007/s11629-006-0091-z.
Lombardo, B., Bortolami, G. (1998): Geology of the Everest – Makalu region. In: Baudo, R., Tartari, G., Munawar, M. (Eds.): Mount Everest-Himalayan Ecosystem. Backuys Publishers, Leiden, 35–64.
Mehta, J. N., Kellert, S. R. (1998): Local attitudes toward community based conservation policy and programmes in Nepal: a case study in the Makalu – Barun Conservation Area. Environmental Conservation 25(4), 320–333, https://doi.org/10.1017/S037689299800040X.
Moravec, F., Daniel, M. (1976): Rhabdochona minima sp. n. (Nematoda: Spiruroidea) from the loach, Neomacheilus inglisi (Hora) of Nepal. Folia Parasitologica 23, 175–178.
Odell, N. E. (1925): Observation on the rocks and glaciers of Mount Everest. Geographical Journal 66, 289–315, https://doi.org/10.2307/1782942.
Odell, N. E. (1948): Geological and some other observations in the Mount Everest region. In: Tilman, H. W. (Ed.): Everest 1938. Cambridge University Press, Cambridge, 143–155.
Pratt-Sitaula, B. (2004): Glaciers, Climate and Topography in the Nepalese Himalaya. UC Santa Barbara, Santa Barbara.
Samšiňák, K., Daniel, M. (1978): Five new species of mesostigmatid mites from Geotrupes beetles collected in the Himalayan region of Nepal (Acari: Mesostigmata). International Journal of Acarology 4(2), 91–100.
Schärer, U. (1984): The effect of initial ^{230}Th disequilibrium on young U-Pb ages: the Makalu case, Himalaya. Earth and Planetary Science Letters 67(2), 191–204, https://doi.org/10.1016/0012-821X(84)90114-6.
Searle, M. P., Simpson, R. L., Law, R. D., Parrish, R. R., Waters, D. J. (2003): The structural geometry, metamorphic and magmatic evolution of the Everest massif, High Himalaya of Nepal – South Tibet. Journal of the Geological Society of London 160, 345–366.
Searle, M. P., Simpson, R. L., Law, R. D., Waters, D. J., Parrish, R. R. (2002): Quantifying displacement on the South Tibetan detachment normal fault, Everest massif, and the timing of crustal thickening and uplift in the Himalaya and Tibet. Journal of Nepal Geological Society 26, 1–6.
Simpson, G. G. (1945): The principles of classification and a classification of Mammals. Bulletin of the American Museum Natural History 85, 1–350.

Smit, F. G. A. M., Rosický, B. (1976): Siphonaptera collected by Dr. M. Daniel in Nepal. Folia Parasitologica 23, 135–159.
Thapa, S., Katuwal, H. B., Gurung, R., Kusi, N., Devkota, B., Shrestha, B., Suwal, T. L. (2018): Pikas in Nepal. Small Mammals Conservation and Research Foundation, Kathmandu, Nepal.
Troll, C. (1967): Die Klimatische und vegetations Geographische Gliederung des Himalaya Systems. Khumbu Himal 1, 358–388, https://doi.org/10.1007/978-3-642-92945-8_1.
Visona, D., Lombardo, B. (2002): Two-mica and tourmaline leucogranites from the Everest – Makalu region (Nepal – Tibet). Himalyan leucogranite genesis by isobaric heating? Lithos 62(3–4), 125–150.
Wager, L. R. (1937): The Arun river drainage pattern and the rise of the Himalaya. Geographical Journal 89(3), 239–250, https://doi.org/10.2307/1785796.
Weigel, I. (1969): Systematische Übersicht über die Insektenfresser und Nager Nepals nebst Bemerkungen zur Tiergeografie. (Survey of Nepal Insectivores a and Rodents and the zoogeographical notes.). Khumbu Himal, Band 3, Lieferung 2, Universitäts-Verlag Wagner, Insbruck-München. (Khumbu Himal, Vol. 3/2, University Publishing House Wagner, Innsbruck-Munich). (In German.)
Zomer, R., Carpenter, C., Ustin, S., Ives, J. D. (2001a): Structure, composition and community ordination of tropical monsoon forest within the Makalu – Barun Conservation Area of eastern Nepal. Phytocoenologia 31(2), 161–184.
Zomer, R., Ustin, S., Carpenter, C. (2001b): Lover cover change along tropical and subtropical riparian corridors within the Makalu – Barun National Park and Conservation Area, Nepal. Mountain Research and Development 21(2), 175–183.
Zomer, R., Ustin, S., Ives, J. D. (2002): Using satellite remote sensing for DEM extraxtion in complex mountainous terrain: landscape analysis of the Makalu Barun National Park of eastern Nepal. International Journal of Remote Sensing 23(1), 125–143.