1 Introduction

Orogenetic processes have influenced climate and biotic development in South Asia on a large scale since the breaking up of Gondwana. Due to its extent in width and height, the Himalaya has an outstanding position within the tertiary orogenetic belt at the southern margin of the former Cretaceous Asian continent. Presently it forms one of the most impressive climatic divides in the world where two faunal realms, Oriental and Palearctic region meet. Since early biogeographical work (Mani 1968) the Himalaya has been mainly regarded as faunal border. However, with ongoing exploration and better known flora and fauna this system of mountain ranges has been understood not simply as habitat for specially adapted high altitude forms but also as a region with high biodiversity (Martens 1979, 1993).

With my increasing knowledge on scarab beetle fauna of the Himalaya or strictly speaking one small part of it (Sericini) I have had the wish for a long time to analyse the faunal composition exemplarily in this group more in detail, with static methods as well as with dynamic ones. Phylogenetic systematics based on computer cladistics provides us a powerful scientific method to explore the dynamics of the processes of dispersal and/ or diversification in the Himalaya. This is what the present thesis aims at.

1.1 The biology and systematics of the group studied

The family Scarabaeidae belongs to the more intensively studied groups of beetles with respect to their biology, taxonomy, and phylogeny. However, Sericine chafers with almost 4000 described species in about 200 genera represent a striking exception, being poorly explored in phylogeny, taxonomy, and larval morphology. Almost nothing, as regards their great diversity, is known about their ecology. The tribe Sericini is most diverse in tropical and subtropical regions (Fig. 1) but absent in Notogea, southern South America, and the south-east of Sulawesi.

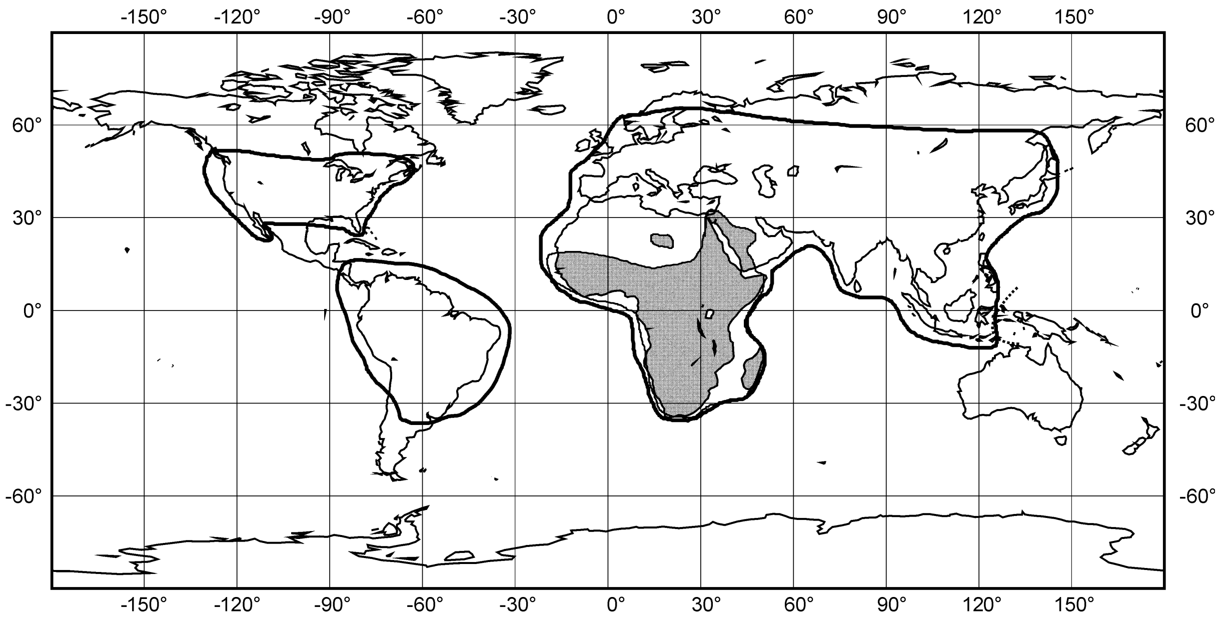


Fig. 1. World wide distribution of the Sericini (bold line). South-eastern ward they have their limit on Sulawesi (dotted line). Its according to Machatschke (1959) presumable sister taxon the Ablaberini (grey shaded) is limited to Afrotropical region.

As with other groups of phytophagous Scarabaeidae, the adults of Sericini are generalist herbivores. *Maladera castanea* (Arrow, 1913) feeds on more than 100 different plant species, and the preferred food plants with succulent roots still number about 30 (Tashiro 1987). The larvae known universally as white grubs, are subterranean feeders on the roots and underground stems of living plants (Ritcher 1966). Many species have been reported to damage cultivations. In *Maladera castanea* most feeding occurs at 5.0-8.0 cm below the surface (Tashiro 1987). The life cycle may take one or two years depending on the climatic conditions (Horion 1958, Tashiro 1987). The average longevity of adults is about one month (Tashiro 1987). In the northern hemisphere sericines overwinter in the larval stage, mainly the third instar, by migrating into deeper soil layers. Many species of Sericine chafers are nocturnal, having an inconspicuous dark or brown colour. Sericines often hide underground during the day. At dusk the beetles come to the surface and feed on nearby plants. Low temperatures may reduce flight activities significantly.

There have been a variety of hypotheses presented for the systematic position of the Sericini throughout the history of scarab systematics. The Sericini have traditionally been classified with other groups of phytophagous Scarabaeidae in the subfamily Melolonthinae (Dalla Torre 1912; Browne and Scholtz 1998). The phylogeny of phytophagous Scarabaeidae has been studied and discussed recently by several authors. However, several of these papers provide no cladistic analysis (Iablokov-Khnzorian 1977; Nikolaev 1998; Machatschke 1959) and the ones that do only consider the Sericini in a superficial way (Browne and Scholtz 1998, 1999; Howden 1982; Jameson 1998; Sanmartin and Martin-Piera 2003; Scholtz and Chown 1995; Zunino and Monteresino 1990). Machatschke (1959) hypothesized the monophyly of the subfamily Sericinae containing the tribes Diphucephalini, "Camentini" (= Ablaberini), and Sericini (Fig. 2) using the following characters: a) labrum and clypeus on one plane, fused producing a labroclypeus; b) the labrum establishes the anterior margin of "pseudoclypeus"; c) anterior coxae conically produced; and d) posterior coxae widened. He also assigned the known genera of Sericini to three subgroups (subtribes): Phyllotocina, Sericina, and Trochalina. While Machatschke (1959) based the monophyly of Sericinae on characters which might be considered as "good" apomorphies, the characters used to argue for the monophyly of Melolonthinae are in great part unambiguously plesiomorphic, such as the unfused labrum and clypeus and the transversal carina of the anterior coxae. Although he proposed the monophyly of Sericinae + Melolonthinae, his arguments are not convincing because he confused apomorphies and plesiomorphies in his argumentation scheme (e.g. position of stigmata within abdominal sternites).

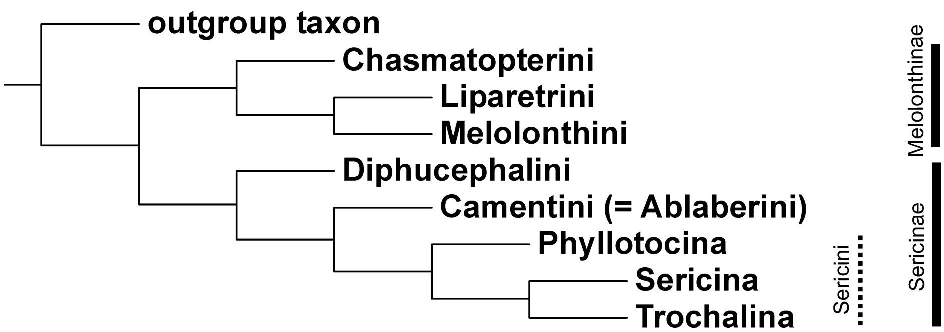


Fig. 2. Phylogeny of Sericini proposed by Machatschke (1959), transposed into a phylogenetic tree, however, an outgroup taxon was not given.

Browne and Scholtz (1998) presented a phylogenetic analysis based on the comparative morphology of articulation and base of the hind wing of Scarabaeidae. They examined numerous genera of sixteen high-ranked scarabeid taxa traditionally classified as subfamilies as well as taxa of uncertain phylogenetic status. According to their phylogeny the Scarabaeidae comprised two major lineages: The 'aphodiine line' (containing Aphodiinae, including Aegialiini, *Aulonocnemis*, and Scarabaeinae), and the 'orphnine line' (containing Orphninae and all major subfamily taxa of phytophagous scarabs). However, their melolonthine lineage comprising the "Melolonthinae", *Acoma*, *Chaunanthus*, *Oncerus*, and the Hopliini, was based on few apomorphies only, in contrast to most other clades. Moreover, they realized that the wing base offered few suitable characters to investigate the Melolonthinae phylogeny in more detail due to a lack of significant differences.

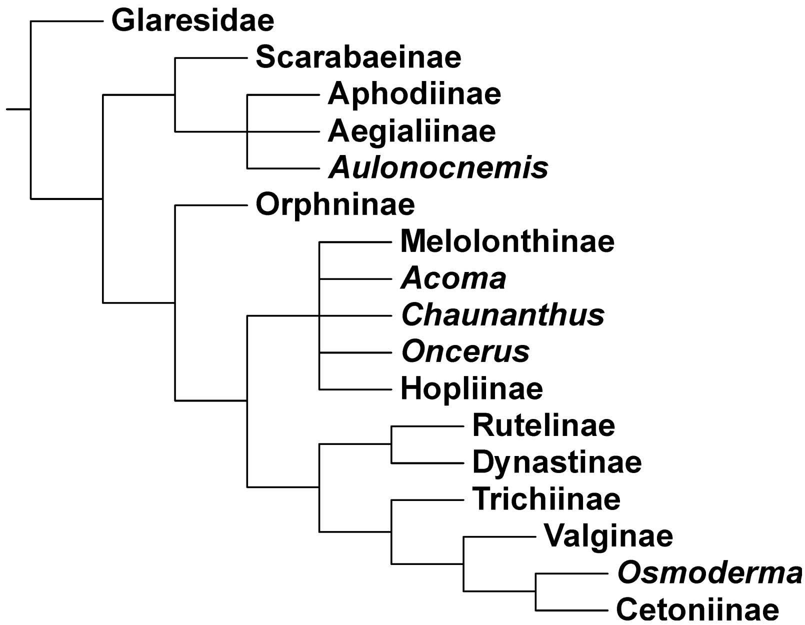


Fig. 3. Phylogeny of Scarabaeidae proposed by Browne and Scholtz (1998).

In contrast to coprophagous Scarabaeidae and "older" lineages of Scarabaeoidea (Pretorius et al. 2000; Browne and Scholtz 1999; Scholtz and Chown 1995; Scholtz and Browne 1996; Scholtz et al. 1994), the phylogeny of phytophagous Scarabaeidae is far from being resolved (Sanmartin and Martin-Piera 2003). This is strikingly evident when trying to place known fossils into the present phylogenetic system (Krell 2000).

The fossil record of the Scarabaeoidea has been reviewed by Iablokoff-Khnzorian (1977), Crowson (1981), and Scholtz (1990). Recently, an excellent summarizing synopsis was presented by Krell (2000). The oldest scarabaeoid are possibly †*Aphodiites* known from Lower Lias (Lower Jurassic) of Switzerland. It was originally thought to belong to Aphodiinae, but later Scholtz et al. (1994) noticed that diagnostic characters attributed to †*Aphodiites* could apply to a *Glaresis*-like beetle. However, Krell (2000) regarded its phylogenetic position still uncertain due to convincing diagnostic characters. Other scarabaeoid-like fossils such as †*Opiselleipon* and †*Geotrupoides* are known from Upper Lias beds and Upper Jurassic beds (Scholtz 1990). Nevertheless Ponomarenko (1995) gave a minimum age for Scarabaeoidea as Middle Jurassic, the fossil record of this epoch is rather doubtful.

The proven first occurrence of Scarabaeoidea is Lower Cretaceous in age (Krell 2000). Fossils resembling modern Geotrupidae and Hybosoridae have been recorded from Lower Cretaceous deposits in China (e.g. †*Protoscarabaeus*). Recently, Nikolaev (1993a,b, 1996, 1998) discovered a number of new fossil forms from Lower and Upper Cretaceous of which a several ones have been assigned to the subfamily Sericinae (†*Lithanomala*) and Melolonthinae (†*Cretomelolontha*) (Nikolaev 1998; Krell 2000). Additional taxa of these lineages assigned to the Melolonthinae have been described from Eocene coal deposits in Germany (†*Eophyllocerus*). Fossils sharing apomorphies with Sericini are known from Oligocene in Europe (*Maladera* †*spinitibialis* Statz, 1952: Rott) and Northern America (*Serica* spp.: Florissant). It is evident from fossil record that the main divisions of modern Scarabaeoidea were distinct from the beginning of the Tertiary.

1.2 The Himalaya - the geographical area studied

1.2.1 Definition of the geographical area

The Himalaya (from Sanskrit *him* = snow, *alaya* = abode) was the name applied in ancient India to the Great Snowy Range of mountains, visible in the north from the Indo-Gangetic Plain (Mani 1968). As now understood, the Himalaya embraces the complex system of nearly parallel ranges, extending over 3200 km, from North Burma in the east to nearly Afghanistan in the west (approximately between 72° and 91° E and 27° and 36°N) (Mani 1968). The Himalaya appears to terminate in the east at the southward bent of the Brahmaputra river and in the west similarly at the bend of the river Indus (Fig. 4). Altitude across the topographic front of the Himalaya increases from approximately 200 meters in the Gangetic foreland basin to more than 8000 meters at the tallest peaks. North of the High Himalaya the Tibetan Plateau has an average elevation of 5000 meters.

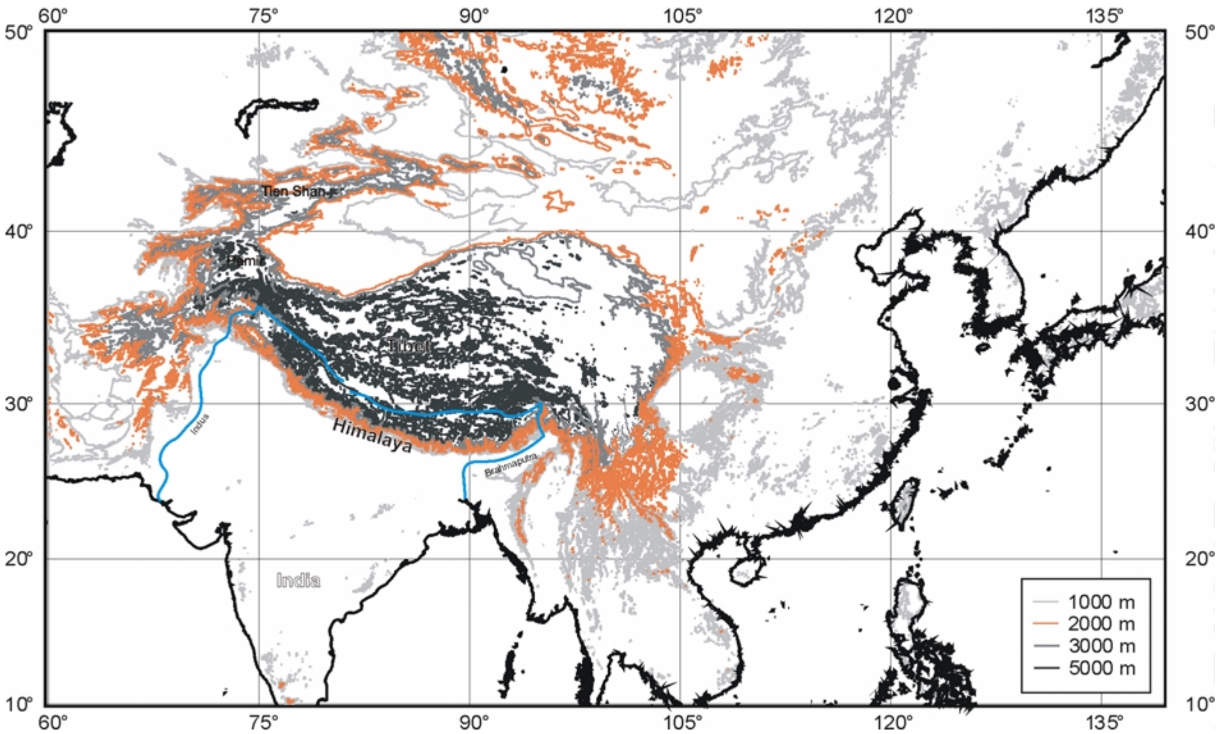


Fig. 4. The geographical extension of the Himalayan range and its surrounding areas. The Himalaya appears to terminate in the east at the southward bend of the Brahmaputra river and in the west similarly at the bend of the river Indus.

1.2.2 Climatic and vegetational characterization of the geographical area studied

The horizontal gradation (N-S, SE-NW)

The Himalaya separates the northern plains of the Indian subcontinent from the high Tibetan Plateau. The southern ranges and slopes are exposed to the rain-bearing monsoon winds. Being subject to high quantities of orographic rain they are densely forested. On the Tibetan side the forests give way to the cold high mountain steppe lands of Central Asia. In the same direction the alpine tree line rises from 3400-3800 meters in the outer southern ranges to 4400-4600 m in Tibet. Similarly, the persistent snow begins at 4500-4600 meters in the south and at it maximum of 6400 m in central Tibet (von Wissmann 1960, 1961). Schweinfurth (1957) distinguished three principal mountain belts within the Himalayan system: the "Outer Himalaya" with luxuriant monsoon forests, the "Inner Himalaya" with moderately moist boreal coniferous forests under the influence of heavy winter snowfall, and the arid "Tibetan Himalaya" with high altitude steppes only.

The Himalayan mountain belt as a whole crosses various horizontal climatic zones (Troll 1967, 1972) which is in its climatic and vegetational arrangement entirely asymmetrical. In the Southeast, in Assam and Bengal as far as Bhutan, the lowlands are covered by tropical evergreen rain forests. Further west in Sikkim and Nepal tropical humid, deciduous monsoon forests (wet sal forests of *Shorea robusta* with screw palm *Pandanus*) are the normal climax vegetation. From West Nepal to the Sutlej river a drier, semi-humid and more subtropical type of deciduous sal forest covers the Piedmont and the "Dun"-basins behind the Siwalik Hills. The Punjab is already part of the arid belt, whose natural plant cover is a subtropical semi-arid thorn steppe with *Acacias*, *Zizyphus*, *Calotropis procera*, fleshy euphorbias etc. Finally in the extreme north-west, in the Himalayan border region towards the Hindukush and the Karakorum, the deep valley bottoms of the Kabul-, Chitral-, Gilgit-, Hunza-, and the Indus valleys are semi-desert and above 2000 meters they give way to the central Asiatic *Artemisia* steppe. In this section the Outer Himalayan belt of wet monsoon forests is absent. Only in the most rainy parts of the Hindukush system, in the mountains of Nuristan (Kafiristan) west of the Kunst valley, and in the eastern part of Wed Koh above the belt of forest steppes (*Pinus gerardiana*) an evergreen mixed monsoon forest belt is developed, with *Quercus dilatata* from 2000 to 2400 meters and with *Quercus semicarpifolia* from 2400 to 2900 meters (Freitag 1971). The boreal Inner Himalayan zone is broadly developed and extends over the main range to the longitudinal Indus valley. Thus, the arid belt extends from Tibet and eastern Pamir southwards through the valleys (Indus gorge, Kunar valley) down into the Punjab plains. In the extreme south-east, in the Assam section east of Bhutan the dry Inner Himalayan zone peters out, the luxuriant wet monsoon rain forests cover mountain slopes and valleys up to the main range and border directly upon the dry Tibetan Highland. Through the Tsangpo gorge the rain forest encroaches upon south-eastern Tibet as far as Gyala and not until further north, in the northern tributary valleys of the Tsangpo does one find boreal coniferous forests (*Pinus*, *Larix*, *Picea*, *Tsuga*), which represent the transition to the highlands steppes of eastern Tibet, i.e. the Inner Himalayan zone.

In accordance with these climatic and vegetational contrasts Troll (1967, 1972) proposed a subdivision of the entire Himalayan system into the following seven natural sections (Fig. 5): 1) the Tsangpo Himalaya, the mountain ranges and valleys in south-eastern Tibet, drained by the left tributaries of the Tsangpo: Gyamda Phu, Po Yigrong, Po Tsangpo including the Zayul valley; 2) the Assam Himalaya, comprising the very wet section in the drainage areas of the rivers Bhoreli, Subansiri, Tsango-Dihan, Dibang and Lohit; 3) the Sikkim Himalaya, extending from Bhutan through Sikkim to eastern and Central Nepal; 4) the Garhwal Himalaya, from western Nepal through Kumaon and Garhwal to the Sutlej; 5) the Punjab Himalaya, from the Sutlej to the Indus, covering the drainage areas of the rivers Bias, Ravi, Chenab and the Jhelum area up to the Pit Panjal range south of the Kashmir basin; 6) the Indus Himalaya, in the north-west with pronounced boreal conditions in the alpine belt (heavy winter snowfall, short growing period), coniferous forests in the montane stage and *Artemisia* steppes and deserts in the deep valleys below 2500 m. The Kashmir basin may be regarded as a transition to the Punjab Himalaya; 7) the Tibetan Himalaya, which comprehends the northern steppe-like parts of the Himalaya sloping from the main crests to the longitudinal valleys of the upper Indus, the upper Sutlej and the upper Tsangpo. These valleys are never lower than 3000 meters. Although Troll (1972) stated that tree growth is here restricted to riverine woodland or artificially irrigated land, Miehe and Miehe (2000) and Miehe et al.

(1997) discussed the possibility of the existence of forests on mountain slopes in recent past which, however, were reduced strongly in consequence of human impact.

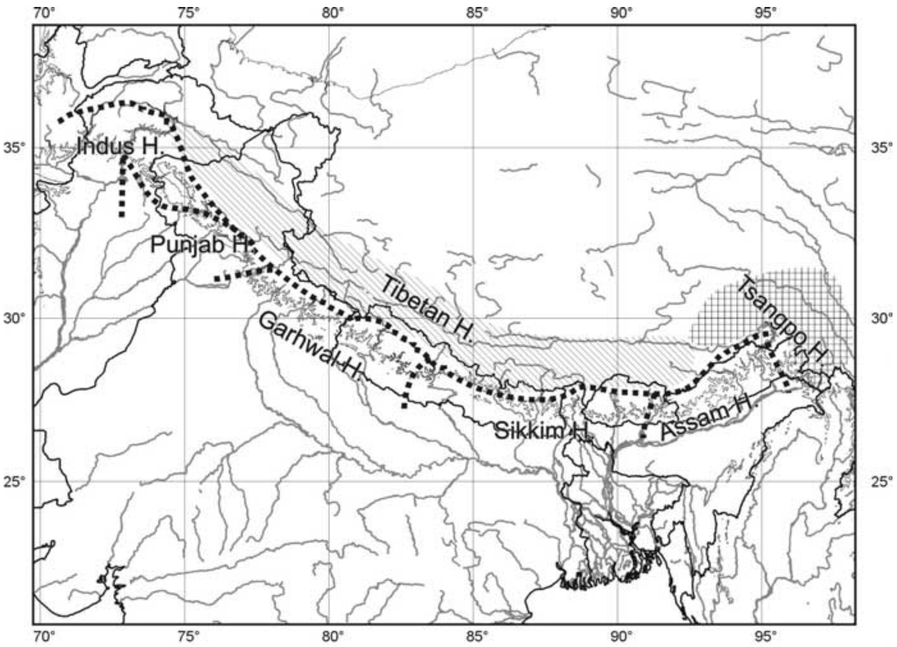


Fig. 5. The horizontal subdivision of the Himalayan system proposed by Troll (1972), modified.

The vertical gradation

A distinct vertical gradation of both climates and vegetation may be observed in all these sections (profiles Fig. 6) (Troll 1972; Miehe 1991). In the Assam Himalaya the tropical rain forest with the dominant trees of the genera *Beilschmedia, Cinnamomum, Cedrela*, *Phoebe*, *Castanopsis*, and with *Pandanus* palm and *Dendrocalamus* bamboo as underbrush rises above 1000 meters. Higher up, on the south-facing slopes, the humidity increases further to 6000 mm rainfall and the tropical evergreen montane forest reaches nearly 4000 meters. The tree line is reached at 3900 meters, but rhododendron scrub reaches higher as a subalpine "krummholz" belt. At 4600 meters the closed plant cover is replaced by the subnival frost debris stage. The climatic snow line does not rise above 5000 meters.

In the Sikkim Himalaya the vertical zonation of the vegetation is similar to the Assam section with two exceptions: 1) the rain forests of the lowest stage up to hundred meters are replaced by the tropical deciduous sal forest, and only the higher stages, the montane and subalpine belts are comparable; 2) in the deep valleys of Bhutan and Sikkim a drier zone of boreal coniferous forests with *Larix griffithii* and *Picea morinda* is inserted between the monsoon-exposed Outer Himalaya and the Tibetan Himalaya. This zone at altitudes from 2000 (2400) up to 3800 meters with a *Juniper*-krummholz on its upper rim replaces the luxuriant montane forests in the Darjeeling area; it is the most eastern extension of the Inner Himalayan zone.

The vegetation of the Garhwal Himalaya represents the subtropical monsoon belt with summer rain. The forests in the foreland belong to the semi-humid tropophilous type of *Shorea* (sal) forest. An additional deciduous forest type of this piedmont and foot hill areas is a more mixed association with species of *Terminalia*, *Anogeissus*, *Dalbergia*, *Cedrela, Bauhinia*, *Erythrina* etc., a subtropical variation of the tropical dry savannah forest. Higher up, in the Siwalik hills as low as 700 meters but further inland at 1500-1600 meters, forests of *Pinus roxburghii* cover the mountain slopes up to 2000 meters. The montane belt in this section is represented by moist evergreen oak forests, reaching from 2000 to 3500 meters. Three substages can be distinguished according to Troll (1972), a lower substage with

Quercus incana as the dominant tree, a middle substage with *Quercus dilatata* and an upper oak-conifer forest with *Quercus semicarpifolia, Picea morinda*, and *Abies pindrow*. Here and further to the west the subalpine rhododendron belt of eastern Himalaya is replaced by a narrow belt of birch forests (*Betula utilis*) from 3500 to 3900 meters, probably as a result of the very long duration of the snow cover. Only *Rhododendron campanulatum* as an underbrush of *Betula* and in a small krummholz belt in 3800 to 3900 meters reminds one of the splendour of the rhododendrons of Sikkim. The interior valleys of western Nepal, Kumaon and Garhwal again are rather dry and represent the Inner Himalayan zone with boreal conifer forests.

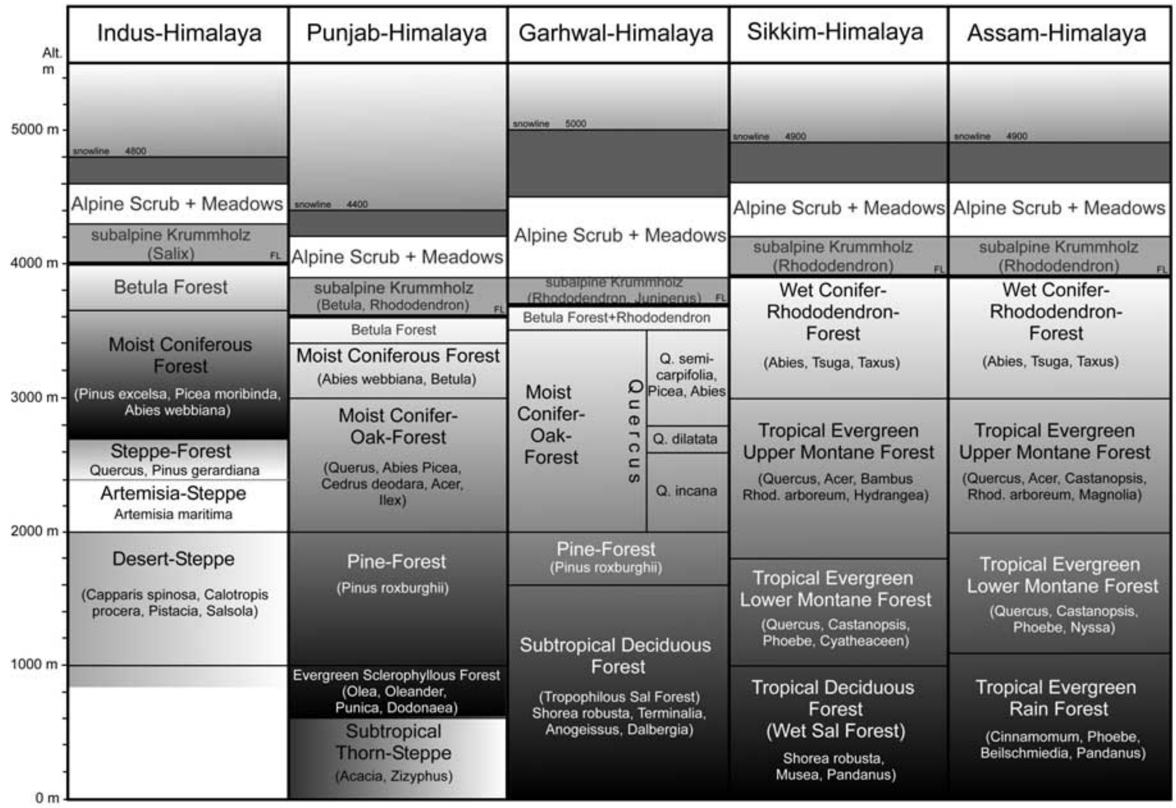


Fig. 6. The vertical zonation of vegetation proposed by Troll (1972), modified.

West of the Sutlej river the Punjab Himalaya begins and, in its foreland, the arid belt of the Middle East. Hence, it follows that the moist monsoon forests have not only an upper alpine limit but also a lower limit, i.e. a limit of aridity. The thorny steppes of the Punjab cover only the plains. Even the foot hills above 600 meters are covered by a sclerophyllous Mediterranean brushwood vegetation with *Dodonacea viscosa* as the prevailing shrub, and with trees of *Olea cuspidata* and *Punica granatum*, and *Oleander* in the torrent-like ravines (Meusel and Schubert 1971). Here, in contrast to the rest of the Indian subcontinent, winter rains begin to supplement and finally to replace the monsoon rains of summer. At higher altitudes this sclerophyllous woodland is replaced by *Pinus roxburghii*, on sunny slopes at 1500 to 2000 meters, on shadowy slopes much lower. The moist evergreen broad leaf forests of the montane belt of the Garhwal section also extend through the Punjab Himalaya from 2200 meters upwards, but they have a sharp continental limit on the crest of the Pir Panjal Range. The Murree and Thandiani Hills between the rivers Jhelum and Indus mark their continuous westwards extension. Evergreen oaks and deciduous maples, horse chestnut and oak trees, *Celtis*, *Ulmus*, *Morus*, a. o., wrapped in ivy and other creepers, are mixed with firs (*Abies pindrow* and *A. webbiana*), pines (*Pinus excelsa*) and spruce (*Picea morinda*). They have a dense undergrowth in sharp contrast to the bare, dry ground covered by the litter of the long-needle-pine. Approaching the upper tree line above 3000 meters, we find the fir trees mixed with *Betula utilis*, then the subalpine birch woodland (up to 3600 m) with an underbrush of *Rhododendron campanulatum* and finally a low krummholz of rhododendron an northern or juniper on southern slopes.

In the Indus Himalaya semi-arid conditions and Central-Asiatic *Artemisia* steppes occupy the valleys up to 2500 and 3000 meters above sea-level. In their upper regions they are often interspersed with *Pinus gerardiana*, juniper (*Juniperus semiglobosa*) and sometimes with *Quercus baloot*. In the innermost valleys, on the upper Indus valley above Skardu, in the Hunza valley in Karakorum and in northern Chitral, where the forest belts peter out completely, these warm steppe lands gradually merge into the cold highland steppes of Tibet and the eastern Pamir. The deep valleys in this innermost region below 2000 meters are desert steppes with some scattered trees (*Pistacia*) or shrubs (*Capparis spinosa*) and poor riverine woods of *Tamarix*. In the moister altitudes above the upper limit of aridity we also miss the exuberant flora and vegetation of the Outer Himalaya completely, The coniferous forest belt has a boreal appearance, comparable with the so-called mountain-Taiga of the Altai. Here as there an undergrowth of the large-leaved herbs of rhubarb (*Rheum webbianum*) and *Bergenia ligulata* is very typical. The forest belt is regularly interrupted by avalanche lanes, in which birches and willows resist the mechanical depressing and the shortening of the growing season. The uppermost timber belt again is represented by *Betula utilis* (timber line at 4000 m), the krummholz belt by a willow scrub of *Salix hastata*. In this parts of the Himalaya the term "alpine" for the subnival stage is completely appropriate. The vegetation, at least on slopes exposed to the north consists of dwarf shrubs (*Juniperus nana* and *J. squamata*, or of *Rhododendron hypenanthum*, of alpine meadows with bright flowers (*Meconopsis*, *Sweertia*, *Rhodiola*, *Pedicularis*, *Iris*, *Aconitum* and many others), or of a dense turf of *Cornresia*. Small peat bogs are covered by the alpine-arctic cotton-grass *Eriophorum scheuchzeri*. Plants adapted to a very short growing season in high summer coin pose very dwarfish associations.

1.2.3 Geological history

The exceptional extent and elevation of the Tibetan Plateau and Himalayan range has generally been attributed to the convergence between India and southern Asia over past 55 Myr (Mattauer et al. 1999). Models advanced to explain the evolution of the present distribution of crust within the Indo-Asian orogen include those that predict wholesale uplift (mantle delamination, delayed under-plating), progressive growth (Indian under-thrusting, Asian under-thrusting, continental injection), lateral responses (orogenic collapse, horizontal extrusion), and inheritance of an elevated terrain (multiple collision, intra-arc thickening). Harrison et al. (1998) argued that a spatially and temporally complex mix of these mechanisms is required to explain the orographic evolution of southern Asia.

The Tibetan Plateau began to form locally in response to the collision of the Lhasa block with southern Asia during Early Cretaceous, particularly in the southern Tibet. This event is well-documented in the northern Lhasa block where a fold and a thrust belt developed between 144-110 Ma and remained substantially elevated until the onset of the collision of Indian and Asia (Harrison et al. 1998). The northward movement of India for some 100 Ma progressively narrowed the Neo-Tethys. The closure of Tethys (early Eocene) was accommodated by subduction of the oceanic floor under the crust of Eurasia. That produced a large volume of magmatic rock that both intruded and were erupted onto the southern margin of Eurasia (Le Fort 1996). Those magmas formed from Palaeocene to Eocene (~60-45 Ma) a mountain range known as the Trans-Himalaya along most of this edge of the Lhasa block. Westward, it branched out of this continental margin to form the Ladakh-Kohistan arc what is probably the largest paleo-arc presently outcropping on earth. In between the two continental margins, in the trench, volcanosedimentary material has been dragged along the subduction and metamorphosed. They exist now as a few patches mostly confined to the north-western Himalaya, where they have been dated as middle Cretaceous (80-98 Ma) (see Le Fort 1996), a period when Tethys was still some 2,500 km wide.

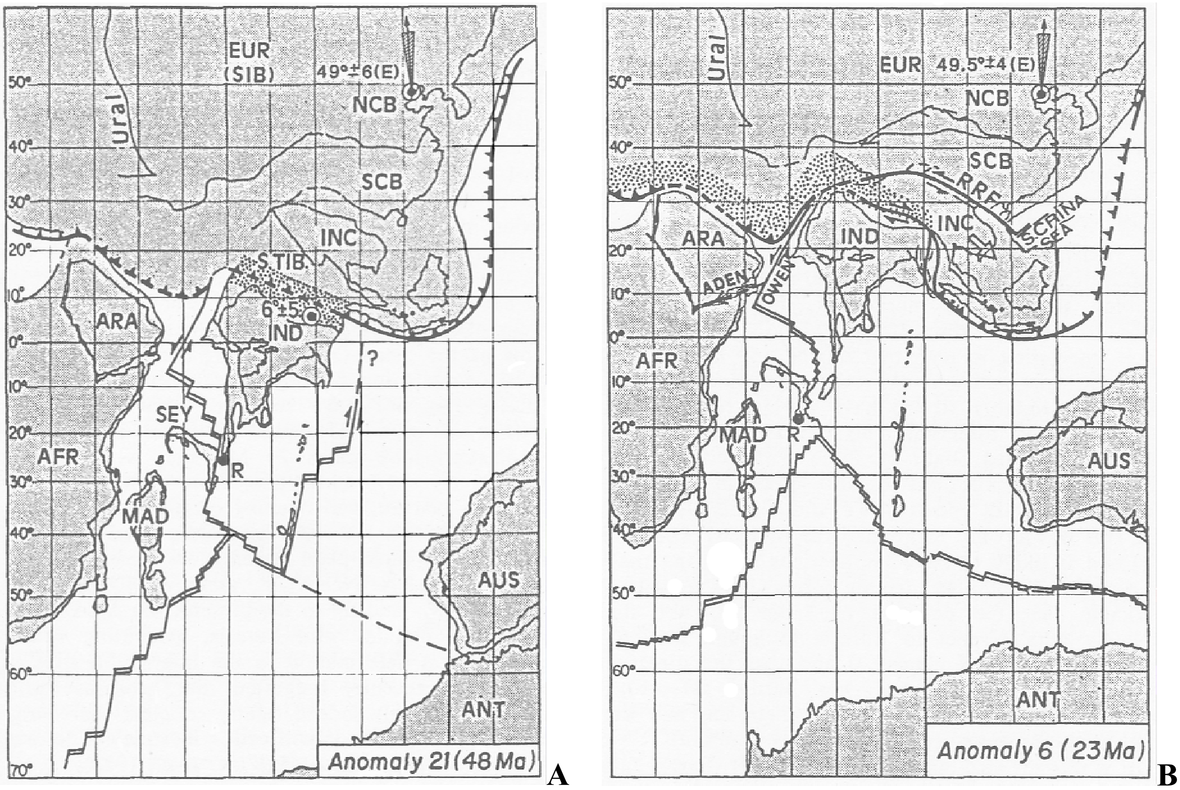


Fig. 7. Paleogeograhic maps of the continents bordering the Indian Ocean (from Besse and Courtillot 1988) during Middle Eocene (48 Ma, A) and Oligocene-Miocene boundary (23 Ma, B).

Sedimentological evidence indicates that the north-west tip of India first collided with Asia at ~ 55 Ma (e. g. Le Fort 1996). By 40 Ma, the two continents appear to have met along the full length of an approximately 3000 km long suture zone. Paleomagnetic evidence reveals that the Indo-Australian plate moved northward by 2600±900 km relative to the Eurasian plate after the initiation of collision (Dewey et al. 1989, Le Pichon et al. 1992). In the same interval, southern Tibet moved north with respect to Eurasia by 2000±600km (Fig. 7; Besse and Courtillot 1988). The first evidence of uplift related thickening due to collision of India with Asia is deformation and clastic sediment production in the Nan Shan and Fenghuo Shan regions of northern Tibet which began at about 45-32 Ma. Several lines of evidence suggest the existence of an early thickening event in the proto Himalaya, referred to as the Eo-Himalayan (58-36 Ma) orogeny (see Harrison et al. 1998). Possibly in response to this thickening, the left-lateral Red River fault was initiated at 35 Ma permitting the eastward extrusion of Indochina until ~ 17 Ma. This had the effect of reducing the magnitude of crustal thickening in Tibet, perhaps by accommodating as much as one-half of Indo-Asian convergence during the Oligocene (37-24 Ma). Thin-skinned thrusting was occurring in the Tethyan Himalaya throughout the Palaeogene while cover rocks on the northern margin of the Indian shield experienced crustal thickening. Although little crustal thickening of Tibet within fold and thrust belts can be documented for the Eocene-Oligocene (58-24 Ma), mass balance considerations all but require that channelled flow in the ductile lower crust (e.g., Zhao and

Morgan 1985; Bird 1991) has continuously thickened the crust, uniformly raising much of Tibet to between 1 and 3 km in elevation.

Thus by the beginning of the Late Oligocene (30 Ma), a relatively low (~2 km) Tibetan Plateau (except, perhaps, along the collision zone between the Lhasa and Qiangtang blocks) was likely in existence while the Tethyan and proto-Himalaya were topographically subdued and the present Himalayan range had not yet begun to develop. At ca. 28 Ma, crustal thickening began in southern Tibet along the Gangdese Thrust (Fig. 8) moving southward to the Himalaya shortly thereafter in a series of south-directed thrusts which appear to be of the same decollement (Yin et al. 1994). Harrison et al. (1998) concluded from geological constraints and calculations taking into account lithosphere shortening and denudation that at ca. 30 Ma, the average paleoelevation of the Himalaya was one kilometer, and the Gangdese Shan (crustal thickening at GT) was at an elevation of 3 ±1 km. The thickening effects from Early Miocene slip on the Main Central Thrust are thought responsible for generating the 24-19 Ma Himalayan leucogranites (Coleman and Parrish 1995; Harrison et al. 1995). This general pattern of propagation toward the foreland was interrupted by the north-directed Renbu Zedong Thrust (RZT) which was active in southern Tibet between 19-11 Ma. Extension in the High Himalaya along the South Tibetan Detachment System occurred concurrently with slip on the MCT and RZT. The Tien Shan thrusts and thickening in the western Kun Lun were also initiated during the Early Miocene (~20 Ma). By ca. 20 Ma, the Gangdese Shan, Tethyan Himalaya, and High Himalaya were now likely a significant climatic barrier, with an average elevation of perhaps 4-5 km, behind which stood a large but still relatively subdued Tibetan Plateau (Harrison et al. 1998). At this point, thickening deformation jumped the Tarim basin to the Tien Shan.

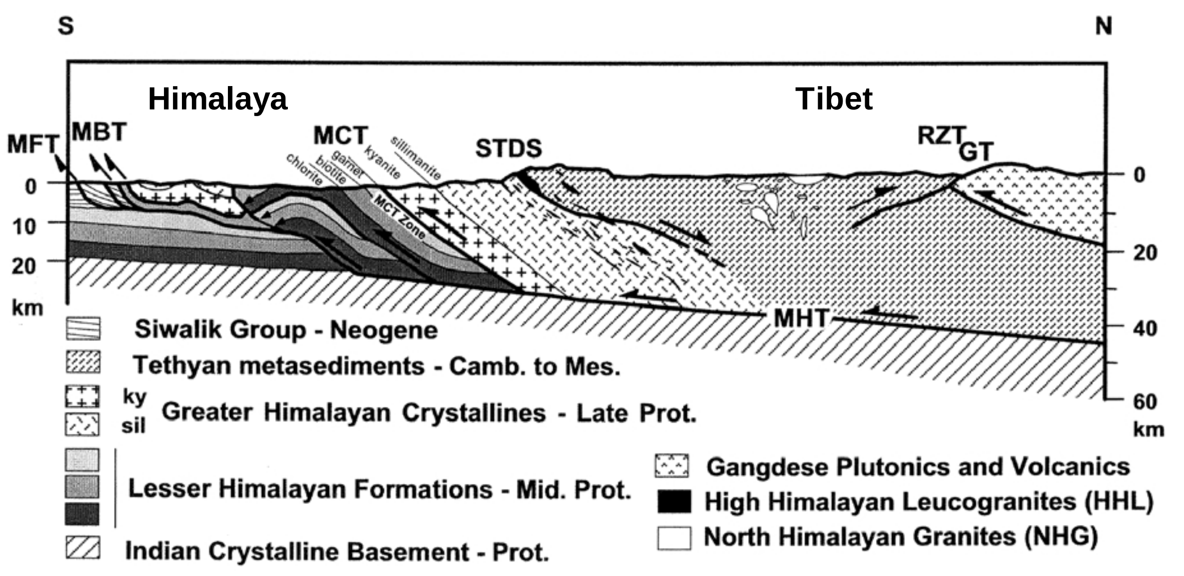


Fig. 8. Generalized cross section through the central Himalaya illustrating the juxtaposition of the major lithostratigraphic units across the major Himalayan faults, inverted metamorphism, and plutonic belts (modified, from Harrison et al. 1999). MFT: Main Frontal Trust; MBT: Main Boundary Trust; MCT Main Central Trust; STDS: South Tibetan Detachment System; RZT: Renbu Zedong Thrust; GT: Gangdese Trust.

Thickening in northwest Tibet, apparently related to transtension along the Altyn Tagh fault, began during the middle Miocene (~15 Ma) (Tapponnier et al. 2001). Subsequent to initiation of the Main Boundary Thrust at ~11 Ma, a broad zone of deformation beneath the MCT fault was active at some time between 10-4 Ma producing the classic Himalayan inverted metamorphic sequences. Shearing within the MCT zone appears to have continued into Pliocene (5-2 Ma). In fact, the Siwaliks originally formed the distal part of the Himalayan piedmont accumulation system and then became incorporated into the range, eroded, and hence recycled during last 5 Ma (Lavé 1997). By ~9 Ma (Harrison et al. 1998), the Tibetan Plateau had attained an average elevation of approximately 5 km and began to differentially extend E-W in a set of N-S trending graben. However, Spicer et al. (2003) conclude at base of their studies of well preserved fossil leaf assemblages from the Namling basin, southern Tibet, that the elevation of the southern Tibetan plateau probably has remained unchanged for the past 15 Ma.

Recent studies of Cenozoic deformation, magmatism, and seismic structure lend support to a model of time-dependent, localized shear between coherent lithospheric blocks (Tapponier et al. 2001). Since India collided with Asia ~55 million years ago, the rise of the high Tibetan plateau likely occurred in three main steps, by successive growth and uplift of 300- to 500-kilometer-wide crustal thrust-wedges (Fig. 9, 10**)**. The crust thickened, while the mantle, decoupled beneath gently dipping shear zones, did not. Sediment infilling, bathtub-like, of dammed intermontane basins formed flat high plains at each step. The existence of magmatic belts younging northward implies that slabs of Asian mantle subducted one after another under ranges north of the Himalaya. Subduction was oblique and accompanied by extrusion along the left lateral strike-slip faults that slice Tibet's east side. These mechanisms, akin to plate tectonics hidden by thickening crust, with slip-partitioning, account for the dominant growth of the Tibet Plateau toward the east and northeast.

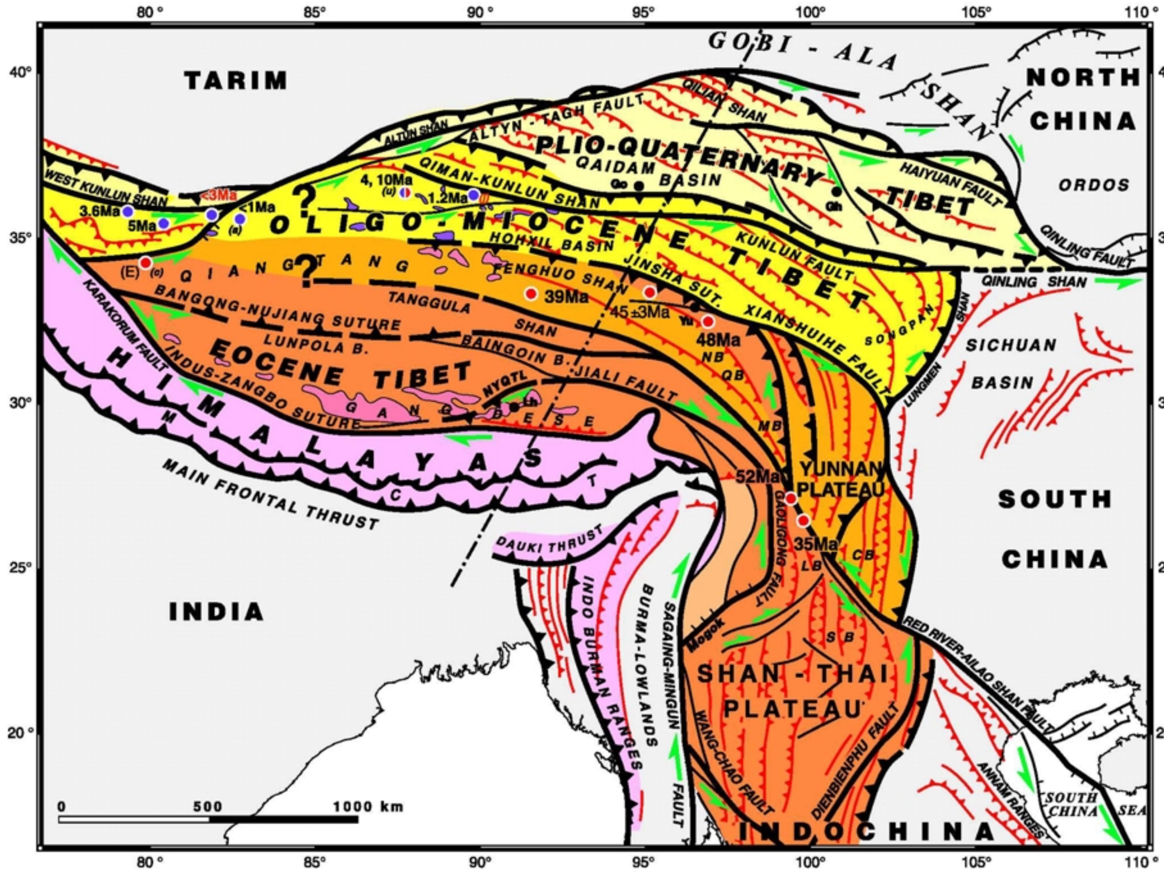


Fig. 9. Simplified map of major tectonic boundaries and Tertiary faults in Tibet, from Tapponnier et al. 2001. Bold black lines are major faults and localized shear zones (megathrust or strike-slip) with largest finite offsets, which may extend into lithospheric mantle. Dashed where uncertain. Thin red lines are crustal thrusts. Red and violet circles are Eocene and Plio-Quaternary magmatic centres, respectively, in central Tibet. Corresponding numbers are ages. Patches with deep pink and violet shades schematise other areas with Eocene–Early Miocene and Late Miocene–Quaternary lavas, respectively. Orange to pale yellow shades represent inferred ages of principal plateau-building epochs at expense of Asian crust. Light pink shade south of Zangbo suture and west of Shan plateau indicates thickened Indian crust. Dashed line shows location of section in Fig. 10. MCT, Main central thrust.

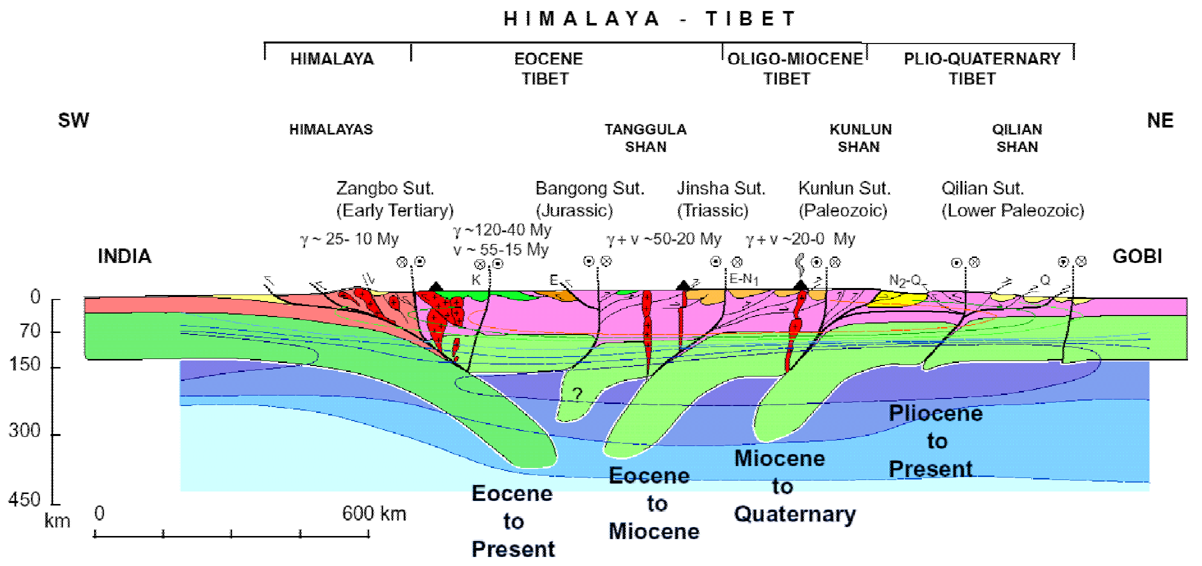


Fig. 10. Schematic lithospheric section of Cenozoic evolution of Himalaya-Tibet orogen. Shades of green represent subducted Indian and Asian lithospheric mantle. Shades of red and pink, Indian and Asian crust, or intrusives. Yellow and dark green shades, ages of sedimentary basins. Relative importance of sedimentary fills is portrayed, but thicknesses are not to scale. Dashed contours (5% intervals) and shades of blue in mantle show variation of L5 rVs 2 with depth (Vs, shear wave velocity), from Tapponnier et al. 2001.

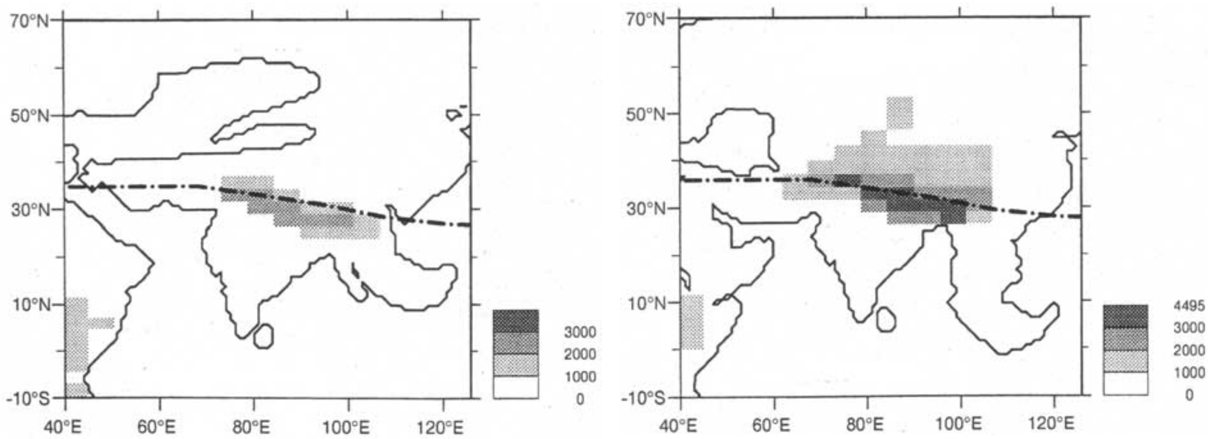
1.2.4 Climatic history

Tertiary

Little is known about paleoclimate of Main Himalayan chain before 8 Ma since sedimentary basis in the Himalaya are rather young or already overformed by erosion and tectonic processes. At the scale of continental Asia, there has been a continuous rise of Solid Phase Accumulation Rates (SPAR) since the onset of India-Asia collision at 50 Ma (Métevier et al. 1999). This evolution of the rates of accumulation in Asian basis does not support a sudden change of climate induced by a sharp altitudinal threshold (Ramstein et al. 1997), but rather implicate that solid phase accumulation rates, on geological timescales, are controlled mainly by tectonics and not by climate (Métevier et al. 1999). However, this observation does not contradict regional evidence for rapid evolution of climate patterns and vegetation (onset of monsoon climate) around 7-8 Ma such as the change (in photosynthesis) from C3 to C4 plants in Pakistan (Quade et al. 1989) and Nepal (Quade et al. 1995) or the appearance of radiolarians and foraminiferal fauna characteristic of upwelling in the Sea of Oman (Prell et al. 1992).

Interiors of large continents are normally arid because of the great distance to ocean moisture sources, but sediments deposited in the western Loess plateau of East Asia were fluviallacustrine through the Oligocene epoch (Wang 1985) indicating a more humid climate. One source of Oligocene moisture in the Asian interior may have been the broad Paratethys sea in westernv Central Asia (Ramstein et al. 1997). As this inland sea shrank during the late Oligocene and early Miocene (Figs 11, 12), it would have left the Asian interior more arid and would also have intensified the continentality, with hotter summers and colder winters. The onset of greater aridity recorded by the early Miocene loess (Guo et al. 2002) of Qinan deposits in northern China (Gansu province) is broadly consistent with this change in land-sea distribution. These Qinan deposits indicate that a winter wind pattern similar to the modern Asian winter monsoon had formed by the early Miocene. However, the finer texture of the

Qinan loess compared with the Quaternary loess deposits of Xifeng (N China, Gansu province) (Guo et al. 2002) suggests weaker wind strength and smaller extent of northern Chinese deserts during Miocene. The alternations between loess and reddish soils in the Qinan deposits indicate cyclical changes in intensity of winter and summer monsoons.



Figs 11, 12. Paleogeography of Himalayan region 30 Ma (Fig. 11, left side) and 10 Ma (Fig. 12, right side) ago (modified after Ramstein et al. 1997). The different palaeoelevations are grey-shaded.

Uplift of the Himalayan-Tibetan plateau (Ruddiman and Kutzbach 1989; Manabe and Broccoli 1990; An et al. 2001) and changes in land-sea distribution (Ramstein et al. 1997) have been invoked as driving forces behind long-term Cenozoic climate deterioration. General circulation model experiments reveal the probable effects of large-scale Tibetan-Himalayan uplift on Asian climate (Ruddiman and Kutzbach 1989; Manabe and Broccoli 1990; An et al. 2001). Uplift strengthens the summer monsoon and brings wetter climates to India and South-East Asia, but this moisture cannot reach the Asian interior because uplifted Himalayan topography blocks flow from the south. As a result, central Asia becomes drier as uplift proceeds. Uplift also produces drier climates in central Asia in the winter season because dry winter monsoon winds blow out of the Asian interior. The combination of summer and winter drying produces year-round aridity and forms deserts. In addition, uplift strengthens the flow of winter monsoon winds from the northwest. These model simulations (Ruddiman and Kutzbach 1989; Manabe and Broccoli 1990; An et al. 2001), combined with geological evidence (Harrison et al. 1992), provide an explanation for the early Miocene loess deposits in Qinan: the southern margin of the Tibetan plateau was sufficiently elevated by 22 Ma (Guo et al. 2002) to cause year-round drying and desert formation in the Asian interior and to produce northwest winds strong enough to carry aeolian particles southeast into the Qinhai Loess plateau (Guo et al. 2002).

Ongoing global cooling during the Cenozoic probably also contributed to regional changes in Asia. Although neither ice sheets nor extensive sea ice appeared in the northern hemisphere until late in the Miocene (Jansen and Sjoholm 1991), climatic cooling had caused Palaeocene evergreen forests and Eocene-epoch deciduous forests along the Arctic margins to yield to mixed coniferous forests by the early Miocene (Wolfe 1985). Oxygen-isotopic values from benthic foraminifers also indicate significant early Miocene cooling of polar oceans (Miller et al. 1987). Cooler high-latitude oceans provide less moisture to continental interiors, promoting continentality at the expense of temperate climates. Continental climates are also generally marked by colder, drier winters with stronger winds.

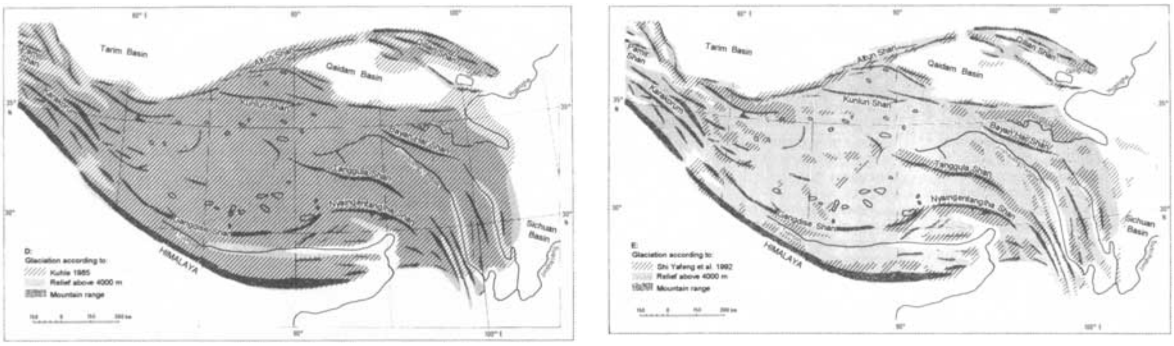
The Miocene sequences of Qinan (China) do not show any obvious long-term intensification of loess deposition between 22 and 6.2 Ma (Guo et al. 2002), however, two intervals with higher dust accumulation rates are observed at 15-13 Ma and 8-7 Ma. The major increases occur after about 3.5 Ma, in the Pliocene and Pleistocene epochs. This suggests that the level of aridity and the strength of the winter monsoon winds in central Asia remained at moderate levels through the Miocene.

Several Miocene plant assemblages have been described (Xu Ren 1981) from Tibet. The Miocene floras of the central and northern Tibet were mainly composed of deciduous broad-leaved trees, though some evergreen species existed somewhere else. Their composition reflects that the surface of central and northern Tibet had been already uplifted to some extent before Miocene. The results of Spicer et al. (2003) indicate due to physiognomy of leave assemblages Tibetan Plateau had its present elevation already at 15 Ma. According to Xu Ren (1981) during the Pliocene, the evergreen broad-leaved trees were gradually declining in their development in northern Tibet. The vegetation of the Tsaidam Basin further changed from deciduous broad-leaved to coniferous forests and then they turned into grasslands and semideserts or deserts, when by that time Tibet and Qinghai were further upheaved. While the vegetation of the Himalaya was still dominated by evergreen oaks and *Cedrus* forests, by the Quaternary evergreen broad leaved trees lack in northern Tibet, and during late Quaternary, the vegetation of most parts of Tibet gradually changed into alpine tundras (Xu Ren 1981).

Pleistocene

The Himalayan mountain range and the Tibetan Plateau form a climatic divide between southern and central Asia that constitutes a formative influence upon the Asian monsoons (Owen et al. 1998). Furthermore, Himalayan climate show considerable geographical variation, dominantly influenced by the SW Indian Monsoon, the mid-latitude westerlies and the El Niño Southern Oscillation. The distribution and style of glaciation throughout central Asia is strongly influenced by these climatic systems. Accordingly follows that variations in Quaternary glaciations in this region were a function of changes in the intensity of these climatic systems. Rapid differential uplift of the Himalaya during late Tertiary and Quaternary times may also have been important in controlling the style of glaciation (Fort 1996).

With the increased attention given to all aspects of global change of climate, the presence or absence of an extensive sheet ice over Tibet during the Pleistocene has become a key issue. This is because of the influence of the Tibetan Plateau on the general circulation of the atmosphere (Bollin 1950) and, in particular, its role in causing variations in the Asiatic monsoon (Ruddiman and Kutzbach 1989; Prell and Kutzbach 1992). At present, two main contrasting views exist. The most extreme is that of Kuhle (1985, 1987), who postulated that an extensive Pleistocene ice sheet on the Tibetan Plateau covered 2-2.4 million km^2 (Fig. 13) and reached up to 2.5 km in thickness. In contrast, Li et al. (1991), Shi et al. (1992), and Derbyshire et al. (1991) expounded the view that ice cover was less extensive (Fig. 14), with an ice cap covering only about 297,000 km^2. In addition, Hövermann and Lehmkuhl (1994), Lehmkuhl (1995), and Lehmkuhl and Liu (1994) provided evidence that glaciation of the eastern margin of the Tibetan Plateau occurred by expanded ice caps rather than an extensive inland ice sheet. An even more limited ice cover was suggested by von Wissmann (1959). The nature and extent of past and present glaciation on the Tibetan Plateau was reviewed recently by Lehmkuhl et al. (1998). Their geomorphological and sedimentological data showed a strong regional control on snowline elevations both today and during former glaciations. Present snowlines rise by about 100 m for each degree of longitude westward, from 4,800 m in the south-eastern part of the Plateau to more than 5,300 m in the northwest margin of the Plateau. During the Last Glacial the snowlines ranged from 4,000 m to 4,700 m between the southeast and northwest of Tibet. The Pleistocene snowline depression, therefore, ranged from 600 m to 800 m. These results, together with other field evidence, show that no ice sheet existed during the Last Glacial Maximum across the north-eastern margin of the Plateau. Rather, glaciers and ice caps extended outwards from the main mountain ranges.



Figs 13, 14. Hypothesized Pleistocene ice sheet on the Tibetan Plateau covered 2-2.4 million km^2 and reached up to 2.5 km in thickness (after Kuhle 1985,1987) (Fig. 13) and Shi et al. (1992) (Fig. 14).

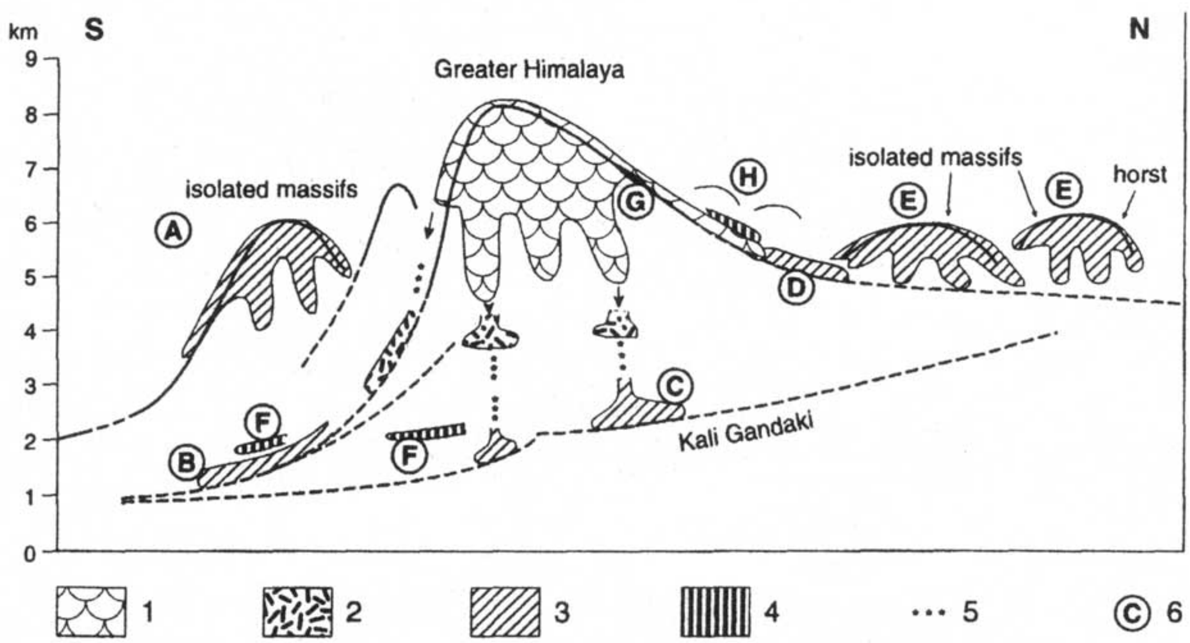


Fig. 15. Various configurations (synthetic) of present and Late Pleistocene glaciation across the Greater Himalaya: a key to assess older glaciation evidence and dating. 1 – present glaciers; 2 – avalanche fed, present glaciers; 3 - extent of Late Pleistocene glaciers; 4 - older glacial remains (either perched or buried); 5 - avalanche tracks, and Late Pleistocene avalanche fed glaciers. A,B,.... mains types of glaciation configurations: A - isolated massifs on south side, the best climatically sensitive areas, also allowing assessment of former glaciation limits; B - glacial tongues in very deeply dissected valleys, derived from avalanche inputs, reconstructed ELAs abnormally low; C - avalanche-fed glaciers: the lowest altitudes are controlled by the steep topography; D - high altitude and low dissection on north slope: ice tongue can expand, with the dryness as a limiting factor; E - isolated massifs on north side, also good indicators for glaciation (same as A); E' - correspond to horst; F - perched remains of glaciation (continuous uplift of the Greater Himalaya), to be sought above the present valley bottoms; G - buried older glacial remains (the continuous uplift causing the expansion of more recent glaciation to override the limits of the former ones); H - perched remains of glaciation (same as F, but on north slope), to be sought upon the deglaciated interfluves. From Owen et al. (1998).

Richards et al. (2000) compared relative chronologies and new optically stimulated luminescence (OSL) dates for the Swat (Pakistan) and the middle Indus valley with chronologies for other Himalayan regions. Their dating seem to confirm that glaciation at the western end of the Himalaya was asynchronous with the maximum extent of northern hemisphere ice sheets, i.e. the Last Glacial Maximum in Oxygen Isotope Stage 2. In support of this view, the maximum extents of glaciation in the Garhwal and Lahul Himalaya in India have been dated at ca. 63 ka, and before ca. 36-43 ka, respectively (Sharma and Owen 1996; Owen et al. 1997). These are during Oxygen Isotope Stage 3, although the Garhwal date is at the very earliest part of the oxygen isotope stage. Furthermore, there is growing evidence that glaciation throughout the Himalaya may even be asynchronous between regions. In the Khumbu Himalaya (Central Nepal), Richards (1999) has shown that the most extensive glacial advance during the last glacial cycle occurred in Oxygen Isotope Stage 2, ca. 18-25 ka.

The asynchronous glacial events in the Himalaya appears to reflect differences in climatic forcing mechanisms across the region (Benn and Owen 1998). In the 'Pakistani Himalaya', the glaciations in Oxygen Isotope Stage 3 (~30-60ka, Richards et al. 2000) were probably coincident with a strengthened and/or a northward extension of the South Asian summer monsoon (Clemens et al. 1991; Emeis et al. 1995). This suggests that the primary control on glacier expansion was enhanced summer snowfall at high altitudes. During Oxygen Isotope Stage 2, the 'Pakistani Himalaya' would have experienced reduced summer precipitation, which would have restricted glacier accumulation despite cooler temperatures. In contrast, the maximum advance of glaciers in the Khumbu Himal occurred during Oxygen Isotope Stage 2 (18-25 ka). Richards (1999) argue that multiproxy data from the Arabian Sea (Sirocko et al. 1991) show that during the period 27-15 ka, low-level summer monsoon winds were predominantly west southwesterlies, rather than the present southwesterlies. The influence of the monsoon, therefore, would have extended further eastward, but would be less to the north and west than at present. This implies that the western Himalaya would have experienced less summer precipitation as compared with the central and eastern Himalaya at that time. This would cause the glaciers in the eastern and central Himalaya to advance, whereas those in the western Himalaya would become less extensive during Oxygen Isotope Stage 2. Various configurations (synthetic) of present and late Pleistocene glaciation across the Greater Himalaya are shown in Fig. 15.

Finkel et al. (2003) provided new data which indicate that glaciations at the south side of the Mount Everest (Nepal) were not synchronous with the advance of the northern hemisphere ice sheets, but the maximum extend of glaciation in the Himalaya occurred earlier than the LGM (Owen et al. 2002). Yet glaciations within the Himalaya were synchronous during the late Quaternary (Finkel et al. 2003) namely during Oxygen Isotope Stage 2. Since chronologies for other glaciations are missing yet, it is not clear, whether these data contradict the conclusions of Richards (1999) and Richards et al. (2000) regarding the timing (synchronous/ asynchronous) of glaciations within the Himalaya. The existence of glacial advances during times of increased insolation suggests that enhanced moisture delivered by an active south Asian summer monsoon is largely responsible for glacial advances in this part of the Himalaya.

Holocene

Evidence on Himalayan climate of Holocene based mainly on punctual data of pollen analyses. Due to great extend of the Himalaya in vertical and horizontal dimension, this type of data is, however, not a suitable proxy for general climatic conditions since similar to present conditions, the climate must have varied considerably locally. Furthermore, data suffer from strong ascending winds present in most regions, rendering the source area often rather variable. Fluctuations of Quaternary climate has been shown by Franz and Kral (1975) and Igarashi et al. (1988) from the Kathmandu valley. It is suggested that climate had been cooler and drier in the past. Franz and Kral (1975) have found a much higher percentage of Graminaceae in comparison to recent and subrecent pollen sequences from Central Nepal.

Franz (1979) concluded that the area relevant for sedimentation of the former lake in the valley must have been free of forests and that the climate must have been more continental due to the occurrence of *Artemisia* and Chenopodiaceae. However, the sequences contained also tree pollen presently occurring in the midland of Nepal. This might indicate that the slopes around the valley were forested during more drier periods, too.

Periods of strengthened monsoon and moister climate were present in the last interstade (58-24 ka, Goodbred in press) and during the postglacial transgression and the hypsithermal (18-7 ka, Goodbred in press) when monsoon intensified (Chauhan 2003), the Himalayan glacier revealed a general pattern of growth in consequence of a simultaneous depression of snowline (see Ducan et al. 1998). During Mid-Upper Holocene, the Himalaya experienced at least two significant episodes of aridity at 5-4.3 and ~ 2 ka (Chauhan 2003). These data revealed based on evidence from oxygen isotope records in the Bay of Bengal are consistent in part with pollen data from Himachal Pradesh (Chauhan et al. 2000) and western Nepal (Yasuda and Tabata 1988). Interestingly, in contrast to the drier western areas, in the eastern Himalaya major vegetational changes resulting from pollen analyses are not evident (Yonebayashi and Minaki 1997). Based on cosmogenic exposure ages of fluvial surfaces in Central Nepal Pratt et al. (2002) speculate that precipitations were elevated around 7±1 ka due to strengthened monsoons. Most pollen analyses reveal generally a shifting between more pine tree dominated assemblages during drier periods and oak dominated forests during more humid and warmer periods (Vishnu-Mittre et al. 1967; Yasuda and Tabata 1988; Chauhan et al. 2000; Sharma and Chauhan 1988). Being mostly fragmentary, presently published pollen analyses let hardly recognize whether the climatic fluctuations evident from changes in pollen frequency in the diverse studies are linked in time within entire Himalayan range.

2 Material and methods

Material examined

In the framework of the previously undertaken faunistic and taxonomic studies (Ahrens 1995a - Ahrens 2004b; Ahrens and Sabatinelli 1996) more than 25.000 specimens from presently approximately 1400 localities have been examined (Fig. 16). A part of this material studied herein was collected personally between 1993 and 1998 on several expeditions to Nepal and Sikkim. Additionally, a very rich material I received from several private collectors and public institutions (Ahrens 1995a, b, 1996, 1998, 1999a, b, c, 2000a, b, c, d, e, 2001a, b, 2002, 2003a, 2004a, b; Ahrens and Sabatinelli 1996) On this exhaustive material the ongoing morphological studies were based on, in search for informative characters for the phylogenetic analysis. Species examined for character coding are indicated for each chapter in the appendix A, abbreviations indicating specimens depository are taken from (Ahrens 2004b). The taxonomic and nomenclatural framework of the present study is based on Ahrens (2004b). IN addition to full names of examined species, references on generic names are completed in appendix D. For further details in procedure of determination of specimens consult Ahrens (2004b).

Preparation of the specimens

Whole specimens were softened in water for one day. For endoskeleton preparation, the specimens were macerated with 10 % KOH at about 80°C until tissue has been sufficiently dissolved. For better effect of the maceration, in large specimens prothorax and abdomen were separated from the rest of the thorax. Subsequently, specimens were washed in water.

The dissection was conducted under Stereomicroscope within a petri dish filled with water. Dissected parts were conserved in vials of suitable size in glycerol or alcohol (70 %). Great part of thoracic endosternites were dry-prepared for immediate access for the comparative study.

Preparation of the genitalia

Whole specimens were softened in water for one day. The male genitalia were extracted pushing the pygidium dorsally. The intersegmental membrane between segments VIII and IX slit and the entire genitalia was pulled out. The aedeagus was fixed air dried with glue on a carton at the same pine with the specimen.

For endophallus preparation, the aedeagus was washed in water after is was macerated with 10 % KOH at about 80°C until tissue has been sufficiently dissolved. The endophallus was pulled out from distal ostium of the aedeagus with help of a very thin insect pin hooked at the tip. In rare cases, when the access via distal ostium was not possible due to deformations or a too small opening, the endophallus was extracted via the basal ostium of phallobase.

For dissection of female genitalia, the entire abdomen was removed after relaxing the specimen in water for a day and macerated with 10 % KOH at about 80°C. After washing the abdomen the tergites including the pygidium were carefully detached from sternites. Finally the membrane between segment VIII and the female genitalia was very carefully removed from the interior face of segment VIII avoiding the detachment of accessory glands from genitalia. Female genitalia as well as male endophallus were conserved in microvials with glycerol.

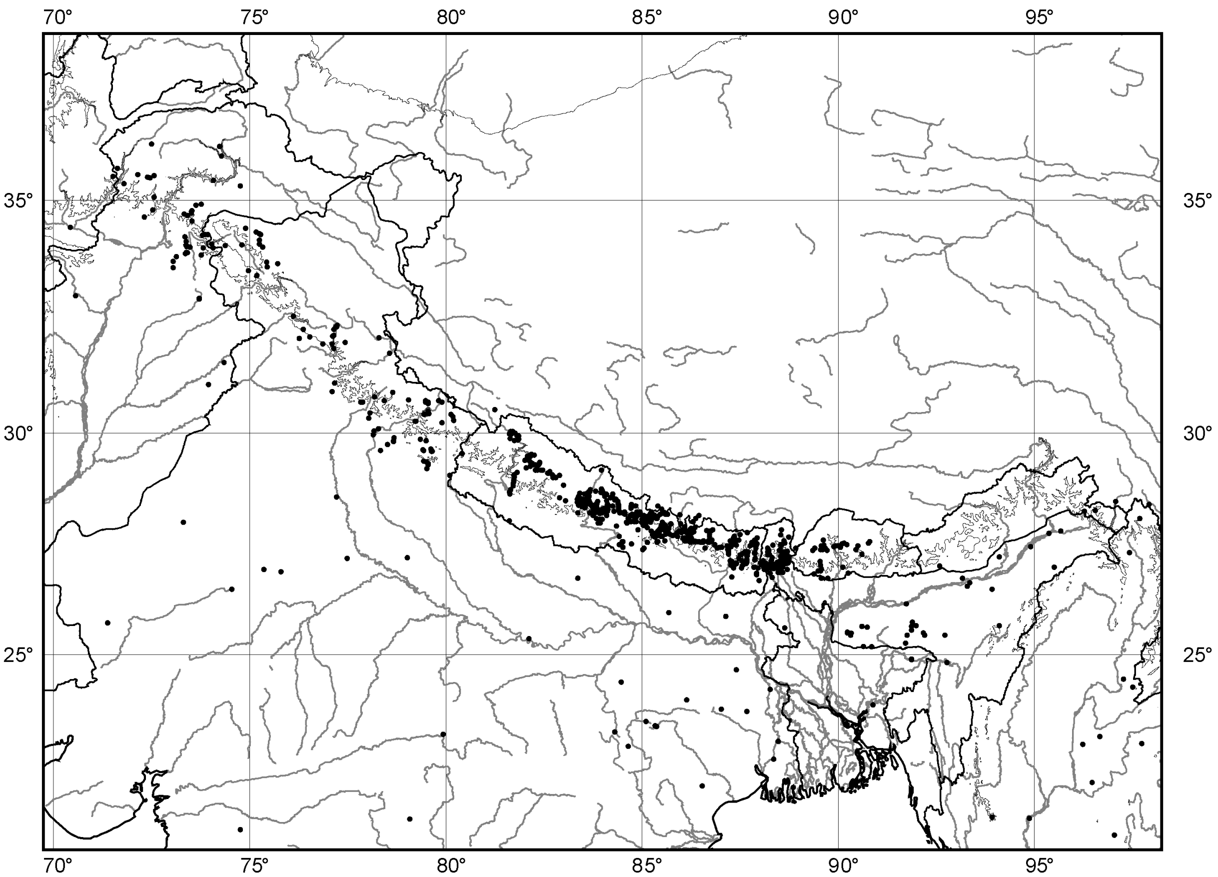


Fig. 16. Map of localities in the Himalaya and adjacent regions from where specimens of Sericini have been examined for this study.

Scanning electron microscopy (SEM)

Specimens for SEM examination were partly cleaned with ultrasound in 70% alcohol or isopropanol. Since setae as well as labial and maxillary palps disrupted during ultrasound, I finally abstained from this treatment in several cases. After air drying the specimens or parts of it were mounted on carbon stickers and coated with gold and palladium (Polaron SC 7640) for 60 or 120 seconds._The specimens were examined with a LEO 1450VP scanning electron microscope (Museum für Naturkunde, Institut für Systematische Zoologie, Berlin) operated between 6 and 10 kV. The images were saved as TIF-files (1084x712 pixels) and finally processed digitally.

Line drawings

Drawing were done with the help of a drawing tube mounted at a stereo-microscope (Olympus SZX-12). The original pencil drawing was traced onto transparent paper with technical ink pens. The original drawings were scanned and digitally processed. For map processing see Ahrens (2004b).

Light microscopic and stereo microscopic images

Images were taken with an Olympus SZX-12 stereo microscope with a digital camera (Olympus C-3030) and finally processed digitally. For light microscopy preparates were placed in a small petri dish filled with water and using a white background.

Morphological terminology and measurement

Explanations of relevant or/and important morphological terms as well as respective length measurements are given in Figs 17A-E as well in the figures accompanied with character states descriptions. Abbreviations used to described the figures are given in the appendix F.

Phylogenetic analysis

Algorithms of cladistic analysis are referred separately for each group of taxa analysed. The phylogenies are based on parsimony analysis which was performed in NONA 2.0 (Goloboff 1999) using the parsimony ratchet (Nixon 1999) implemented in NONA, run within WINCLADA vs. 1.00.08 (Nixon 2002). Settings were adapted to the respective data set of the group under investigation and are given for each analysis separately.

For parsimony analysis of endemism (Rosen 1988) and in some cases for cladistic analysis heuristic search was performed with PAUP 3.1.1 (Swofford 1993).

The use of resampling methods (particularly the bootstrap) has been questioned as a means of assessing confidence limits on phylogenies (Carpenter 1992, 1996; Kluge and Wolf 1993). This is principally because these tests rely on the assumption that the characters are "independently and identically distributed" (Felsenstein 1985) and that they have been randomly sampled - two assumptions violated by most phylogenetic data. Morphological data sets are particularly susceptible to these problems as they are often replete with examples of redundant (inapplicable) and correlated characters, although molecular data sets are not immune from this (e.g. ribosomal RNA genes which code for a secondary structure).

However, as an estimate of the robustness of a data set, these resampling techniques can be useful as a means of discovering ambiguity between characters. Bremer support (Bremer 1988, 1994), parsimony jacknife (Farris et al. 1996) and bootstrap values (Felsenstein 1985) were evaluated using NONA.

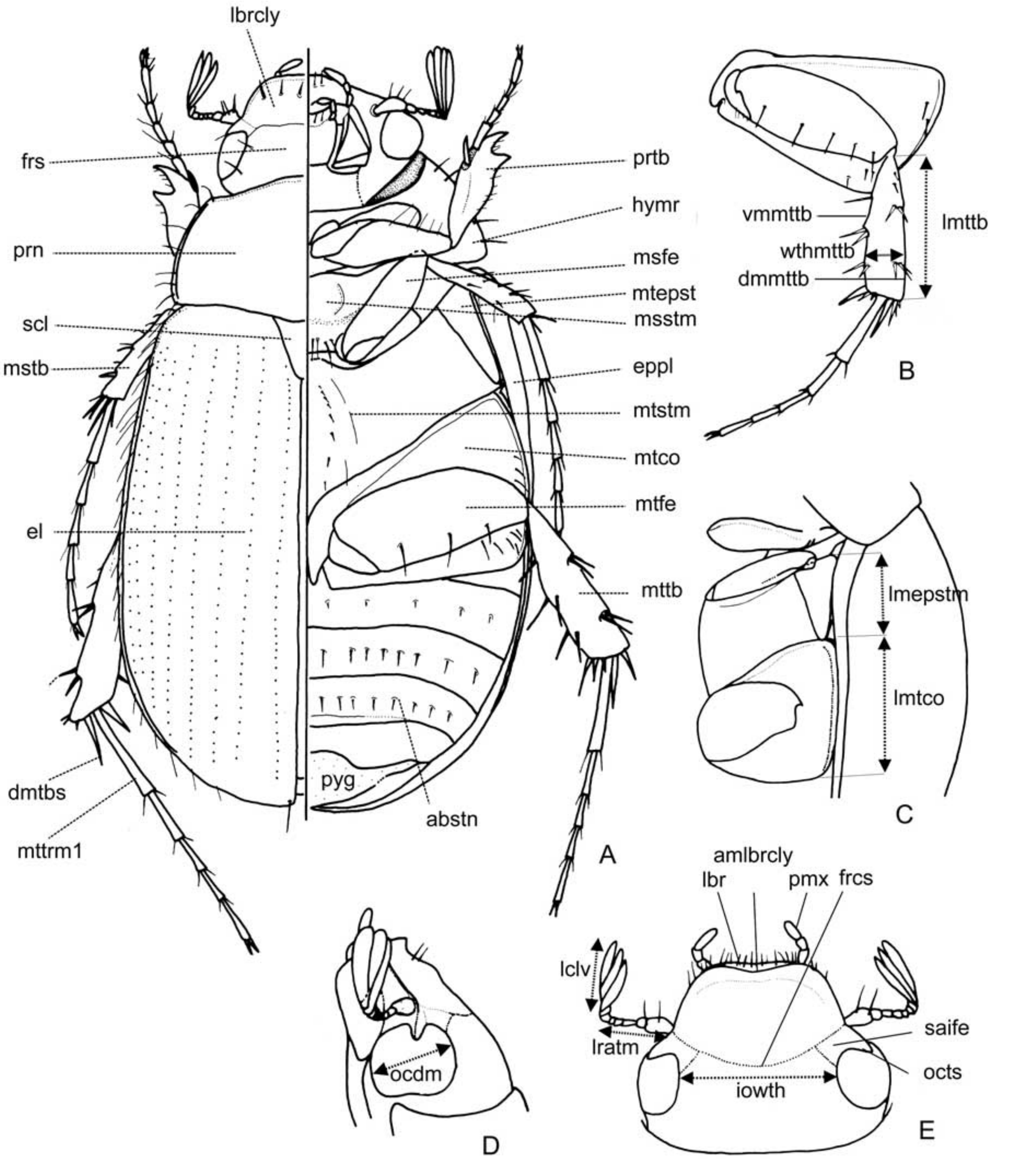


Fig. 17. A: schematic body of a sericine beetle (left, dorsal view; right, ventral view); **B:** posterior leg of a sericine beetle, ventral view; **C:** schematic body (pterothoax) of a sericine beetle, lateral view; **D:** head, lateral view; **E:** head, dorsal view.