4 Biogeography of the Himalayan Sericini - a synthesis

4.1 The state of knowledge of the Himalayan fauna of Sericini

In a separate monograph (Ahrens 2004b) I summarized the available information on the Himalayan sericine-fauna: before the commencement of my revisionary study about hundred valid species of Himalayan Sericini were known from inadequate descriptions only (Sabatinelli 1993). Subsequently, the descriptions of 218 additional species and subspecies (appendix E) were published by the present author (Ahrens 1995a, b, 1996, 1998, 1999a, b, c, 2000a, b, c, d, e, 2001a, b, 2002b, 2003a, 2004a, b; Ahrens and Sabatinelli 1996) based on the complete revision of all formerly described taxa. Furthermore, another six sericine species from the Himalayan region were recognized from the material at hand in the course of this study and are described separately (not included in appendix E). Thus, in all, 324 species of Sericini can be recognized at present from the Himalayan region. However, this figure can not be considered the final number of species of Sericini in the Himalayan region, since the eastern Himalaya (especially Arunachal Pradesh) is still widely unexplored. In fact, the level of taxonomic knowledge on sericines among the different region of the Himalaya is quite diverse, as shown in Figure 115, where recorded species diversity and the number of examined specimens are compared for the separate regions of the Himalaya (see Fig. 118).

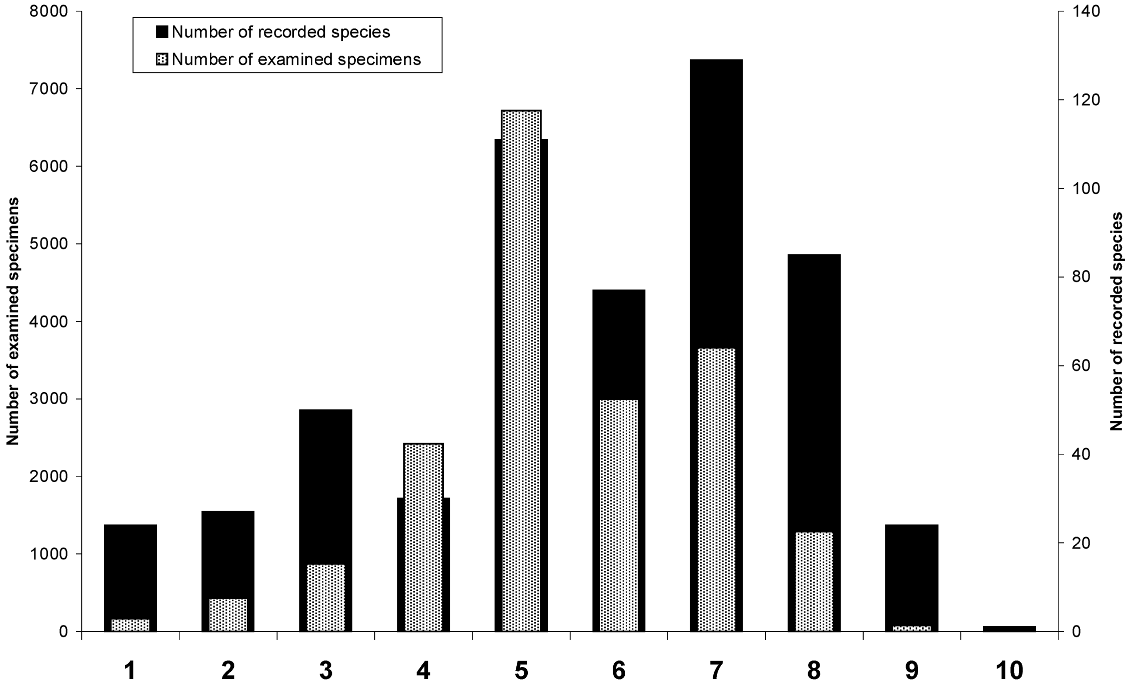

Fig. 115. Species diversity and state of exploration within the different regions of the Himalaya (from Ahrens 2004b, modified). 1 – Indus Himalaya, 2 – Punjab H., 3 – Garhwal H. (Uttar Pradesh), 4 – West Nepal, 5 – western Central Nepal, 6 – eastern Central Nepal, 7 – East Nepal / West Sikkim, 8 – East Sikkim / Bhutan, 9 - Assam-H., 10 - Tibetan H.

In this respect, a look at the rates of discovery of the sericine species is also informative. For this approach, not the date of the description of a species is plotted, as this would reflect just the activities of single specialists, rather than the rate of species discoveries (Fig. 116). The year when the first specimen of a species was collected is used as an indicator of its discovery [however, when collection data were lacking the date of first description was used]. The cumulative number of species discovered in an area follows an almost straight graph for the last 50 years, at least in theory. In the beginning, relatively few species were discovered.

A reason for that may be that appropiate techniques such as light trapping were not yet readily available. In the Himalaya played a role both collecting techniques and the general inaccessibility of remote regions. From time to time exponential growth phases are apparent, with a subsequent phase of saturation. This phenomenon is supposed to coincide with the opening of a hitherto unexplored region, such as by the Bhutan expeditions by the Natural History Museum Basel in the seventies (Baroni Urbani et al. 1973).

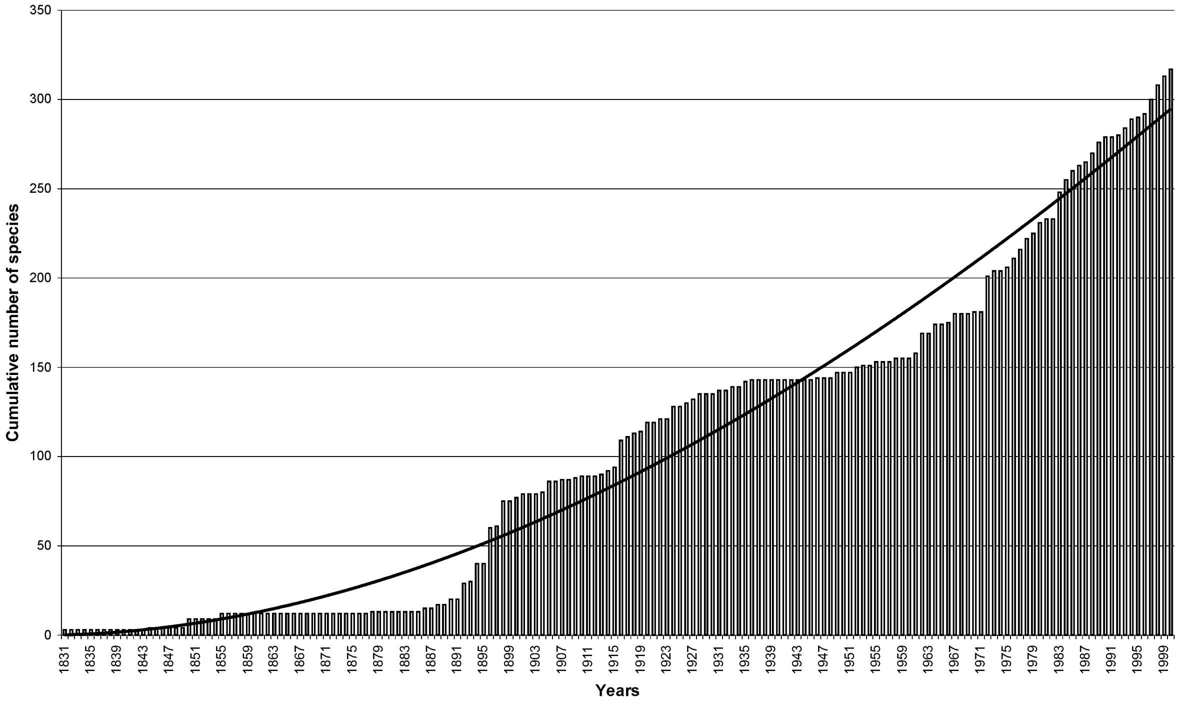

Fig. 116. Discovery of Himalayan sericine species. Numbers are based on the date of collecting of the first specimen of a species, not on the date of its publication. Also undescribed species are counted. Cumulative numbers of species discovered per year. Continuous line shows general trend (3rd order polynomic trend curve, calculated by Microsoft Excel).

4.2 Chorology

4.2.1 Regional diversity of Sericini

The species composition of the Himalayan Sericini differs significantly from adjacent regions. This becomes apparent, when depicting the species in common with the neighbouring areas, as shown in figure Fig. 117. The number of species shared with other regions is rather low compared to the total amount of species dwelling in the Himalaya, meaning that the Himalayan fauna is highly endemic at species level. For Himalayan species shared with other regions, it must be expected, that this pattern is due to rather recent dispersal.

Figure 115 not only provides information on the present level of exploration of Himalayan Sericini, but permits also preliminary conclusions on specimen frequency and species diversity in the Himalaya. The number of recorded species principally increases from west to east. In a few cases, such as Central Nepal where investigations have been very intensive, the number of recorded species is higher due to the high total of specimens collected. Although less explored, in Bhutan the number of species found is higher than in eastern Nepal. This pattern of impoverishment of fauna from east to west is in accordance with general patterns reported, for example, by Dobremez (1976).

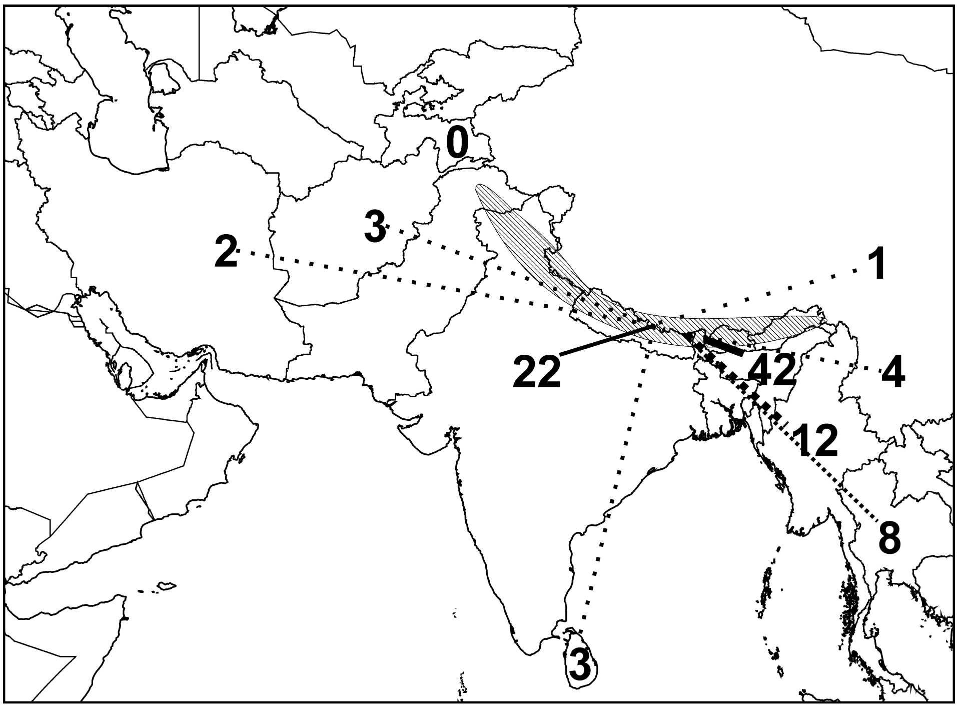

Fig. 117. Species of Sericini occurring in the Himalaya (diagonally shaded) shared with the adjacent regions, such as Afghanistan, Indian subcontinent, Iran, Khasi Hills (Meghalaya), Myanmar, Sichuan, Yunnan, Sri Lanka, Tajikistan, and Thailand.

The large north-west to south-east extension of the Himalaya and its exposition to south-east monsoon, result in a considerable climatic differentiation (see chapter 1.2.2). Major variables are the temporal sequence and amount of precipitation as well as duration of snow cover according to mean temperatures (Mani 1968; Troll 1972). The westwards diminishing humidity determines the expression of the tree line and snowline as well as the vertical sequence of biota and their qualitative and quantitative composition (Troll 1972; Dobremez 1976; Miehe 1991). Thus, it seems suitable to examine the Sericine fauna according to their horizontal and vertical differentiation based on principal patterns observed by previous studies (Troll 1967, 1972; Mani 1968; Dobremez 1976; Martens 1979).

The faunal similarity of ten geographical sections of the horizontally subdivided Himalaya was quantitatively analysed (Tab. 1) using the Jaccard coefficient (Jaccard 1902). These geographical sections of the horizontally subdivided Himalaya are based principally on the climatic-vegetational classification of Troll (1972), which was partly refined to involve additional patterns of other studies (Mani 1968; Dobremez 1976; Miehe 1990). The clusters produced by the UPGMA-clustering based on Jaccard coefficient coincide generally with the climatic subdivision of the Himalayan range (Troll 1972): section 1 - Indus Himalaya, 2 - Punjab Himalaya, 3+4 - Garhwal Himalaya, 5-8 - Sikkim Himalaya, 9 - Assam Himalaya, 10 - Tibetan Himalaya.

Due to high endemicity, similarity between the several regions is generally low. Highest concordance result between sections three und four (= Garhwal Himalaya), Indus Himalaya (section 1) and Punjab Himalaya (section 2) as well as between the western Central Nepal (section 5) and eastern Central Nepal (section 6). Section seven (East Nepal/ West Sikkim) shows higher affinity to section eight (East Sikkim / Bhutan) than to eastern Central Nepal (section 6). The subdivision into a western (section 1-4) and an eastern cluster (section 5-8) is highly interesting. This should be mainly derived from the higher similarity of the West Nepal (Section 4) to the more westerly sections. This would indicate that the “Nepal Himalaya” is faunisticly not a natural “unit”, but just geographical. Otherwise, the limitation of the sections seven and eight, at the level of the Tista river, might also be influencing these patterns, since this geographic “limit” is not an efficient barrier for all biota (in vertical dimension). Notable is the rather isolated position of the Tibetan Himalaya and of the presumably insufficiently investigated Assam Himalaya.

Tab. 1. Faunal similarity based on the Jaccard coefficient (Jaccard 1902) of the horizontal regions of the Himalaya (from Ahrens 2004b): 1 - Indus Himalaya, 2 - Punjab Himalaya, 3 - Garhwal Himalaya (Uttar Pradesh), 4 - West Nepal, 5 - western Central Nepal, 6 – eastern Central Nepal, 7 - East Nepal / West Sikkim, 8 – East Sikkim / Bhutan, 9 - Assam Himalaya, 10 – Tibetan Himalaya. Highest similarity is highlighted by bold value numbers.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
1	x	**38**	14	17	5,5	4,1	3,4	3,8	2,1	0
2	-	x	**31**	**33**	13	12	6,1	5,7	4,1	0
3	-	-	x	**40**	**26**	15	11	7,1	2,8	0
4	-	-	-	x	19	13	6,7	4,5	1,9	0
5	-	-	-	-	x	**38**	16	8,9	2,3	0
6	-	-	-	-	-	x	19	12	4,1	0
7	-	-	-	-	-	-	x	**33**	7	0
8	-	-	-	-	-	-	-	x	6,9	0
9	-	-	-	-	-	-	-	-	x	0
10	-	-	-	-	-	-	-	-	-	x

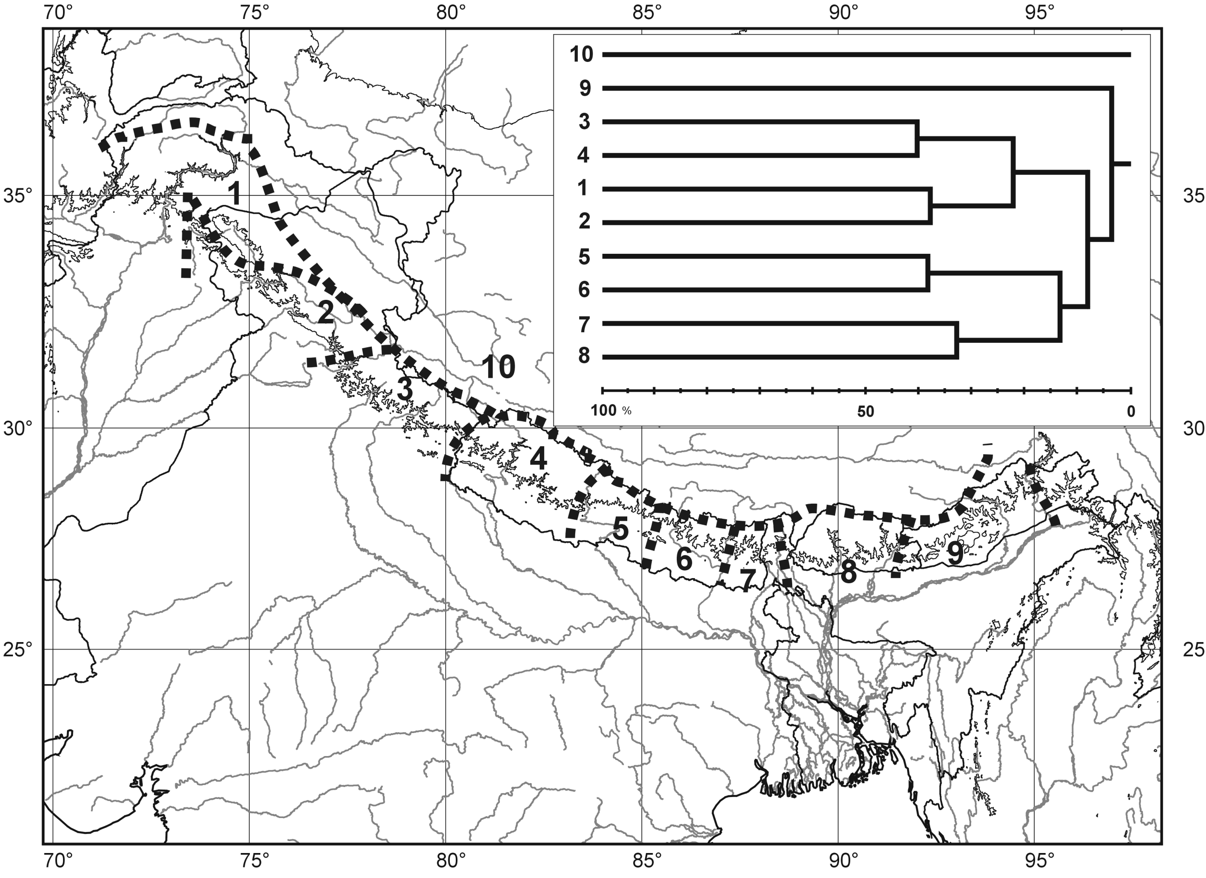

Fig. 118. UPGMA-Cluster based on the faunal similarity apparent from the Jaccard coefficient of the horizontal regions of the Himalaya (from Ahrens 2004b): 1 - Indus Himalaya, 2 - Punjab Himalaya, 3 - Garhwal Himalaya (Uttar Pradesh), 4 - West Nepal, 5 - western Central Nepal, 6 – eastern Central Nepal, 7 - East Nepal / West-Sikkim, 8 - East-Sikkim / Bhutan, 9 - Assam Himalaya, 10 – Tibetan Himalaya.

Considering the distribution of monophyletic species groups such as the genera *Calloserica*, *Lasioserica*, or *Nepaloserica*, westerly of the Kali-Gandaki river (meaning from section 4 to 1) one recognizes a distinct impoverishment. On the other hand, there is a notable 'concentration' of diversity in the western Himalaya (Indus and Punjab Himalaya) in groups such as the *Sericania kashmirensis* – group, or *Xenoserica*. This led to assume for the Himalaya at least two centres of diversity (Ahrens 2004d), a north-western one, and a south-eastern one.

This pattern is also apparent from parsimony analysis of endemism (PAE, Rosen 1988). As with phenetic analysis of biogeographical assemblages, the starting point is a data matrix of the occurrence (presence/absence) of taxa with respect to a set of sample localities. Presence of a taxon is regarded as a derived or 'advanced' character within a sample locality (or region), and absence as 'primitive' (Rosen 1988). The PAE represent an ecological scheme of relative favourable conditions of the environments for the sampled taxa, localities and regions, i.e. a hypothesis of contemporaneous ecological conditions. 'Sister regions' or localities would then be those that were most closely related ecologically. Alternatively, PAE may represent also schemes of successive emergences of biota- that is, relative recency of biotic interchange between 'sister localities' or, conversely, historical sequences of biotic divergences and isolations. It is therefore without cladistic biogeography not possible to distinguish how far a single PAE pattern is ecological and/or historical (Rosen 1988).

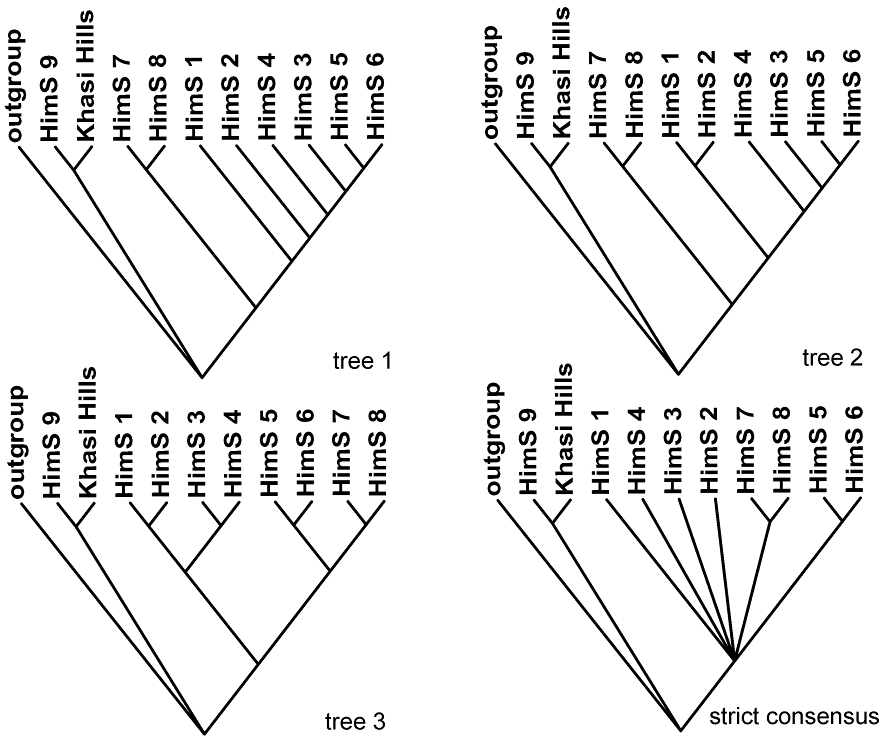

Fig. 119. Parsimony analysis of endemism of the horizontal regionalized Himalaya and a hypothesized „outgroup" region, whose species inventory was coded with "0". HimS = regional section of the Himalaya (with reference to Fig. 118). Length of most parsimonious trees: 244 steps, CI: 0.627, RI: 0.627.

From nine of the ten regions analysed above, under inclusion of Khasi Hills (India, Meghalaya) as well as a hypothesized "outgroup" region, whose inventory was coded entirely with "0" resulted with heuristic search performed in PAUP 3.1.1. (Swofford 1993) three most parsimonious trees (Fig. 119). Their strict consensus, however, provides however only little new information, due to polytomy of most regions. Nevertheless, similar to results of species similarity (Fig. 118), dendrograms reveal close relationships between sections five and six, as well as between sections seven and eight. The diverse groupings of the single sections in the three dendrograms might be explained, a) by the existence of at least two centres of endemism, which overlap in the territory of West Nepal, and b) by the impoverishment of the species diversity from east to west in most groups occurring in the Himalaya. The phylogenetic analysis of the montane elements of the Himalayan Sericini have shown, that at least the phenomenon a) is not a result of recent climatic conditions, only. The Tibetan Himalaya could not be included into PAE, since it has no species in common with other regions of the Himalaya (Ahrens 2004b).

4.2.2 Chorological characterisation of Himalayan Sericini

A number of different types of distributional ranges are recognizable among the Himalayan Sericini. These range patterns are closely related to the ecology of the species as well as to their evolutionary history. The more principal among these patterns are summarized in Figs 120 and 121. Their portion of the total amount of species occurring within the Himalayan range is presented in Table 2.

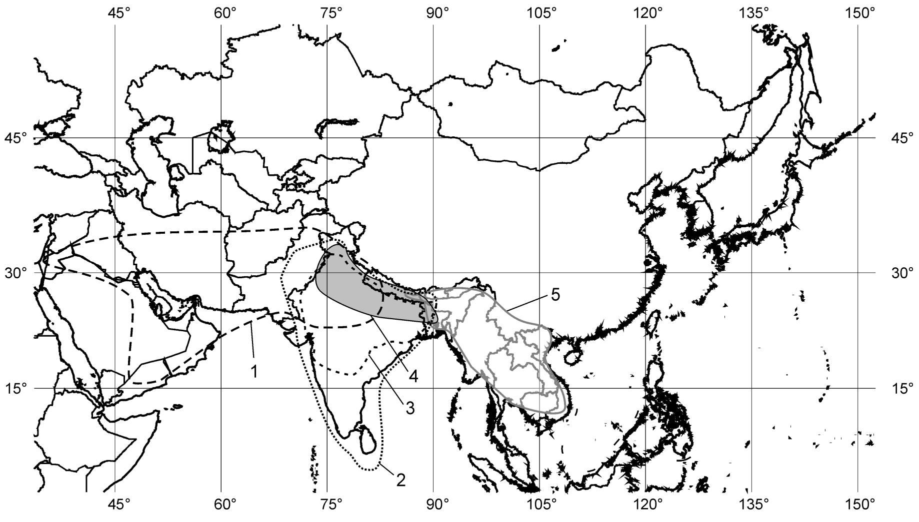

Fig. 120. Principal wide-range chorotypes occurring within the Himalayan range: **1 -** Indo – East Mediterranean; **2 -** Himalayan – Indian; **3 -** Himalayan – Dekkanean; **4 -** Himalayan – Gangetic; **5 -** Himalayan – Indochinese.

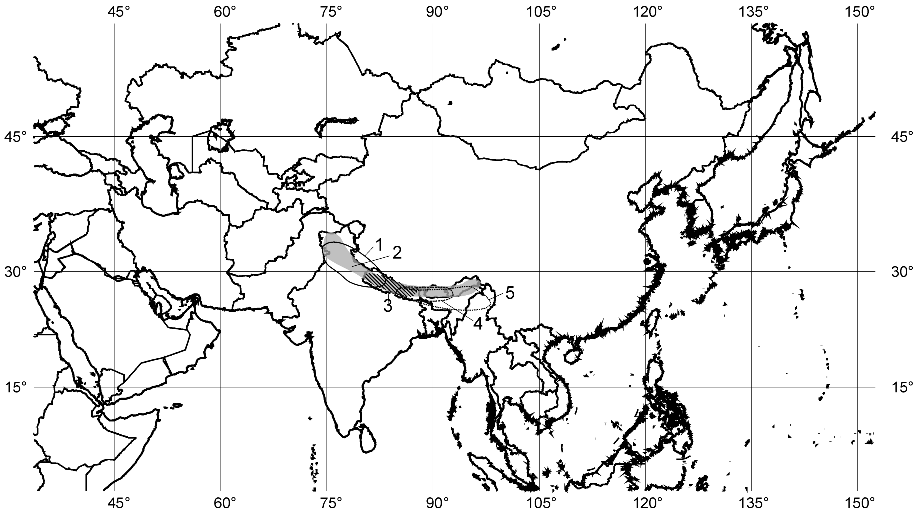

Fig. 121. Principal small-range chorotypes occurring within the Himalayan range: **1 -** West Himalayan; **2 -** Himalayan; **3 -** Nepalese; **4 -** East Himalayan; **5 -** Himalayan – Khasian.

A notable part of the species occurring at low altitudes in the Himalaya have extensive ranges on the Indian subcontinent, representing the Himalayan – Indian chorotype, the southerly less extensive Himalayan-Dekkanean chorotype, and the Himalayan – Gangetic chorotype. Most of these species also have there their closest relatives (e.g. *Maladera marginella*, *M. nagporeana* or *Hemiserica nasuta*). The largest number of common species are shared by the Himalaya with the Khasi Hills and the lowland of Assam (Fig. 117), resulting in another chorotype, the (East-) Himalayan – Khasian. The endemic forms may be subdivided into regional endemics and locally endemic species. The latter comprising about 60 % of all Himalayan species are generally limited to a single massif or river valley. Taxa with Central-Asian or Middle Asian chorotype, which are generally inhabitants of the steppe highlands and alpine belt, are absent in the Himalaya.

Tab. 2. Portion (%) of principal chorotypes of the total amount of species occurring within the Himalayan range.

Chorotype	%	Chorotype	%
Indo – East Mediterranean	0.32	West Himalayan	2.87
West Nepalese	0.32	East Himalayan	3.50
Himalayan - Yunnan	0.64	Nepalese	3.50
Himalayan - Indochinese	0.96	Central Nepalese	3.82
Himalayan - Gangetic	0.96	Himalayan	6.69
Himalayan - Dekkanean	1.27	(East) Himalayan - Khasian	7.32
East Nepalese	1.59	local endemics	60.51
Himalayan - Indian	2.87	uncertain	2.23

4.2.3 Species richness at different altitudes

Naturally, phytophagous insects are not only affected by the abiotic changes of the environment along an altitudinal gradient, but also by the changes of the vegetation. However, since sericines are soil dwelling herbivore generalists, this generality becomes modified in a particular manner. Comparing related taxa within monophyletic groups of Himalayan Sericini, a rather homogeneous altitudinal distribution is apparent generally (Ahrens 2004b, see chapters 3.2.4 and 3.2.7). This pattern of altitudinal distribution which is not much more distinct regionally (e.g. Fig. 122) contrasts interestingly with the above noticed high degree of endemism among the species. But also among genera or larger monophyletic species groups, a clear altitudinal differentiation is not evident (Fig. 123) as is for example known for many other Himalayan arthropods, such as dung beetles (Aphodiinae; Stebnicka 1986, 1990), Dermaptera (Brindle 1974) or Carabidae (Martens 1993). A very vast altitudinal tolerance (3400 meters) is reported for *Nepaloserica procera rufescens* by own collecting in the Annapurna Himal (Ahrens and Sabatinelli 1996). Similar to this wide ecological tolerance, for this and several other species an occurrence is found on both sides of the Himalayan main chain, such as for *Lasioserica nepalensis*, *Serica eberti* und *S. thibetana*. In this context it is worth pointing out that in Sericini, excluding a few single taxa such as *Oxyserica pygidialis annapurnae* and *Calloserica capillata*, a faunistic differentiation could not be proved for the ecologically very dissimilar dry 'Inner valleys' and the humid southern slope of the Himalayan main range (Ahrens 2004b).

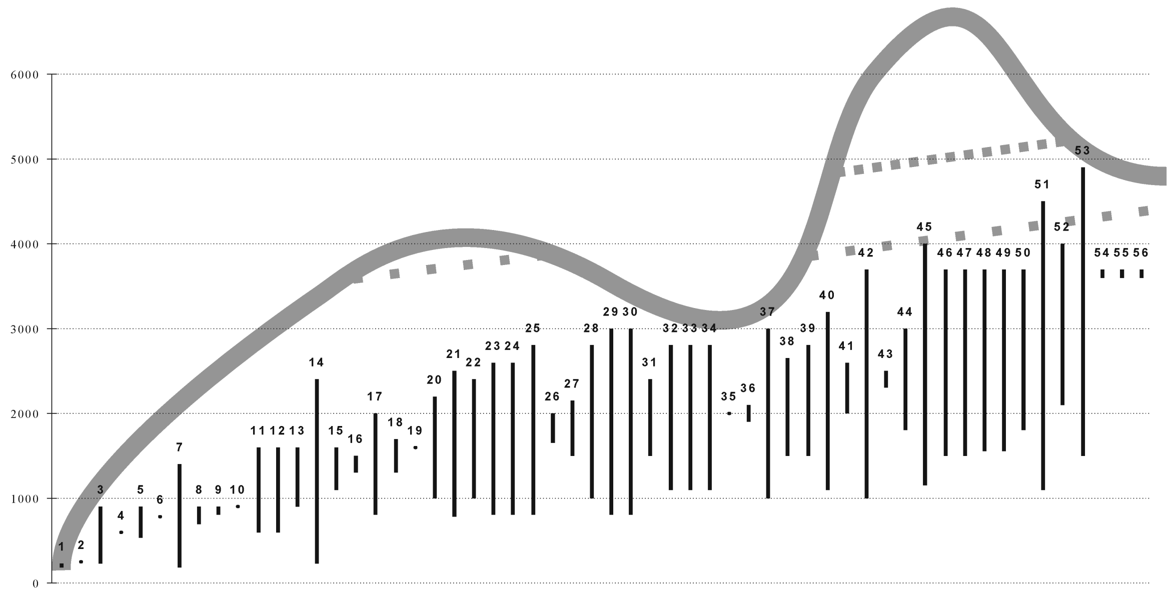

Fig. 122. The altitudinal distribution of Sericini in the Annapurna Himal (part of section 5; from Ahrens 2004b): 1: *Maladera siwalikiana*, 2: *M. lugubris*, 3: *M. allopruinosa*, 4: *M. raptiensis*, 5: *M. thomsoni*, 6: *Calloserica begnasia*, 7: *M. affinis*, 8: *M. tumida*, 9: *M. quinquidens*, 10: *M. sikkimensis*, 11: *M. sericella*, 12: *Pachyserica gracilis*, 13: *Chrysoserica stebnickae*, 14: *M. marginella*, 15: *Microserica myagdiana*, 16: *M. ferruginea*, 17: *M. pokharae*, 18: *M. emmrichi*, 19: *Tetraserica ferrugata*, 20: *Lasioserica modikholae*, 21: *Serica jaegeri*, 22: *L. piloselloida*, 23: *L. maculata maculata*, 24: *Pachyserica olafi*, 25: *M. simlana*, 26: *Neoserica kaskiensis*, 27: *S. khajiaris*, 28: *Mi. interrogator*, 29: *Mi. schulzei*, 30: *Oxyserica pygidialis pygidialis*, 31: *S. incognita*, 32: *M. joachimi*, 33: *Mi. gandakiensis*, 34: *Mi. pruinosa*, 35: *S. khasiana*, 36: *Sericania mela*, 37: *Neoserica garlangensis*, 38: *S. tukucheana*, 39: *M. himalayica thakkholae* s, 40: *Amiserica krausei*, 41: *Nepaloserica lamjungi*, 42: *S. nepalensis*, 43: *C. poggii*, 44: *N. muelleri muelleri*, 45: *S. thibetana*, 46: *O. pygidialis annapurnae*, 47: *S. ramosa*, 48: *S. eberti*, 49: *S. panchaseana*, 50: *N. schmidti*, 51: *L. nepalensis*, 52: *N. mustangia*, 53: *N. procera rufescens*, 54: *N. telbrungensis*, 55: *S. arborea*, 56: *S. guidoi*.
C.= Calloserica, *M.= Maladera*, *Mi.= Microserica*, *L.= Lasioserica*, *N.= Nepaloserica*, *O.= Oxyserica*, *S.= Serica*.

Most species dwell in the montane and submontane belt, as apparent from Fig. 124. The lower montane forest at 1500-2200 meters harbours more species than the tropical zone from sea level to 800 meters. The species number decreases constantly towards the alpine zone, with a few taxa able to extend its range from upper montane forest higher (e.g. *Lasioserica nepalensis*, *Nepaloserica procera rufescens*), and a few exceptions with so far as known exclusively alpine occurrence, such as *Anomalophylla mandhatensis* and *Xenoserica brachyptera*. However, it is to be supposed, that this pattern (Fig. 124) is presumably also influenced by human activity, which had lead to a widely extended deforestation below ~2000 meters, accompanied by an intensive cultivation of most soils below that altitude. Although this accumulation of diversity about 2000 meters coincides with hypothesized boundary of Palaearctic and Oriental realm being a zone of interference of more tropical and temperate species, interestingly a similar concentration of diversity has been found in other tropical mountain ranges for lower montane forests too, such as in New Guinea (Riedel 2002), where no distinct interference zone of elements of two faunal realms exists. In fact, in addition to the interference effect, for many local endemics an exclusive occurrence for this altitude has been recorded (Ahrens 2004b).

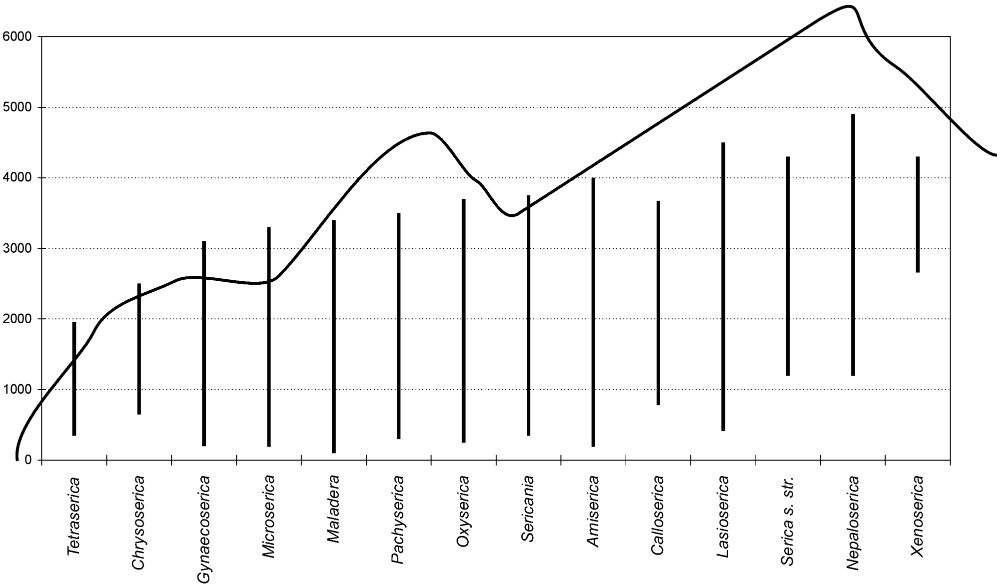

Fig. 123. The altitudinal distribution of the genera occurring in the Himalaya.

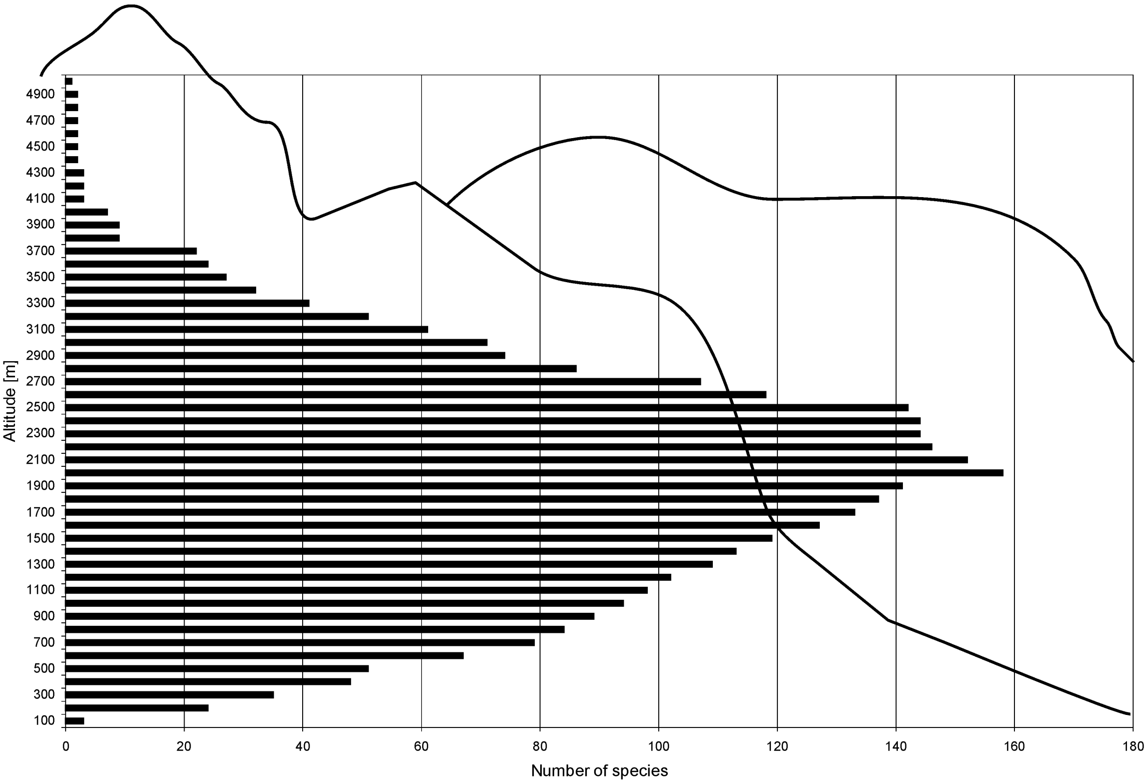

Fig. 124. Diagram illustrating the change of number of Himalayan sericine species with altitude. Note maximum diversity at 2000-2500 m altitude.

4.3 Biogeographical implications

Although the evolution of the montane biota in Asia and especially the Himalaya has received some attention (e.g. Martens 1997, 1993; Holloway 1986), there have been relatively few attempts to explicitly test biogeographical theories with species-level phylogenetic hypotheses (Denton and Hall 2000; Schimmel 1993).

Among the montane lineages, the following general patterns of diversification have been hypothesized:

(1) Himalayan xerophilous forms, such as *Sericania*, are supposed to have occurred in the northern and drier parts of Tibet; this corridor should have been responsible for their interference with areas of north-eastern Asia and with progressing uplift of northern Tibet. In case of *Sericania*, the basal lineages have been separated into a North-West Himalayan and East Asian clade.

(2) The hypotheses of phylogeny of taxa of the more humid areas of the Himalayan southern slope, such as *Omaladera* and *Lasioserica* generated in this study provide evidence to suggest multiple events of radiation in Himalayan Sericini along the southern slope of the Himalaya which may be regarded as a main source of the high diversity within this region. This hypothesis is mainly supported by the congruent cumulative ranges of certain distal clades of species, such as in *Lasioserica* (Fig. 69) or *Serica* (Fig. 106). The fact, that a great number of diverse sericine groups performed a strong diversification within these mountain chains, lead to a safe assumption that the presence of mountain ranges with the characteristics similar to the present Himalaya predate those diversification processes. There is comparatively high evidence from range positions of closely related species for allopatric geographical speciation in *Lasioserica* with the majority of closely related Central Himalayan species occurring allopatrically or parapatrically. However, in the more easterly distributed lineages, this pattern is altered to the contrary, with a great portion of closely related species occurring sympatrically. This differentiated pattern might be attributed to the climatic gradient in present and past which has characterized this mountain range at least since the onset of monsoon climate with its humid south-eastern summer winds.

The occurrence of numerous basal lineages in the Himalaya, additionally, lead to assume that the Himalaya was in historical framework a “refugium“, too, being able to buffer fluctuations of climate by “orobiom-shifting”. These ‘refugia’ might be related also to special topographical structures such as large river valleys which were able to cross the Great Himalayan chain, as apparent in case of *Xenoserica*. In the Himalaya presently very restrictedly occurring basal lineages of e. g. *Lasioserica* or *Serica* should be interpreted as relics of former widely distributed clades. The taxa of these clades became extinct in great part, probably also in consequence of competition of the strongly radiating younger lineages.

The phylogenies found show a congruent pattern in groups with similar vertical and/or horizontal distribution. Patterns of vertical and/or horizontal distribution are shown to be of crucial importance for gene flow, dispersal capacity, and for the opportunity to occupy new habitats. In lower montane species, major distal clades are generally restricted to the Himalaya, as revealed in *Calloserica*, *Omaladera* or *Lasioserica*. Similar patterns result from preliminary cladistic analyses of *Microserica*, *Nepaloserica*, and *Oxyserica*.

(3) As apparent from phylogeny of *Serica*, major distal clades of middle to upper montane species show a stronger interference with the mountain regions of eastern Tibet. This would implicate that flight-active organisms of the medium and upper montane belt had in present and/or past better opportunities for dispersal along and across higher mountain chains as encountered in the Himalaya or eastern Tibet. Probably, the taxa capable of flight were enabled during warmer and drier periods to cross higher passes and ranges, when the snow line was elevated, reaching adjacent valleys or even the Tibetan Plateau, where they have been meeting along the Yangtze suitable conditions for a long distance-dispersal. Interestingly, in basal lineages of groups mainly occurring in lower montane forests, these interferences are also present, although ranges at the eastern margin of the Tibetan Highland are displaced more southerly. With the advancing uplift of southern and central Tibet as well as of the Yunnan Plateau and later also of the north-eastern Tibetan Plateau, these highlands became an effective geographical divide for the taxa of these lineages.

(4) Although being frequently recorded at the eastern slope of Tibet in humid habitats of middle-montane belt, for example in *Anomalophylla* no species occur in very similar habitats at the southern slope of the Himalaya. This group has diversified at eastern margin of Tibetan Highland, with extension north-easterly and westerly (*A. mandhatensis*). Due to the presumably harsh periglacial conditions during the Pleistocene, and because of evidence of high age of the present elevation in southern Tibet (Spicer at al. 2003), it should be supposed that the latter extension is a result of a rather recent dispersal, may be during an interglacial stage or during later warm periods, such as in the middle Holocene (Gasse et al. 1991).

Most of the forms occurring in lowland and in the colline regions of the Himalaya represent taxa with extensive ranges having here a limit of their distribution. To these belong the taxa with range belonging for example to Himalayan-Indochinese or to Himalayan-Indian chorotype. Among the forms of the lowland areas, only a very few developed monophyletic lineages, such as the taxa belonging to *Maladera* (subgenus *Cycloserica*). For this group results of cladistic analysis reveal a separating effect of the Himalayan-Alpine belt favouring the split up of a Middle Asian and a Himalayan lineage. Based on geological evidence, that first higher elevations (with barrier effect northerly) in the region of the present Himalaya and the Tibetan Plateau were achieved during Oligocene (Tapponier et al. 2001, Harrison et al. 1998), it is hypothesized that two *Cycloserica* lineages existed before they dispersed into the two separated areas (Fig. 37), the northern Indian subcontinent and the Middle Asian lowland.

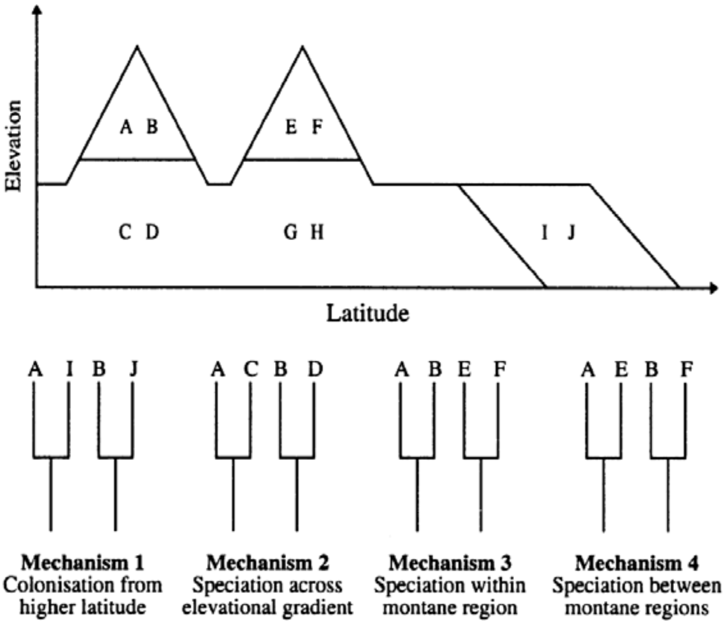

Fig. 125. Geographic mechanisms of speciation in montane regions and predicted resultant phylogenetic relationships between sister taxa (from Willmott et al. 2001).

Due to the lack of sericine fossils in the Himalaya, to discuss the course and the influencing factors for the diversification the number of assumptions augment drastically for each hypothesis. For example, parapatric speciation can not really be proved, if it is not shown by the fossil record that at the moment of the dispersal or the vicariance event, the stem species was present in the relevant area. The same applies to the dating of a splitting event of two lineages by a hypothesized geographic barrier.

Geographic mechanisms of speciation in montane regions and predicted resultant phylogenetic relationships between sister taxa have been discussed by Willmott et al. (2001) using of Neotropical butterflies. They discussed four mechanisms for speciation (Fig. 125). Due to the extreme extension in height, high relief energy, and due to the strong climatic differentiation between the northern and the southern face of the Himalaya as well as between slopes differently exposed to climate, also the possibility of speciation between great valleys separated by high mountain chains should be taken into consideration.

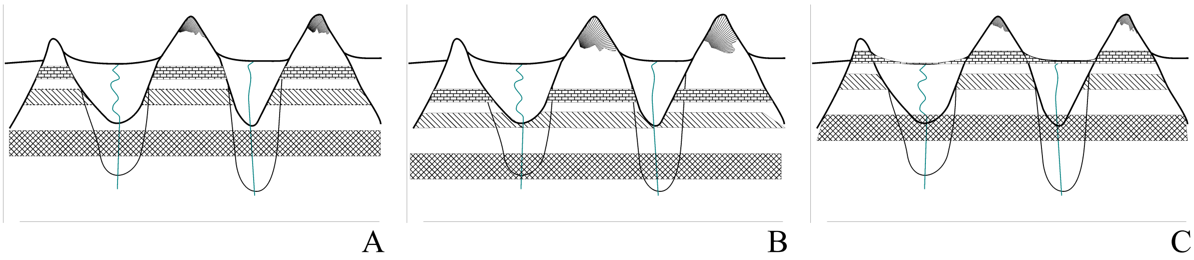

Fig. 126. Model of hypothesized scenario of effects caused by climatic fluctuations in the Himalaya, resulting in snow line depression, but also in a shifting of orobiomes along the altitudinal gradient. The scenario would result in differentiated facilities of dispersal and altering periods of vicariance. A- present climate; B- Glacial period with snow line depression and extension of glaciers; C- warm period, with regression of glaciers and upward shift of forest line. Under assumption C species of upper montane forest would have been able to cross high passes or mountain chains which have been a barrier during A and B; in similar manner dispersal was facilitated to lower montane species during cold period (B). Diagonally shaded: lower montane forest belt; brick-like shaded: upper montane forest belt; cross shaded: lowland and colline belt.

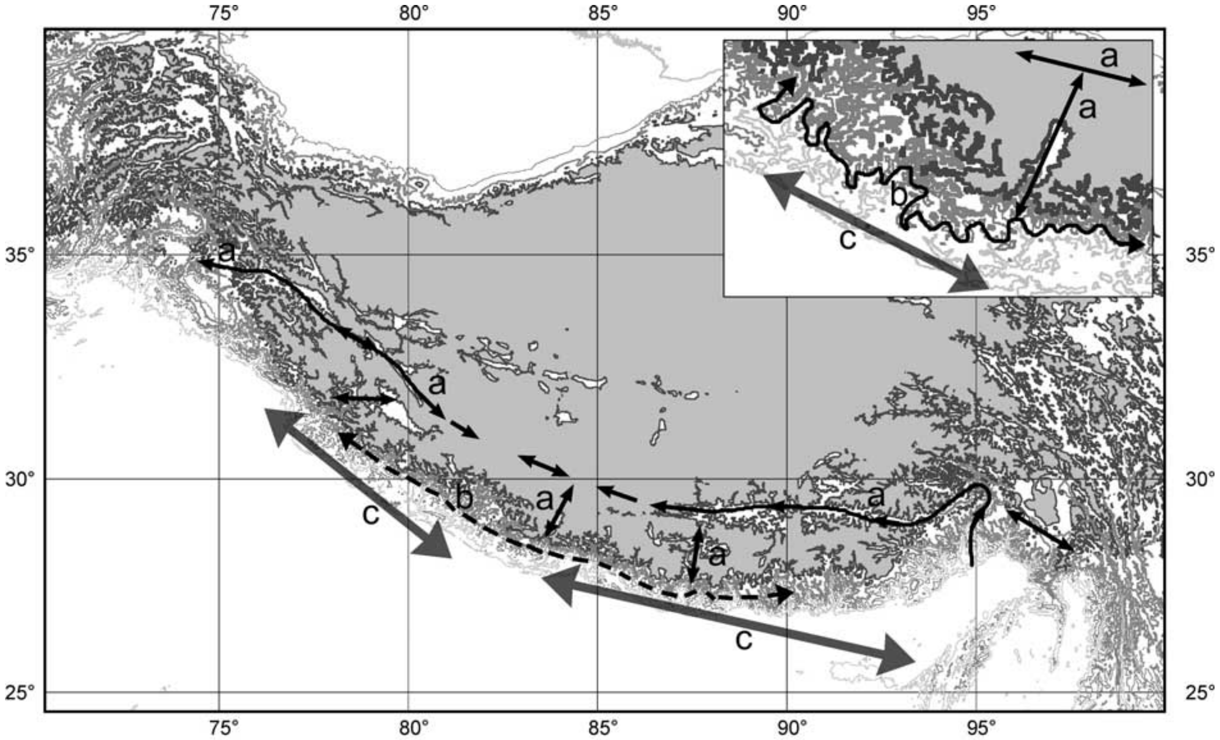

Fig. 127. Hypothetical path-ways for dispersal applied to present Himalayan topography, in the framework of past climatic fluctuations resulting in hypothesized 'up and down shift' of orobiomes. Individuals of species which disperse in montane belt (b) along the southern slope of the Himalayan range have much longer ways (detail map right above) than those of the lowland species (c) or than taxa which have (had) been able to reach the Tibetan Plateau (a).

Assuming parapatric speciation, a model shown in Fig. 126 can be hypothesized, which brings into one context potential geographic barriers and fluctuating climate, resulting in an alternating scenario of opportunities of dispersal and vicariance. Such in geological terms frequently changing climatic conditions have been reported from Miocene to present (e.g. Gasse et al. 1991; Quade et al. 1995; Métevier et al. 1999; Pratt et al. 2002; Chauhan 2003; Goodbred in press), and patterns of the present distribution in several sericine taxa are consistent with this hypothesized model. But also before this epoch with better preserved geological and palaeobotanical evidence, fluctuations should have occurred, although they may have been less radical before the onset of monsoon (8 Ma; Prell et al. 1992). These mechanisms, however, persisting for long geological intervals could explain multiple radiation as hypothesized and thus the high diversity in the High mountains of Asia as found in the Himalaya.

This scenario applied three-dimensionally for present Himalayan topography would result in a number of hypothetical path-ways for dispersal of the species of the lowland, of lower montane and upper montane belt (Fig. 127). Individuals of species which disperse (or dispersed) along the southern slope of the Himalayan range in montane belt have much longer ways (b, detail map right above Fig. 127) than those of the lowland species (c) or than taxa which have (had) been able to reach the Tibetan Plateau (a), such as the taxa of upper montane belt during warm periods.