

ON THE PROBLEM OF POSSIBLE LAST-GLACIAL FOREST-REFUGE-AREAS
WITHIN THE DEEP VALLEYS OF EASTERN TIBET

With 6 figures, 2 tables and 4 photos

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Zusammenfassung: Zum Problem der Existenz letzteiszeitlicher Waldrefugien in den tiefen Tälern Osttibets

Aufgrund des bei sechs Expeditionen gewonnenen Materials wird die Frage untersucht, ob es auf dem Tibetischen Plateau letzteiszeitliche Waldrefugien gegeben hat, oder ob diese nur an der Peripherie des Plateaus zu erwarten sind. Die Aussagen beruhen auf pollenanalytischen Studien hochgelegener Moore, die seit dem Übergang von der Letzten Eiszeit in das Holozän oder mindestens seit dem unmittelbaren Beginn des Holozäns gewachsen sind, auf dendroklimatologischen Untersuchungen eines sehr umfangreichen Probennetzwerkes verschiedener Nadelholzarten und auf florengeographischen Analysen anhand der vorliegenden Literatur.

Es wurden die folgenden Resultate erzielt:

- 1) Alle drei methodischen Ansätze legen die Schlussfolgerung nahe, dass während des Hochstandes der Letzten Eiszeit in dem Gebiet der oberen meridionalen Stromfurchen ein oder mehrere Waldrefugien bestanden haben. Dies erweist die Einwanderungsgeschichte wichtiger Holzarten in einem 60 bis 180 km von den meridionalen Stromfurchen im Nordosten gelegenen Moor, aber auch die Herausbildung offenbar eigenständiger physiologischer Baumrassen dort und die heutige Verbreitung endemischer Pflanzentaxa, die zu einem beträchtlichen Teil Waldarten sind.
- 2) Es ist unklar, ob es sich nur um ein einziges Refugium oder um mehrere gehandelt hat.
- 3) Die eigentliche Geschichte derartiger Refugien bleibt gegenwärtig unbekannt, da geeignete Stellen, an denen sich tiefere Seen oder auch lange wachsende Moore gebildet oder erhalten hätten, in den meridionalen Stromfurchen fehlen.

Summary: Based on the results of our six expeditions to the Tibetan Plateau, it was investigated whether, during the last glaciation, forest refuge-areas had only existed at the periphery of the Tibetan Plateau, as it is generally suggested, or within the deep East-Tibetan river gorges, as well. This investigation was done by pollen analyses on peat-bogs, which date from the Late-glacial to Holocene transition or at least from the very beginning of the Holocene, and by dendroclimatological studies and studies on the distribution pattern of various botanical taxa with the support of international literature.

The following results were obtained:

- 1) All three methodical approaches equivocally point to forest-refuge areas in the region of the deep East-Tibetan river gorges, which seem to have existed during the last glaciation.
- 2) It is unknown, whether one or more of these refuge-areas existed.
- 3) The history of these refuge-areas still remains unknown.

1 The problem

The huge mountain systems of the Tibetan Plateau and its periphery are extremely rich in botanical and zoological taxa although the plateau itself is geologically relatively young (BURBANK et al. 1993; summaries of the relevant literature: FRENZEL 1998, 2002). Thus, a very rapid evolution of various taxa might have taken place in these most interesting areas. However, the Tibetan Plateau has experienced a considerable number of strong climatic changes during the Quaternary.

On the one hand, they might have triggered an extinction of various taxa, but on the other hand, severe selection might have caused the formation of new, better adapted taxa, too. When investigating these problems it is of great interest whether the Tibetan Plateau had experienced the formation of ice masses during the glacial ages, how often and how rapidly this might have happened, and of which dimensions these glaciations were. Investigations of the extent of the Pleistocene glaciations on the Tibetan Plateau have a long history (see references in FRENZEL 1998; FRENZEL a. LIU 2001).

In the context of the problems discussed here, the hypothesis of masses of inland ice, which are said to have covered most parts of the Tibetan Plateau during various glacial ages, is of utmost importance. This hypothesis has been discussed and pushed forward most intensively by KUHLE (e.g. 1984, 1986, 1987, 1991a, b, 2000, 2002). However, several authors were able to demonstrate that inland ice never existed (see references in FRENZEL and LIU 2001). Moreover, it could be shown that the deep valleys, running more or less meridionally in the eastern part of the Tibetan Plateau repeatedly contain a sequence of thick loess layers, which are interrupted by well developed fossil soils, which evidently have been formed during interglacial times in formerly forested areas. The oldest fossil forest soils we saw in East-Tibetan loess sequences seem to correspond in both character and stratigraphical position to the S₅-fossil soil of the Chinese loess plateau, which may be correlated with the Holsteinian or even with a group of older interglacials (FRENZEL 1998). The occurrence of these loesses suggests (for palaeogeographical reasons) that the valleys, in which they can be found, had been free of ice during several Middle and Upper Pleistocene glacial ages. Thus, besides the well known refuge areas in the lowland areas at the southern and eastern fringes of the Tibetan Plateau, glacial refuges in which various plant and animal species could have survived the phases of harshest climatic conditions during various ice ages might also have existed in the extremely deep valleys within the plateau area itself. However, because these valleys are so extremely deep, they have very steep slopes on which peat bogs or lakes, which might have stored animal and plant remains, could not develop or were not preserved till today. Thus, for accepting or discarding this hypothesis it is necessary to look for such sites outside these valleys. During the expeditions to the Tibetan Plateau geological borings for pollen-analytical investigations could be made in several Tibetan lakes and in peat bogs, which may help to answer the question just mentioned. As shown by the itinerary (Fig. 1), our expeditions covered the study area quite well. Answers might also be found by the study of the dendroclimatological reactions of more than 1,000 tree trunks which were bored or sawn during the expeditions. Of course, these trees can only show changes in climate, which have happened during the last 2,000 to 2,500 years and cannot be used to decipher the history of climate and of forest vegetation during the last glacial period. Yet, if it can be shown that the dendroecological characteristics of trees from the interior parts of the Tibetan Plateau point to special genetical lines which behave in a different way to trees growing in the periphery of the plateau (FRENZEL 2000), this might

help to answer the question of glacial refuge areas of a forest vegetation. The flora of the Tibetan Plateau is generally regarded as poor in botanical taxa of different taxonomical ranks compared to the floras of Western Sichuan, Western Yunnan and the Himalaya-Karakorum system. This might favour the view that during glacial times the Plateau was either covered by ice or that the climatic conditions were too harsh for permitting a somewhat remarkable plant cover to develop there. Yet, the Flora Xizangica (WU 1983 till 1987) is rich in information about endemic taxa thriving in various parts of the Tibetan Plateau; YING et al. (1993) explicitly state: "The Qinghai-Tibet Plateau region forms a separate division of its own – the high altitude frigid zone. The climatic conditions have apparently been unfavourable for the development of endemic genera, although there are a large number of cold resistant endemic species in this region" (p. 11, see p. 17, too). MIEHE and MIEHE (2000a) stressed roughly the same for Tibetan alpine pastures. HUANG (1988) regarded the relatively great number (14.7%) of endemic taxa in the (Mt. Everest) Qomolangma-Xixabangma flora as an indication for the youthfulness of this flora and the rapid uplift of the mountain-system mentioned. However, from a biological point of view one would argue just the opposite, since the evolution and the spread of new taxa needs time. Thus, the 14.7% of endemic taxa there would favour the view that this centre of endemic taxa is not young, but old. These interpretative difficulties may be overcome by an overall analysis of the distribution patterns of various taxa, endemic to the regions concerned.

The distribution pattern of forest vegetation in Tibet as it is documented by the map of vegetation in China (ZHANG 1988), the "Atlas of the Tibetan Plateau" (Academia Sinica, Inst. of Geogr. 1990), MIEHE et al. (1998) and our own observations is outlined in figure 3. Here, only the general distribution pattern of mountain forests and of isolated tree stands is shown. These forests are mainly confined to the slopes of the deeply incised gorges and to their widely branched tributaries. We did not differentiate the great variety of ecological mountain forest types there, with the exception of pure open juniper forests (mainly *Juniperus tibetica*), juniper scrubland (*Juniperus pingii* var. *wilsonii*) and the thorny scrub formations. These scrubs are probably a type of secondary vegetation, that developed after the removal of the original forest vegetation by man. This is supported by the fact that even at present various tree species can be found there at inaccessible sites (FRENZEL 2000).

The mountains from the Himalaya in the West to the eastern fringe of the Tibetan Plateau are extremely

rich in coniferous species. According to LI WENHUA (1993), 18 species of *Abies*, 12 *Picea* species, 5 *Larix* species, 6 *Pinus* species and 5 erect *Juniperus* species occur in this region, even if the systematic status of some of these taxa is still under debate. These species are not distributed homogeneously but their distribution patterns show general concentrations in different regions (Fig. 5). This may help to understand the historical background of the very diverse pattern of different types of vegetation on the Tibetan Plateau. In trying to do so, we will rely on pollen analyses of peat-bogs outside the valleys, on the dendro-climatological sensitivity and on the distribution patterns of various plant taxa to

answer the question as to last-glacial forest refuge-areas within the deep river gorges in eastern Tibet and western Sichuan.

2 Outlines of the late-glacial immigration patterns of various tree taxa onto the Tibetan Plateau

Figure 1 shows the most interesting sites for pollen analyses. For this type of analyses several hundred sporomorphs (pollen-grains and spores) have to be analysed per sample. Regrettably, for the area concerned, this has only been done very rarely or the number of



Fig. 1: Expedition routes of the authors (1989, 1992, 1994, 1996, 1999, 2001) and locations of pollen profiles (1. Kakitu; 2. Qinghai Hu; 3. Qamdo Airport; 4. Hai ze Shan; 5. Nianbaoyeze Shan; 6. Hung Yuan; 7. Lake Shayema)

Expeditionsrouten der Autoren (1989, 1992, 1994, 1996, 1999, 2001) und Ortsangaben der Pollenprofile (1. Kakitu; 2. Qinghai Hu; 3. Qamdo Airport; 4. Hai ze Shan; 5. Nianbaoyeze Shan; 6. Hung Yuan; 7. Lake Shayema)

sporomorphs per sample has not been mentioned in the literature. Thus, only a very small number of sites can be taken into consideration here, not least because for studying the immigration history of the forest vegetation they should cover the Late-glacial to Holocene transition or at least the very beginning of the Holocene.

JARVIS (1993) studied the vegetation history at Lake Shayema in south-western Sichuan (No. 7 in Fig. 1), situated at an elevation of 2,400 m a.s.l. It can be shown that the amount of tree- and shrub-pollen has been extremely high here and never dropped below 90% of the total pollen sum since 11000 ¹⁴C yrs. B.P. Already at the very beginning of the sequence, pollen of *Quercus cf. lepidobalanus*, *Betula*, *Picea*, *Abies*, *Tilia* and others had reached remarkably high values. Evidently, the site was situated within a glacial refuge area of the exacting forest vegetation. An even much richer late-glacial forest vegetation (16000 to 10000 cal. B.P.) was described by SUN et al. (1986) from the immediate vicinity of Kunming (1,886 m a.s.l.). This is well understandable considering that Kunming is situated about 500 m deeper and 370 km more to the south than Lake Shayema.

Just the opposite situation was encountered on the Kakitu Mountain (No. 1 in Fig. 1), situated at an elevation of 4,620 m a.s.l. on the southern side of the Qilian Shan-system. Here, from before 9400 ± 185 yrs. B.P. up to at least 8660 ± 135 B.P., the amount of tree pollen was always negligible. This was interpreted quite correctly by the author (BEUG 1987) as having been caused by long-distance transport only.

In the Qinghai Hu (3,268 m a.s.l.; No. 2 in Fig. 1; LISTER et al. 1991) the tree-pollen percentage is already relatively high between 11000 and 10000 B.P. (20% to more than 40%), and at about 9700 B.P. it still increases systematically to more than 40%. Regrettably, the exact data of these pollen analyses were not given, yet evidently the site studied has been very near to last-glacial forest refuge areas.

The situation changes when comparing with one another the next three pollen sites: the huge peat bog of the Zoige Basin at Hung Yuan (32°48'N, 102°34'E, 3,490 m a.s.l.; No. 6 in Fig. 1), has developed within a tectonic basin drained by the Hoang He. It was investigated by THELAUS (1992), WANG (1987) and FRENZEL (1994). The full glacial, interstadial and interglacial vegetation history of the basin itself was analysed by LIU et al. (1994).

SCHLÜTZ (1999) studied the pollen flora of several peat bogs in the Nianbaoyeze Shan (No. 5 in Fig. 1). One of the bogs dates from the Late-glacial to Holocene transition. It is situated at an elevation of 4,170 m a.s.l. in an area which has been formed by glaciers of the last glaciation.

In the Hai ze Shan (No. 4 in Fig. 1) a swimming peat bog has developed in a glacial lake of the last glaciation, which is surrounded by lateglacial lateral and terminal moraines descending from the nearby mountains.

The three bogs mentioned could be dated appreciably well by radiocarbon. In their basal parts they show sediments dating from the Late-glacial or at least of the earliest Holocene. The flora of their sporomorphs was always counted in an identical way, so that

Table 1: Percentages of arboreal pollen of three selected profiles during the early and middle Holocene

Prozentuale Anteile von Gehölzpollen in drei ausgewählten Profilen während des frühen und mittleren Holozäns

years B.P.	Hai ze Shan 1)					Nianbaoyeze Shan 2)					Hung Yuan 3)				
	4,100 m a.s.l.					4,170 m a.s.l.					3,490 m a.s.l.				
	31°58'33"N, 99°06'E					33°22'N, 101°03'E					32°48'N, 102°34'E				
	<i>Picea</i>	<i>Abies</i>	<i>Betula</i>	<i>Junip.</i>	<i>Salix</i>	<i>Picea</i>	<i>Abies</i>	<i>Betula</i>	<i>Junip.</i>	<i>Salix</i>	<i>Picea</i>	<i>Abies</i>	<i>Betula</i>	<i>Junip.</i>	<i>Salix</i>
9200	2.5	0.0	6.5	4.5	2.0	4.5	3.0	6.5	2.0	4.0	19.0	1.5	20.0	5.5	1.0
9000	9.5	1.0	14.0	2.5	0.5	2.5	2.5	7.5	2.0	6.5	30.0	2.5	6.0	6.0	0.5
8000	11.0	0.0	10.0	0.0	2.0	4.5	2.5	6.0	2.5	0.5	29.5	0.0	12.0	5.0	0.0
7000	11.5	2.0	12.0	1.0	1.2	3.0	1.0	3.0	2.0	0.5	38.5	4.0	11.0	5.0	0.0
6000	12.0	1.0	11.0	2.0	2.0	5.5	1.5	8.0	2.0	1.0	29.0	15.0	7.5	3.0	1.0
5000	10.0	1.0	7.5	1.0	0.0	2.0	0.5	6.0	2.5	0.0	21.0	4.0	10.0	5.0	0.5
4000	2.5	0.0	4.0	2.0	0.0	2.0	1.0	7.0	2.5	0.0	?	?	?	?	?

¹⁾ own investigations, No. 4 in Fig. 1

²⁾ SCHLÜTZ (1999), No. 5 in Fig. 1

³⁾ FRENZEL (1994a), No. 6 in Fig. 1

the respective percentage-values can be directly compared with one another (Tab. 1). The values are given without those of the *Cyperaceae*.

The peat bog of Hung Yuan is situated in a mountainous region, which even at present is covered in several places by fir- and spruce forests. The trees are clad with long thalli of *Usnea longissima*, indicating a high atmospheric humidity at the sites of these forests. The site is located in the very vicinity of those regions, which have been studied in terms of their modern tree-taxa by CHENG (1939) and by PATSCHKE (1912). The wealth of these taxa points to the immediate vicinity to last-glacial forest refuge areas.

The peat bog studied by SCHLÜTZ (1999) in the Nianbaoyeze Shan (No. 5 in Fig. 1) is situated in alpine meadows and steppe-like vegetation types. However, dense *Abies* and *Picea* forests occur only some 30 km to the south. These forests are not well shown in the "Atlas of the Tibetan Plateau" (1990).

The peat-bog of the Hai ze Shan (No. 4 in Fig. 1) is situated at the north-eastern foot of a mountain system, which even at present contains some isolated stands of spruce and several dicotyledonous shrubs.

From table 1 it can be seen that in the surroundings of the peat bog of Hung Yuan the immigration of various tree species had happened already at the Late-glacial to Holocene transition. This is indicated by the

typical immigration sequence of taxa well known from other regions of the Northern Hemisphere (FRENZEL 1994). Immediately at the very beginning of the Holocene (at about 9200 B.P.), the share of tree-pollen of those genera which are given in table 1 was remarkably high (47% of the total pollen sum discussed here) and this amount remained nearly constant till about 7000 B.P. Afterwards, it changed to ca. 58% and declined at about 5000 B.P. to approx. 40%. The rapid immigration and the relatively high tree-pollen values point to the fact that an important refuge area must have been very near so that immediately after the late-glacial improvement of climate had been felt several tree taxa could immigrate there.

In the pollen diagram of the Nianbaoyeze Shan (No. 5 in Fig. 1) the situation is different: from the very beginning, the tree-pollen percentage of those taxa given in table 1 only reached approximately 16–20%, with very low values of *Picea* and *Abies*. This situation lasted till about 6000 B.P., when the sum of tree-pollen declined considerably. It seems that the site was relatively far away from last-glacial refuge areas of a tree-vegetation and that the Holocene immigration of the tree-taxa had proceeded only very slowly.

The third site to be discussed here is the swimming peat bog in the Hai ze Shan (No. 4 in Fig. 1). Here, the tree-pollen values began at a comparatively low level

Table 2: Site description of the maximum latewood chronologies used for cluster analysis

Standortbeschreibung der zur Clusteranalyse herangezogenen Chronologien der maximalen Spätholzdichte

No. in Figs. 2, 3	Location	Elevation	Site name	Species name	Cluster
1	31°40'N/ 102°49'E	3800-3950	Zhegu	<i>Abies fabri</i>	II A
2	32°42'N/ 102°12'E	3750-3850	Aba	<i>Abies sp.</i>	II A
3	30°42.5'N/ 101°21'E	3920	Daofu	<i>Picea c.f. retroflexa</i>	?
4	30°42.5'N/ 101°21'E	3920	Daofu	<i>Larix potaninii</i>	?
5	31°49'N/ 99°07.5'E	4350	Lhamcoka B	<i>Picea balfouriana</i>	I B
6	31°49'N/ 99°05.5'E	4150	Lhamcoka D	<i>Picea balfouriana</i>	I B
7	31°57'N/ 98°52'E	4270	Chola Shan A	<i>Picea balfouriana</i>	I B
8	31°58'N/ 98°51'E	4350	Chola Shan C	<i>Picea balfouriana</i>	I B
9	30°18'N/ 99°30'E	4350	Litang	<i>Picea balfouriana</i>	I C 2
10	29°40'N/ 98°31'E	4300	Gartog	<i>Picea balfouriana</i>	I C 2
11	31°05'N/ 96°57.5'E	4500	Qamdo	<i>Picea balfouriana</i>	I C 1
12	31°14'N/ 96°29'E	4400	Riwoqe A	<i>Picea balfouriana</i>	I C 1
13	31°18'N/ 96°29'E	4300	Riwoqe B	<i>Picea balfouriana</i>	I C 1
14	29°48.8'N/ 95°41.5'E	3580	Bomi	<i>Picea cf. linzhiensis</i>	II D 2
15	29°53'N/ 94°53'E	4000	Gyalaperi A	<i>Abies delavayi var. motouensis</i>	II D 3
16	29°54'N/ 94°53'E	3820	Gyalaperi B	<i>Larix griffithii</i>	II D 3
17	29°35'N/ 94°46'E	4300	Nyingchi A	<i>Abies delavayi var. motouensis</i>	II E 1
18	29°35'N/ 94°45'E	4050	Nyingchi B	<i>Abies delavayi var. motouensis</i>	II E 1
19	?	>4000	Kongpo	<i>Picea sp.</i>	II D 2
20	29°59'N/ 93°59'E	3900	Basum Co	<i>Abies delavayi var. motouensis</i>	II D 1
21	28°55'N/ 93°14'E	3700	Langhsien A	<i>Abies delavayi var. motouensis</i>	II E 2
22	28°55'N/ 93°14'E	3700	Langhsien B	<i>Larix griffithii</i>	?

as in the Nianbaoyeze Shan, but at about 9000 B.P. they had already risen to values of ca. 28%. This percentage was generally held till 6000 B.P. At 5000 B.P. it had declined to about 20%. This tendency continued till about 4000 B.P. (8.5%). The relatively strong share and fast immigration of the tree-taxa and the appreciably high arboreal pollen values suggest that, in contrast to the Nianbaoyeze Shan, last-glacial forest refuge areas should have been very near the site studied. The lake investigated is situated at the north-eastern margin of a mountain system, the maximal elevations of which reach approx. 6,500 m a.s.l. Yet to the north-east of the lake, there is a soft-rolling landscape with elevations of between 4,100-4,800 m a.s.l., which probably did not

host last-glacial forest refuge-areas. However, to the west of the Hai ze Shan, at a linear distance of about 60 km, the very deep valley of the Yangtze jiang is situated, followed by other comparably deep valleys like that of the Mekong etc. The floor of these valleys lies at about 3,200 to 4,000 m a.s.l. It seems possible that forest refuge areas existed in these deep valleys.

3 Dendro-ecological division of eastern Tibetan forests

The tree-ring network that has been established during several extensive collection campaigns comprises about 50 investigation sites (Fig. 3) and a total of more

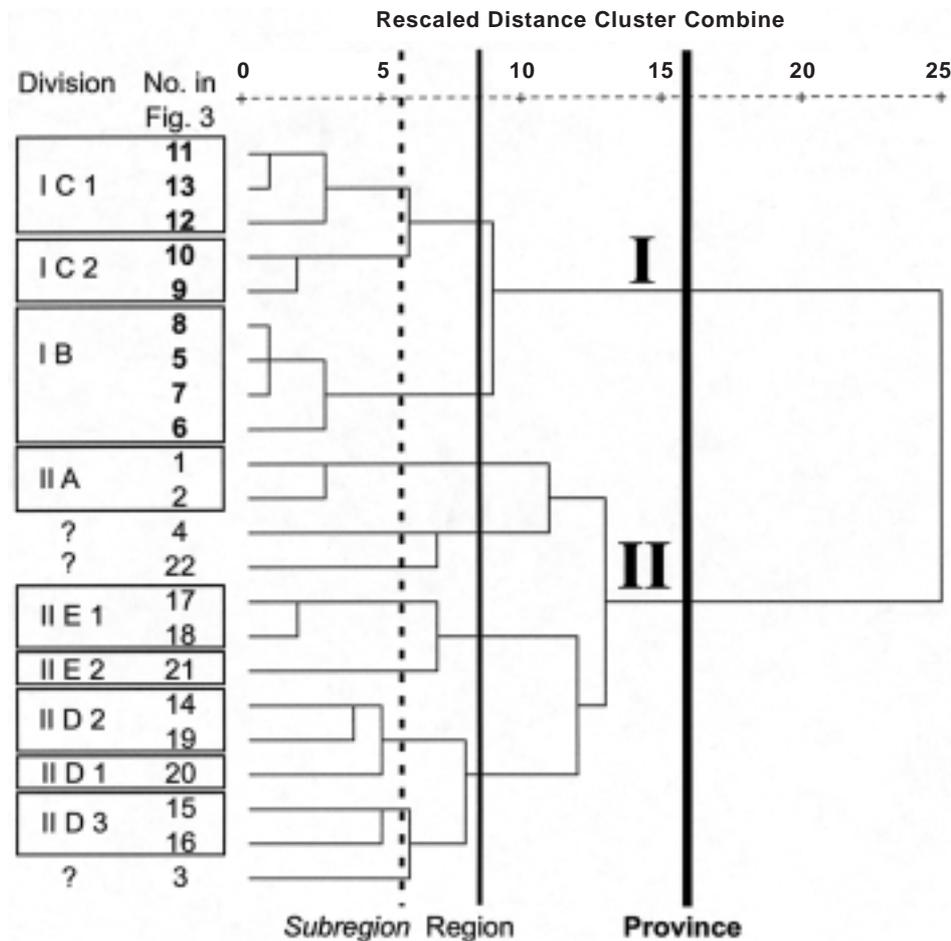


Fig. 2: Results of hierarchical cluster analysis (HCA) of the set of maximum latewood chronologies. For the chronology description see Tab. 2, for the spatial extension of the resulting spatial units see Fig. 3

Ergebnisse einer hierarchischen Clusteranalyse (HCA) einer Gruppe von Chronologien der maximalen Spätholzdichte. Eine Beschreibung der Chronologien erfolgt in Tab. 2, die räumliche Ausdehnung der ermittelten Einheiten ist in Fig. 3 dargestellt

than 1,000 trees. Apart from total ring width, maximum latewood density (MLD) was registered at 22 sites (Tab. 2). For a regional division, the set of MLD-chronologies was chosen, since this dataset contains sample plots from high elevation sites only, which are in a vertical distance of less than 400 m from the local upper forest line, with the exception of the sites Langhsien and Bomi. Chronologies from valley sites and from juniper forests that are restricted to drought-sensitive south-facing slopes have been analysed by BRÄUNING (2000, 2002a), but were excluded from the following calculations to guarantee a maximum of homogeneity within the data set. In contrast to ring width, MLD shows a significant positive visual correlation to summer temperature at all sites investigated (BRÄUNING 1999). This finding is corroborated by principal component analysis (PCA): the first eigenvector has a positive loading at all MLD sites and explains a common variance of 55%, which points to a very strong common climatic signal governing MLD. Thus, differences between the chronologies reflect patterns of regional

climate variability and are not caused by differences in ecological site conditions. In general, however, a dendro-ecological division of eastern Tibet based on ring width corroborates the results based on MLD.

The samples from site 19 (Kongpo) have been collected at a sawmill in Lhasa, where huge stems of freshly cut timber were delivered in July 1999. According to the information of the sawmill manager, the timber originated from a site above 4,000 m in the Kongpo region. The exact location, however, was not known. Thus, the position of the respective symbol of site 19 in figure 3 does not represent the exact location; however, this is of no relevance for the spatial division presented below.

Before establishing the chronologies, the age trend of the individual tree MLD curves was removed by subtracting a linear trend or a horizontal straight line (BRÄKER 1981). The chronologies were standardised by subtracting the mean and by division through the standard deviation. As a measure of similarity, a hierarchical cluster analysis (HCA) was applied. The method used

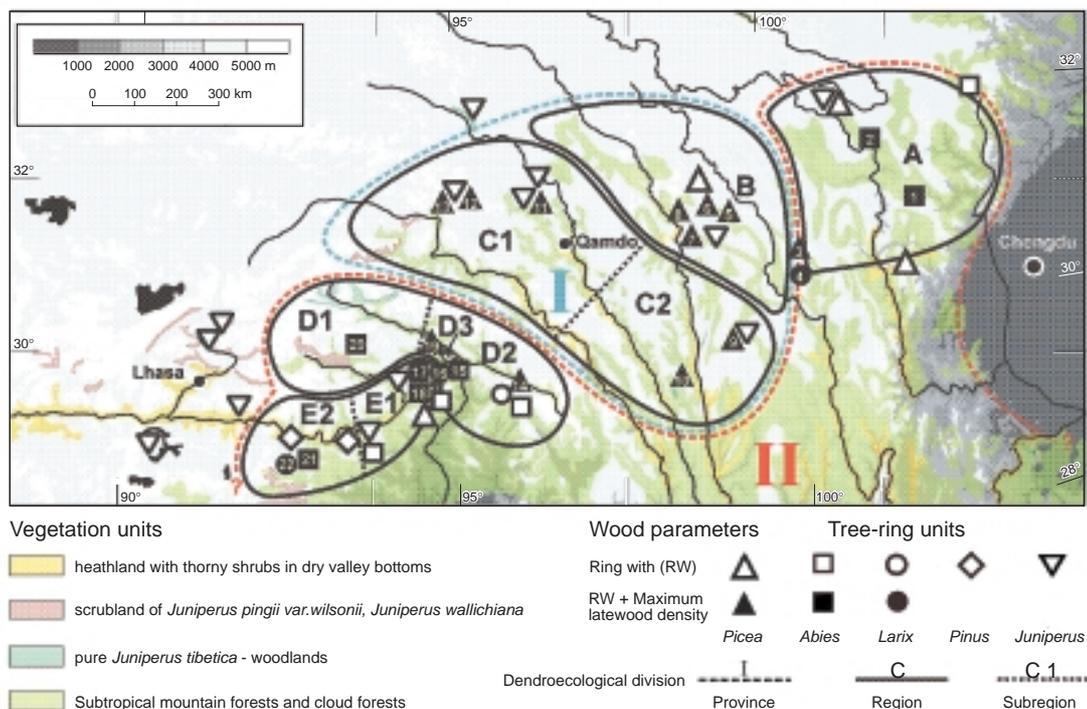


Fig. 3: Distribution of present vegetation (after ZHANG 1988; Academia Sinica 1990; MIEHE et al. 1998 and own observations) and tree-ring network with dendro-ecological division (the western and eastern borders of Province II are not yet known due to lack of data). For further explanations see Fig. 2 and Tab. 2

Verteilung der heutigen Vegetation (nach ZHANG 1988; Academia Sinica 1990; MIEHE et al. 1998 und eigenen Beobachtungen) sowie Darstellung eines Jahrring-Probennetzwerks mit dendroökologischer Gliederung (die westlichen und östlichen Begrenzungen der Provinz II sind mangels Probenmaterial noch nicht bekannt). Weitere Erläuterungen in Fig. 2 und Tab. 2

disturbances. On the other hand, larch is known to be affected by insect infestations in the European Alps, which cause rhythmic patterns in the growth curves. These factors that are characteristic for the ecological behaviour of larch might cause similarities in tree-ring curves that are to a certain degree independent of climate. On the other hand, we have no explanation for the fact that the spruce chronology from Daofu, too, does not form one cluster together with any chronology from the neighbouring areas. It is possible that very moist local site conditions bias the climatic signal in the chronologies. Also, the two chronologies from Gyalaperi (subregion II D 3) might be influenced by local climatic conditions caused by a nearby glacier.

As can be seen two major growth provinces can be distinguished, which are separated from the forest stands at the southern and eastern margins of the Tibetan Plateau receiving plenty of monsoonal rainfall (Province II in Fig. 3). These two major growth provinces are formed by the forests of the continental interior areas at the upstreams of the deep river gorges (Province I). It is noteworthy that all chronologies that are clustered in Province I are composed of *Picea balfouriana*. This means that chronologies of this species have a higher similarity to each other than to chronologies from other spruce species, which are growing nearby. Usually, the similarity of tree-ring chronologies is decreasing with increasing distance, as was shown for North America (SCHWEINGRUBER et al. 1993) and the western European Alps (ROLLAND 2002). This special behaviour of *P. balfouriana* might point to a general ecological capability of this spruce better to withstand a relatively dry and continental climatic regime than other *Picea* species. It is suggested that this disposition might have been acquired by the selection caused by the harsh conditions during the last glacial period, when the intensity of the summer monsoon was low and the general climatic character in the possible refuge areas of the valley bottoms in eastern Tibet was more continental than it is today.

4 Contributing aspects of the recent distribution-patterns of various plant taxa

Till now it could be shown that there are some indications of last-glacial forest refuge-areas in the region of the northern deep river gorges of eastern Tibet. This hypothesis might be checked by other plant-geographical criteria, most of all by the distribution patterns of various botanical taxa in the eastern part of the Tibetan Plateau. For analysing this, the following monographs were taken into consideration: HULTÉN

1958, 1962; MEUSEL 1943; YING et al. 1993 (maps of the distribution patterns of 557 endemic taxa of the Chinese flora); CHEN 1987; WANG a. ZHANG 1994.

When studying the history of various distribution patterns of plant-taxa it is generally thought that the differentiation of a new species will need much more time than that of a new subspecies or even a new form, because it is suggested that the differentiation of a new species will need the activity and combination of many more genes than that of a subspecies or a variety or even a form. Yet, one has always to consider that the systematic differentiation of botanical taxa of different systematic ranks will be done most of all by visual comparison of morphological features, not by genetical experiments or macromolecular investigations. Moreover, the meaning of the term 'species' or 'subspecies' very often differs from country to country or from research-group to research-group. These difficulties have also been dealt with by DICKORÉ (1995), too, when investigating the monocot flora of the Karakorum. Thus the following remarks should not be taken too literally. This can sometimes easily be seen in the field, when for instance cones of *Picea*, collected in various sites, are compared with one another: repeatedly it seemed that continuous transitions from one "species" to another did exist. This means that our knowledge about the distribution pattern of various botanical "taxa" on the Tibetan Plateau will strongly depend on the intensity with which the botanical studies have been done in this vast and geomorphologically very diverse region. Thus, only some remarks about interesting tendencies in the distribution patterns of various botanical taxa can be given, which might add to our knowledge of the historical problems discussed.

According to the literature, the eastern part of the Tibetan Plateau can be divided into various floristic regions (Fig. 4). For the construction of this map all the relevant plant-taxa have been taken into consideration, irrespective of their taxonomic rank, because it is the aim to identify more or less well-defined regions of independent speciation of the plant-taxa studied. In this respect the region within the northern deep river gorges is most interesting. It is evidently situated at approximately the same sites as those of the dendro-ecologically differentiated regions and like those, which on the basis of considerations about the immigration patterns to the sites studied in table 1 might have served as refuge areas for the Hai ze Shan region. CHEN (1987) mentions that within the northern deep river gorges the following tree-"species" can be found (Fig. 5):

Picea retroflexa Masters

Picea aurantiaca Masters

Picea balfouriana Rehder et Wilson
Picea likiangensis (Franch.) Pritzl
Abies ernestii var. *salouenensis* (Bord.-Rey et Gaussen)

Cheng et L.K.Fu

Abies squamata Masters

Larix potaninii var. *macrocarpa* Law

Pinus densata Masters

Additionally should be mentioned

Sabina tibetica Kom.

Sabina convallium (Rehd. et Wils.) Cheng et W.T.Wang

Sabina saltuaria (Rehd. et Wils.) Cheng et W.T. Wang

It is interesting to note that for the same region YING et al. (1993) mention 27 endemic taxa (shrubs and herbs), 13 of which are characteristic of various types of *Abies* to *Pinus* forests. The remaining 14 taxa, on the other hand, characterise alpine meadows, rocks and talus scree. Taking all this together and taking into account that even at present this region has not been studied sufficiently by botanists, the conclusion may be drawn that these plant-geographical distribution patterns point to the former existence of a forest refuge-area within the region studied here. On the other hand, all the data given in the monographs mentioned clearly demonstrate that the refuge areas in the easternmost part of the Tibetan Plateau, i.e. western Sichuan and north-western Yunnan, that of the southern deep river gorges and that of the Himalayas, most of all its western part, must have been much more important as forest refuge-areas than the region mentioned here (the northern deep river gorges). In this respect it is interesting to note that KOTLLA et al. (1997) have convincingly described by means of vegetation history a last-glacial forest-refuge area in the mountainous regions of Kumaun (29°30' to 31°00'N, 78°30' to 81°00'E), just in opposition to steppe-vegetation, which had thrived at the same time in the North-Indian lowlands. On the other hand, the observations of JARVIS (1993), SUN et al. (1986), LIU et al. (1986) and of MAXWELL (2001) concerning, southwesternmost Sichuan, western Yunnan and Cambodia point into the same direction as those, which have been discussed here for the East Tibetan river gorges, i.e. to last glacial forest refuge areas.

Thus, it seems that a last-glacial forest refuge-area within the region of the deep river gorges can also be traced with the modern distribution patterns of botanical endemic taxa. This area has been of much less importance, however, as far as the "species"-richness is concerned, than the other refuge areas in the eastern, south-eastern, southern and south-western parts of the Tibetan Plateau. At any rate it must be suspected that the forest-refuge stands in the northern deep river

gorges moved slope downwards during stadial times, since the climate on the Tibetan Plateau has been much colder and drier at that time than it is at present (FRENZEL et al. 1992; for more literature see also FRENZEL 1998, 2002).

5 Discussion

On the preceding pages facts have been compiled, which favour the view that during the last glaciation one or more refuge areas of forest vegetation might have existed within the deep river gorges of eastern Tibet, which would have contributed to the very early immigration of forest plants into eastern Tibet after climate had improved. The question is whether the deep valleys were deep enough and orientated in an appropriate way so that forest plants could have escaped the extremely cold and severe climatic conditions, which characterised the Plateau during full-glacial times, and also whether these plants might have got enough moisture.

During full-glacial times the summer monsoon system was weakened considerably yet it still existed, as can be seen from the configuration of the last-glacial snowline there (WISSMANN 1959; FRENZEL 1959, 1993; FRENZEL a. LIU 2001; Fig. 6). Thus, summer moisture should have had the possibility to penetrate deeply into the eastern part of the Tibetan Plateau. At present it is fascinating to see how the summer monsoon moves into these valleys forming clouds on mountain systems, which are running diagonally to the main direction of the winds (Photos 1, 2). Yet, it is quite a different problem whether the valleys have been deep enough to harbour these forests at lower elevations during glacial times or not.

Long lasting and numerous meteorological data-sets, which may help to understand the climatic regime trees experience at the upper tree limit are lacking, since all of the small number of Tibetan meteorological stations are situated at the valley floors, were operated for short periods only and these periods were not the same everywhere. BÖHNER (1996) has theoretically improved the situation considerably by climate modelling. However, the vertical distance between the bottoms of the valleys and the upper tree limit in the deeply incised East-Tibetan river gorges amounts to more than 1,200 m (BRÄUNING 1999, Photos 3 a. 4). Thus, estimations of the vertical temperature lapse rates are crucial to formulate more or less correct assumptions about the climatic conditions at the upper tree-line. In a survey about the distribution of spruce-fir forests in China, LI and CHOU (1984) suggested a temperature gradient





Photo 1: Monsoon clouds over the upper Mekong valley east of Qamdo (Photo: FRENZEL, 23/07/1996, 4,700 m)

Monsunwolken über dem oberen Mekongtal östlich Qamdo

Photo 2: Monsoon clouds in the valley end of a tributary of the Mekong west of Qamdo (at site 11 in Fig. 3). In the foreground mixed forests of *Picea balfouriana* and *Juniperus tibetica* (Photo: BRÄUNING, 24/07/1992, 4,500 m)

Monsunwolken im Talschluß eines Nebenflusses des Mekong westlich von Qamdo (bei Standort 11 in Fig. 3). Im Vordergrund Mischwälder aus *Picea balfouriana* und *Juniperus tibetica*

Photo 3: Remnants of *Picea balfouriana* forests (upper left, ca. 4,200 m) above the upper Mekong valley (3,200 m) south of Qamdo (Photo: BRÄUNING, 01/07/1996, 3,500 m)

Reste von *Picea balfouriana*-Wäldern (oben links im Bild, ca. 4200 m) über dem oberen Mekongtal (3200 m) südlich von Qamdo

Photo 4: Remnants of *Picea balfouriana* forests (upper right) above the upper Salween valley (Photo: BRÄUNING, 30°05'N/ 97°17'E, 3,300 m)

Reste von *Picea balfouriana*-Wäldern (oben rechts im Bild) über dem oberen Salweenental (3200 m) südlich von Qamdo

of $-0.57\text{ °C}/100\text{ m}$ for the warmest month. OHSAWA (1990) used a lapse rate of $-0.6\text{ °C}/100\text{ m}$ to model forest limits in various regions of tropical and subtropical Asia including south-western China. TANG and OHSAWA (1997) found a maximum lapse rate of $-0.6\text{ °C}/100\text{ m}$ on the Emei Shan at the eastern fringe of the Tibetan Plateau before the start of the monsoon season in May. BÖHNER (1996) assumed vertical temperature lapse rates for the deep river gorges area for January of $-0.6\text{ °C}/100\text{ m}$ and for July of $<-0.55\text{ °C}/100\text{ m}$, respectively. However, CRAMER (2000) found temperature lapse rates of $-0.69\text{ °C}/100\text{ m}$ in July and $-0.67\text{ °C}/100\text{ m}$ in January in the continental mountain ranges of the Karakoram around Gilgit. In the upper Bagrot valley, lapse rates between $-0.6\text{ °C}/100\text{ m}$ and more than $-0.8\text{ °C}/100\text{ m}$ were found. These conditions are not representative of the deep river gorge area nowadays but they probably existed in the region during glacial and late glacial times under a more continental climate (FRENZEL et al. 1992).

The highest elevation of the upper tree-line in Tibet occurs at about the 30th degree of latitude (LI a. CHOU 1984; FRENZEL 2000), towards the north and towards the tropic the elevation of the upper tree-line is decreasing again (LI a. CHOU 1984; OHSAWA 1993; MIEHE a. MIEHE 2000b). The results of our own investigations during the expeditions mentioned are given in figure 4. *Picea balfouriana* reaches elevations of up to 4,500 m west of Qamdo (31°N), stands of *Juniperus tibetica* can even exceed 4,600 m on south facing slopes, single trees can be found up to more than 4,700 m. Several authors tried to correlate the elevation of the upper forest line in Tibet with meteorological parameters. Whereas no correlation can be found with temperatures of the coldest month, significant positive relationships occur with temperatures of the growing season. LI and CHOU (1984) calculated average temperatures of the warmest month of about 10–12 °C for the upper limit of spruce forests in eastern Tibet, whereas LI BOSHEG (1993) gives an average temperature of 7–10 °C in the warmest month (July) and an annual rainfall requirement of 500 mm. However, isolated forests of *Juniperus tibetica* can be found near Buddhist monasteries in southern central Tibet in areas with an annual rainfall of about 300 mm, only (MIEHE a. MIEHE 2000b). According to LI WENHUA (1993), the cold-tolerant juniper species can endure temperature conditions of 8 °C in the warmest month at the upper tree limit. Presently, the mean temperature of July at Qamdo (31°11'N; 3,241 m) is 16.05 °C (mean for 1951–1990). Accepting a temperature lapse rate of 0.6 °C/100 m, the mean temperature of the warmest month at the upper forest line for spruce (4,500 m) and juniper (4,600 m–4,700 m)

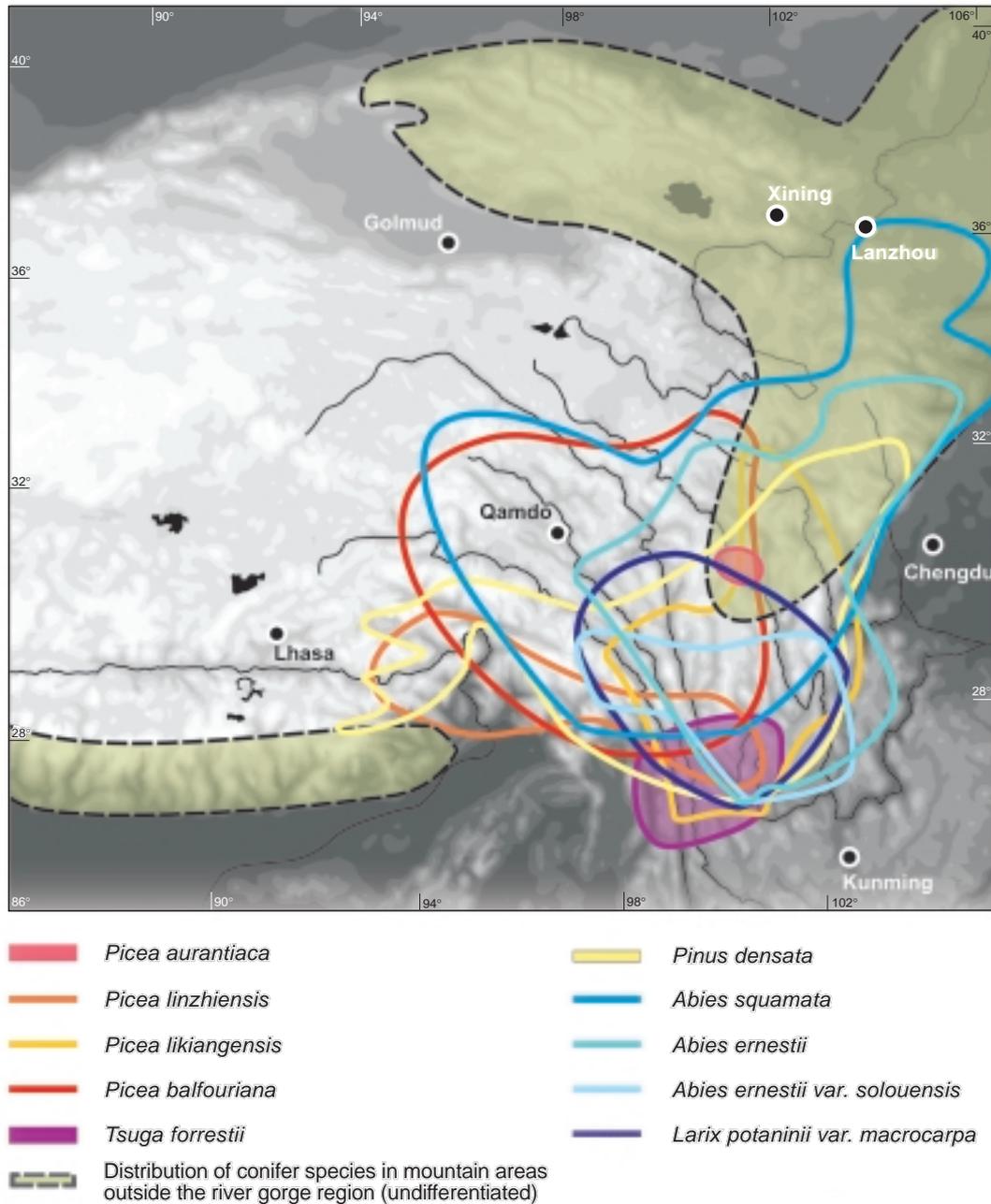


Fig. 5: Distribution pattern of selected conifer taxa in south-eastern Tibet, western Sichuan and northern Yunnan (after CHEN 1987; FARJON 1990 and own observations)

Verbreitung ausgewählter Nadelholztaxa in Südost-Tibet, West-Sichuan und Nord-Yunnan (nach CHEN 1987; FARJON 1990 und eigenen Beobachtungen)

would be about 8.55 °C and 7.95 °C, respectively. Thus, even a supposed temperature depression of 8 °C during the LGM (Last Glacial Maximum; FRENZEL et al. 1992) should at least allow the juniper forests to grow around the upper Mekong valley as far north as approx. 31°N.

Estimations of the depression of the annual mean temperature during the LGM range from 5 °C (GUPTA a. SHARMA 1992) or 6 °C (LEHMKUHL a. HASELEIN 2000; BÖHNER a. LEHMKUHL 2003) to 8 °C (FRENZEL et al. 1992). The last-mentioned value was calculated from the distribution pattern of probably last-glacial

permafrost features (FRENZEL a. LIU 2001). BÖHNER and LEHMKUHL (2003) suggest a depression of 5.0 °C of summer temperatures in the subtropical regions of southern Tibet. Depending on the region, this temperature depression results in a depression of the equilibrium line altitude (ELA) of 700–1,200 m, if a temperature lapse rate of -0.6 °C to -0.7 °C/100 m is assumed (GUPTA a. SHARMA 1992). From field evidence of glacial deposits, FRENZEL and LIU (2001) reconstructed a depression of the ELA of 300 m in the north at around 32°N, to 700–1,000 m in the south (at 25°N) of the area under concern. Similar values are given by LEHMKUHL (2003). Even if we assume a temperature depression of 8 °C (after FRENZEL et al. 1992) during the LGM and a temperature lapse rate of -0.8 °C/100 m

or -0.7 °C/100 m, a lowering of the upper forest line of between 1,000–1,150 m seems to be realistic. Thus, the position of the upper limit for spruce and juniper would have run at an elevation of approximately 3,500–3,350 m or 3,600–3,450 m, respectively. Since the bottom of the Mekong gorge close to Qamdo has an elevation of about 3,200 m (Photo 3), there should have been space enough on the lower parts of the slopes to allow the occurrence of a narrow coniferous forest belt. These assumptions are corroborated by recent palaeoecological models (BÖHNER a. LEHMKUHL 2003).

Thus, these climatological considerations show that the existence of last-glacial (stadial) forest refuges within the deep East-Tibetan river gorges seems to be possible, even at the latitude of Qamdo (Fig. 4). This con-

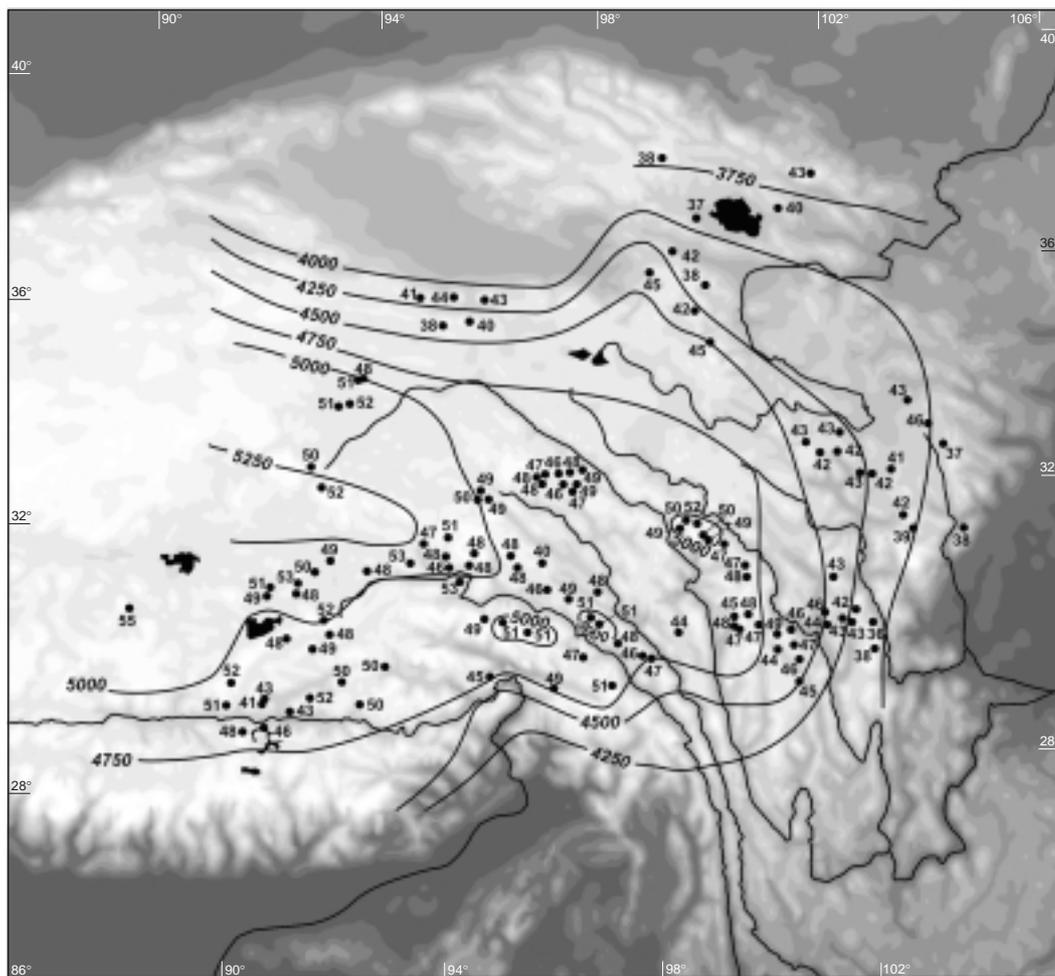


Fig. 6: Elevation of the last-glacial (LGM) climatical snowline in eastern Tibet. The numbers given (hundreds of meters) result from own observations in the field and from studies of various topographical maps (details in FRENZEL a. LIU 2001)

Höhe der letzteiszeitlichen klimatischen Schneegrenze (LGM) in Ost-Tibet. Die Ziffern (hunderte von Metern) ergeben sich aus den eigenen Feldbeobachtungen und einer Analyse verschiedener topographischer Karten (Einzelheiten in FRENZEL a. LIU 2001)

firms the conclusions drawn from the pollen-analytical, dendro-ecological and the plant-geographical data. Of course, all these observations and considerations are not an exact proof that in the region mentioned glacial forest refuge areas existed, yet the probability for this is appreciably great. This conclusion may be corroborated by the fact that a near-by peat bog, to the west of the Qamdo airport (30°44'N, 96°50'E, ca. 4,500 m a.s.l.; No. 3 in Fig. 1), has already shown a remarkably high percentage of arboreal pollen from the very beginning of peat formation (ca. 9160 ¹⁴C yrs. B.P.). This might point to the last glacial existence of tree refuge areas within the deep valleys. But on the other hand, just here it cannot be ruled out that these forests, which exist there even at present high up on the inaccessible mountain flanks, migrated very early from refuge areas farther in the south. Yet from all what has been discussed here, we formulate the working hypothesis that these northern East-Tibetan river gorges harboured during the stadials of the last glaciation forest refuge sites.

Some 30 km to the southeast of Qamdo one of us (B. F.) dug up a geological profile on a low terrace of the

river Mekong, which contained loesses, interrupted by a fossil cernozem-like soil (FRENZEL a. LIU 1994). Regrettably due to weathering the soil and the loess layers did not contain any pollen grains so that the problem of the existence of glacial forest refuge areas could not be studied there.

It is possible that a macromolecular analysis of the DNA of various tree-taxa of the region might help to answer this question, if it would be done on a very broad geographical scale.

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