

## The Pleistocene Vegetation of Northern Eurasia

The recent vegetation of northern Eurasia resulted from a relentless contest between steppe and forest.

Burkhard Frenzel

In a discussion of evolution of vegetation in northern Eurasia during the Pleistocene, some matters of general interest should first be considered. Northern Eurasia embraces all of Europe; those regions of Siberia and the middle of Asia which lie to the north of the Black Sea, the Caucasus, the Elburz Mountains, the Tien Shan Mountains, and the mountains of southern Siberia; and, finally, Korea. The Pleistocene began with the end of the Pliocene (the end of the Tertiary) and closed with the dawn of postglacial times. During this epoch, which seems to have lasted for about a million years, there were several marked changes in climate, causing, in some periods, a tremendous accumulation of snow and ice in higher latitudes and, in others, migration of animals such as the hippopotamus as far north as the middle of England (Fig. 1). The division of the Pleistocene in the Northern Hemisphere that is shown in Table 1 seems to be relatively correct. But Russian scientists have often advanced the hypothesis that the climatic history of Siberia during the Pleistocene differed from that of other regions at the same latitudes. According to this hypothesis, the climate of the center of Asia was always governed by an extreme conti-

mentality, and glaciations occurred there only when mountainous areas were uplifted or during times when the periphery of the continent was experiencing interglacial conditions and masses of damp air could penetrate much farther into the interior than they could when the periphery was covered with ice. If this hypothesis is valid, the glaciations of Siberia cannot be directly correlated with those of the Far East or of Europe (1, 2). But it seems to me that both the vegetational and the climatic history of the postglacial period and the vast transgressions of the polar sea during the last interglacial (the Eemian, Boreal, and Kazantsev transgressions) provide strong evidence in support of a theory of synchronicity of interglacial and glacial phases, respectively, all over the continent (1, 3, 4). Apparent differences between accepted dates for glacial and interglacial phases in some regions of northeastern Eurasia and in western and central Europe should be explained, not by hypothesizing divergent geological or climatological evolution, but in terms of the inadequacy of our knowledge.

If one accepts the general division of the Pleistocene shown in Table 1, one must nevertheless admit that serious problems of Pleistocene history do exist. They are caused primarily by the fact that, for several regions of Europe,

there seem to have been more climatic oscillations than are shown in Table 1 (5, 6). Perhaps this may be explained in terms of interruptions of interglacial conditions during the three earliest interglacial periods (the Tiglian, Waalian, and Cromerian) by pronounced cold spells, which resulted in the establishment of subarctic plant communities in central and western Europe within the warm phases (6, 7). A cold spell seems to have occurred during the Holsteinian interglacial also, and another during the Eemian; in these two cases the cold spell separated the interglacial proper from a very pronounced interstadial phase, which may have consisted of several minor climatic oscillations (1, 4, 7-10).

Another difficulty encountered in trying to reconstruct climatic and vegetational evolution during the Pleistocene of northern Eurasia arises from the fact that the orography of the coastlines changed within this relatively long period. From Figs. 2-7 it may be seen that two general trends governed the shape of the continent. (i) During the glacial phases the ocean retreated, leaving a broad land bridge between Asia and North America, and during interglacial phases the ocean spread onto the continent, drowning vast lowlands in northern Europe and northern Siberia and repeatedly separating the mountains of the Taimyr Peninsula and those of Scandinavia from the body of the continent. (ii) In the area of the Caspian Sea there was an opposite trend: during glacial periods the low temperatures caused a considerable reduction in the rate of evaporation of the surface water of the Sea, and there were huge transgressions; whereas during the interglacials the rate of evaporation was high (at times, it seems, higher than that of today) and there were large regressions.

The displacement of coastlines governed the continent's overall oceanity or continentality of climate, but the character of local climates, which is of utmost importance both for the distribution of different types of vegetation and for the vegetation's chances of

The author is professor of botany at the University of Hohenheim, Stuttgart-Hohenheim, Federal Republic of Germany.

Table 1. Division of the Pleistocene in the Northern Hemisphere.

Northwestern and central Europe	Eastern Europe	North America
Weichselian glaciation	Valdai glaciation	Wisconsin glaciation
Eemian interglacial	Mikulino interglacial	Sangamon interglacial
Saalian glaciation	Dneprovsk glaciation	Illinoian glaciation
Holsteinian interglacial	Likhvin interglacial	Yarmouthian interglacial
Elsterian glaciation	Oka glaciation	Kansan glaciation
Cromerian interglacial	? interglacial ?	Aftonian interglacial
Menapian cold period	Cold period of the Bakou transgression	Nebraskan glaciation
Waalian warm period	?	?
Eburonian cold period	Cold period of the Apsheron transgression	?
Tiglian warm period	Warm period of the Apsheron transgression ?	?
Praetiglian cold period	Cold period of the Akchagyl transgression	?

surviving unfavorable conditions, was essentially modified by tectonic movements of the mountain areas of northern Eurasia. In general these mountains, with the exception of those of the Alpine belt, of Scandinavia, and of the Kamchatka Peninsula, seem to have been uplifted by about 200 to 300 meters during the Pleistocene. This uplift resulted in an increase in the differences between the climates (relatively oceanic) at the periphery of the continent and those (strongly continental) at the center; moreover it caused a tremendous local variability of climate, which made it possible for vegetation to survive, and even for new species to evolve, in some regions of the continent during the Pleistocene (4).

The last question of general interest that concerns us here is the Pleistocene history of permafrost, since perennially frozen ground seriously affects vegetation. It seems (4) that permafrost did not exist in most parts of northern Eurasia at the end of the Pliocene. But as soon as the first significant deterioration of climate began (the Praetiglian glacial period), the area of permafrost must have spread far to the south. Figure 8 outlines present-day knowledge of the expansion and retreat of the permafrost area since the beginning of the next-to-last glaciation (the Saalian).

In any study of the Pleistocene history of vegetation of northern Eurasia, all these events and factors must be considered.

### History of Pleistocene Vegetation

The starting point for the Pleistocene evolution of vegetation was the very end of the Pliocene—that is, according to Dutch terminology, the Reuverian. Various types of forest vegetation were then characteristic for northern Eurasia

(Fig. 2) (1). The distribution of these types suggests that no zone of true tundra vegetation existed, despite the fact that the northern coastline of Siberia ran farther to the north than it does today. At the same time the southern border of the forest belt extended farther to the south than it does now, and forest-steppe vegetation seems to have been widely distributed. From this it appears that the climate was warmer and moister than it is today. This view is corroborated by a comparison between recent and past distribution of several botanical species. The mean temperatures for July must have surpassed those of today by about 2° and 3°C in central and western Europe, and by 4° to 5°C in eastern Europe. Moreover, in eastern Europe and in Siberia, mean temperatures for January and mean annual temperatures must have been about 5° to 10°C higher



Fig. 1. Distribution and age of finds of Pleistocene *Hippopotamus* in central and western Europe. (1) Weichselian glaciation; (2) Eemian interglacial; (3) Holsteinian interglacial; (4) Elsterian glaciation; (5) Cromerian interglacial; (6) early Pleistocene; (7) age unknown. [From Frenzel (4)]

than those of today, and mean annual precipitation must have been about 300 millimeters greater than it is in the same regions today (4). So, in general, the climate was much more oceanic than it is now, perhaps because the mountain systems were appreciably lower. Nearly all vegetation types known to have been present during this period differed remarkably from their present-day relatives; they included numerous species now found only in southeastern Asia and in North America (Fig. 9). But in northeastern Yakoutia (Siberia), coniferous forests of recent type (the taiga) began to form. One is surprised to note that in Caucasia and on the western slopes of the Tien Shan and the Dzungaric Alatau, isolated forests rich in subtropic elements existed at this time, separated from the northern forest vegetation by a broad belt of steppe vegetation.

Several investigations, in the Netherlands, in central Europe, and in eastern Europe (11–13), have shown that climatic conditions changed pronouncedly several times toward the end of the Pliocene but that these climatic oscillations did not reach their greatest amplitude until the beginning of the Pleistocene, during the Praetiglian. To give a better understanding of the consequences of these climatic changes, it seems appropriate to compare three glacial periods (Praetiglian, Saalian, and Weichselian) with three interglacials (Cromerian, Holsteinian, and Eemian) from the standpoint of plant geography.

The most striking feature of the vegetation of the glacial periods (Figs. 3–5) was undoubtedly the wide distribution of steppe vegetation within the belt of interglacial forests. But apparently the glacial periods differed from one another with respect to the dominating types of open vegetation (1): forest steppes seem to have prevailed during the Praetiglian, open steppes during the Saalian and Weichselian. Moreover, reliable traces of permafrost during the Praetiglian are lacking in Europe, though plenty of fossil forms indicative of permafrost which date from the middle and late Pleistocene have been found there (4). Finally, the earliest Pleistocene faunas of central, western, and southeastern Europe are related to modern savanna faunas of Africa, so it might be argued that the vegetation and climate of the Praetiglian in these parts of Europe resembled the vegetation and climate of dry and relatively warm regions. But during the Praetiglian the forest-steppe of

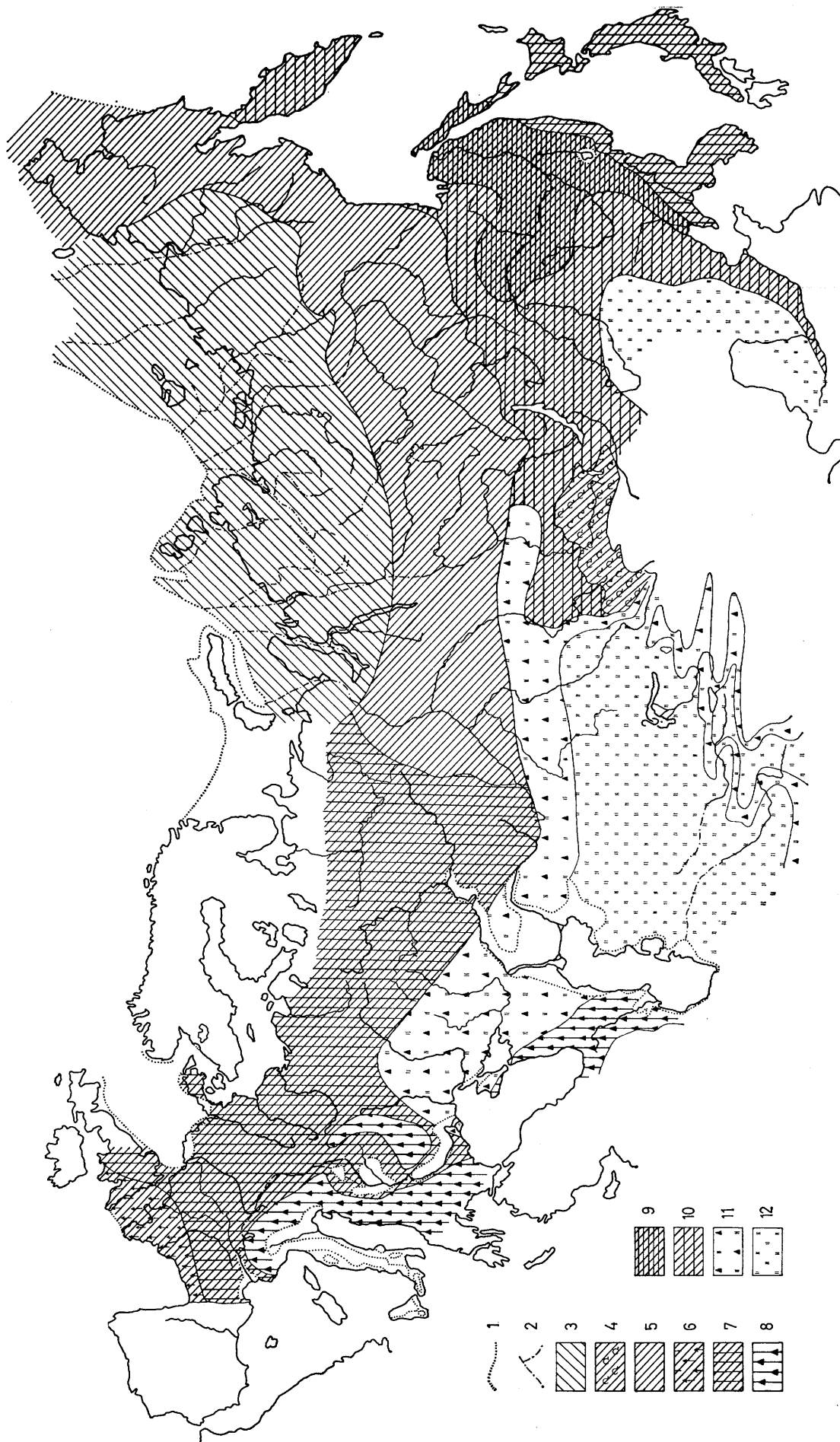


Fig. 2. Plant-geographical conditions at the end of the Pliocene (Reuverian). (1) Coastlines; (2) rivers; (3) pine-spruce-larch taiga with *Pinus sibirica* and some birch and alder; (4) forests of spruce, fir, and hemlock, with pine and birch in some abundance; (5) forests of spruce, fir, and hemlock and recent North American pines (*Pinus strobus* and others); (6) forests of pine, *Sequoia*, and ericaceous undergrowth; (7) mixed forests of conifers and deciduous broadleaf trees (*Juglandaceae*, *Sciadopitys*, *Sequoia*, *Taxodium*, and others); (8) mixed forests of southern Europe and of the Colchis (*Abies*, *Picea*, *Tsuga*, *Chamaecyparis*, *Keteleeria*, and hygrophilous broadleaf deciduous trees); (9) East Asian forests of spruce and hemlock mixed with thermophilous deciduous broadleaf species (*Juglandaceae*, *Castanea*, and others); (10) forests of spruce, hemlock, and fir, with only a small admixture of thermophilous and hygrophilous broadleaf species; (11) forest-steppe; (12) steppe, desert, and alpine steppe vegetation. [From Frenzel (1)]

the Netherlands had a subarctic character (11). Also, in several regions of Europe thick layers of loess were accumulating (1) and the soil was frozen during at least several months of the year. These conditions existed in the northwestern part of Germany and perhaps to the north of the Caspian Sea, in the southern part of the Ukraine, and in Bavaria. Moreover, in several regions of northern Eurasia traces of inland ice or of mountain glaciations have been observed (Fig. 3). These observations show that mean annual temperature was lower by about 10°C than it is today, and that annual precipitation was roughly 200 to 250 millimeters less than it is now (4). Virgin forests seem to have disappeared during the Praetigian in most regions of northern Eurasia, with the exception, perhaps, of central Siberia, the Mediterranean area, and Caucasus. Even in the Mediterranean region and Caucasus vegetation had suffered from the cold, dry climate, hence subalpine forests grew in northern Italy and in Caucasus (15), where nowadays forests of deciduous or even evergreen broadleaf trees thrive.

In contrast to the Praetigian, during

the Saalian and Weichselian the forest-steppe vegetation was confined (Figs. 4 and 5) to some mountainous regions where local climates were less severe than the climate in general: the western and eastern Alps, the Carpathian Mountains, the southern part of the Ural Mountains, the Kazakh Mountains, and the mountainous regions of central and southern Siberia. Here the most frost-resistant species of ancient forest vegetation could survive, in several, presumably very small, areas of retreat, at a time when the lowlands were nearly devoid of trees. Small groves of pine, spruce, larch, birch, and alder grew in these regions of refuge, perhaps in the southern parts of the Carpathian Mountains, associated with hazel and oak (1, 3, 16-20). In place of the subalpine forest of the Praetigian, various steppe plant communities covered most regions of the Iberian and Apennine peninsulas during the height of at least the last two glaciations, when simultaneously in northern Spain, southern France, northern Italy, and northwestern and western Yugoslavia thick layers of loess were accumulated by winds blowing dust over vast treeless areas (21).

There is considerable doubt about the character of the vegetation in open areas at the height of these glaciations. It might be argued that the extreme glacial climate produced a wide distribution of tundra vegetation (the recent occurrence of arctic-alpine species in the flora and fauna of northern Eurasia seems to corroborate this view). But though several fossils and microfossils of glacial floras and faunas, dating from various glaciations, have been reported (1), traces of vast glacial tundras are very scarce. Such traces of tundra vegetation as have been reported seem to be restricted to areas which at the time had relatively oceanic climates, such as the southern part of England and the Netherlands (22). But beginning with central and eastern Belgium, steppe-like communities seem to have been much more characteristic—communities dominated by *Artemisia*, *Chenopodiaceae*, and several herbs and grasses, together with appreciable numbers of halophytic plants (plants which today grow chiefly in soils having a high content of chloride and sulfate salts) (17, 18, 23). The presence of halophytic plants led Russian paleobotanists to suggest that soils must have been salty in eastern

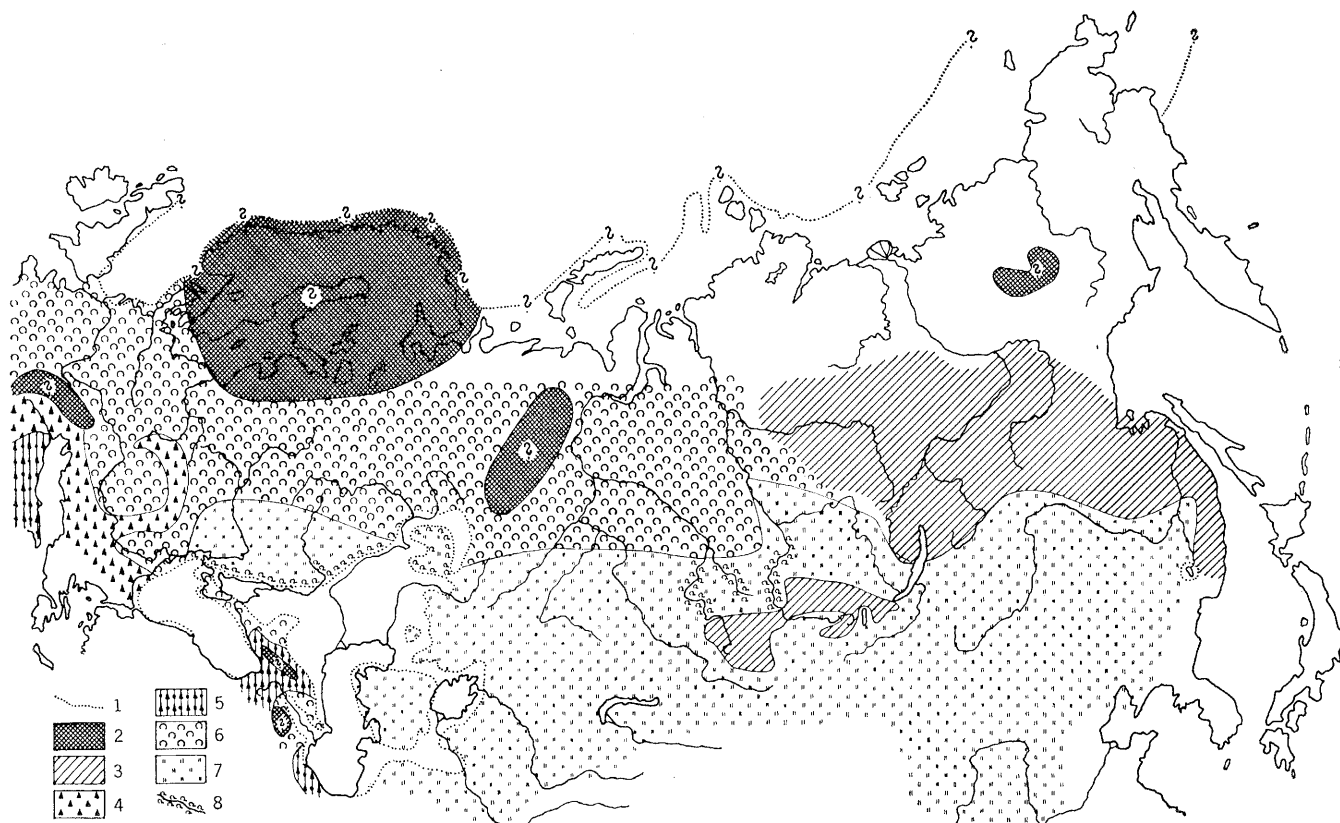


Fig. 3. Plant-geographical conditions during the Praetigian glacial period. (1) Coastlines; (2) glaciers; (3) forests of pine, spruce, and larch; (4) forests of pine, spruce, and fir; (5) forests of spruce, fir, and beech, together with mixed forests of the Colchis type; (6) subarctic parkland and forest-steppe with some loess sedimentation; (7) steppe and desert; (8) galeria forest. [From Frenzel (4)]

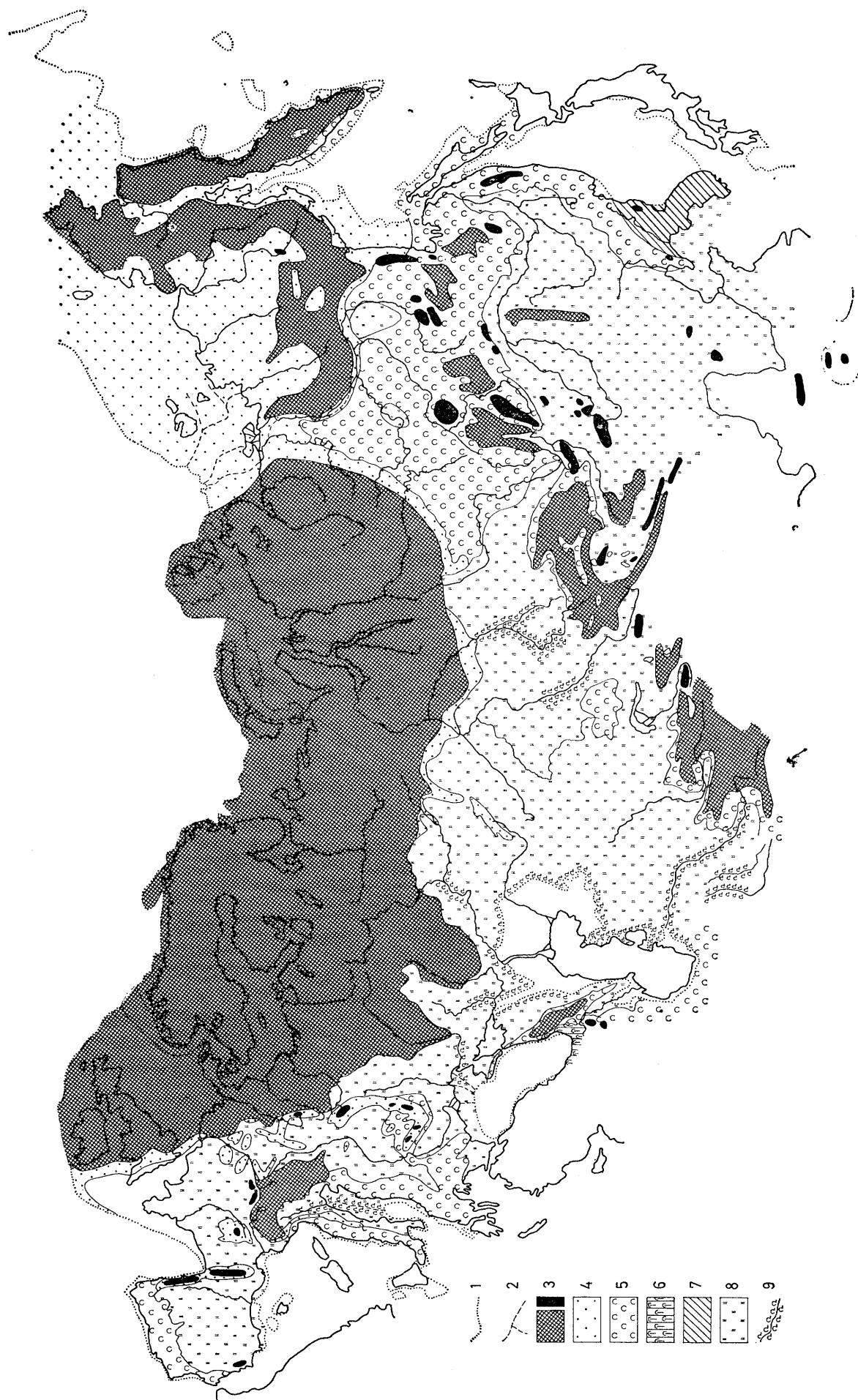


Fig. 4. Plant-geographical conditions at the height of the Saalian glaciation. (1) Coastlines; (2) rivers; (3) glaciers; (4) tundra; (5) groves of extremely cold-resistant conifer and deciduous trees within the prevailing steppe vegetation; (6) conifer and broadleaf forests of the Colchis region; (7) taiga vegetation (cold-resistant conifers with a small admixture of thermophilous broadleaf species); (8) steppe and desert-steppe, in general with loess sedimentation; (9) riverine forests. [From Frenzel (7)]

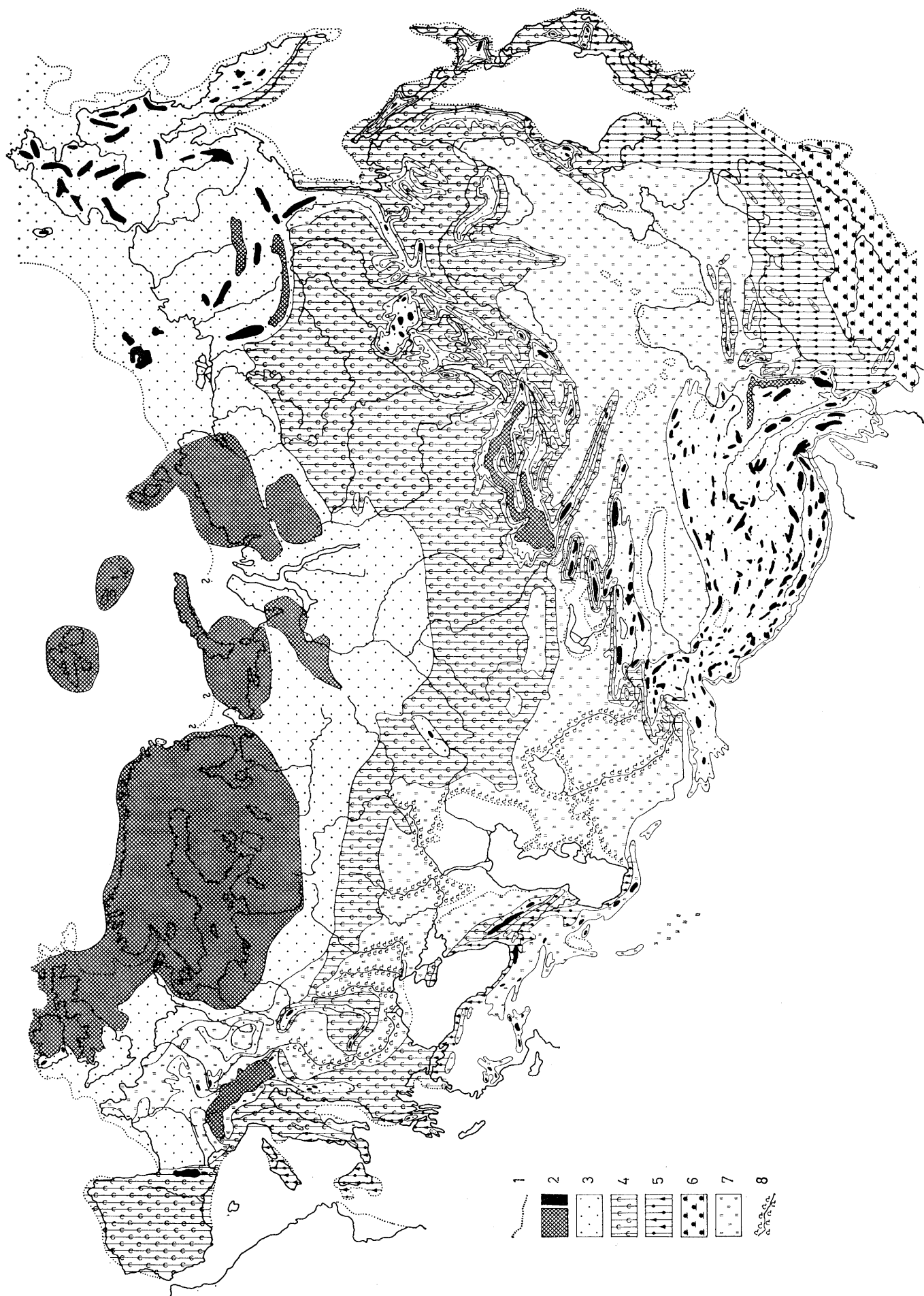
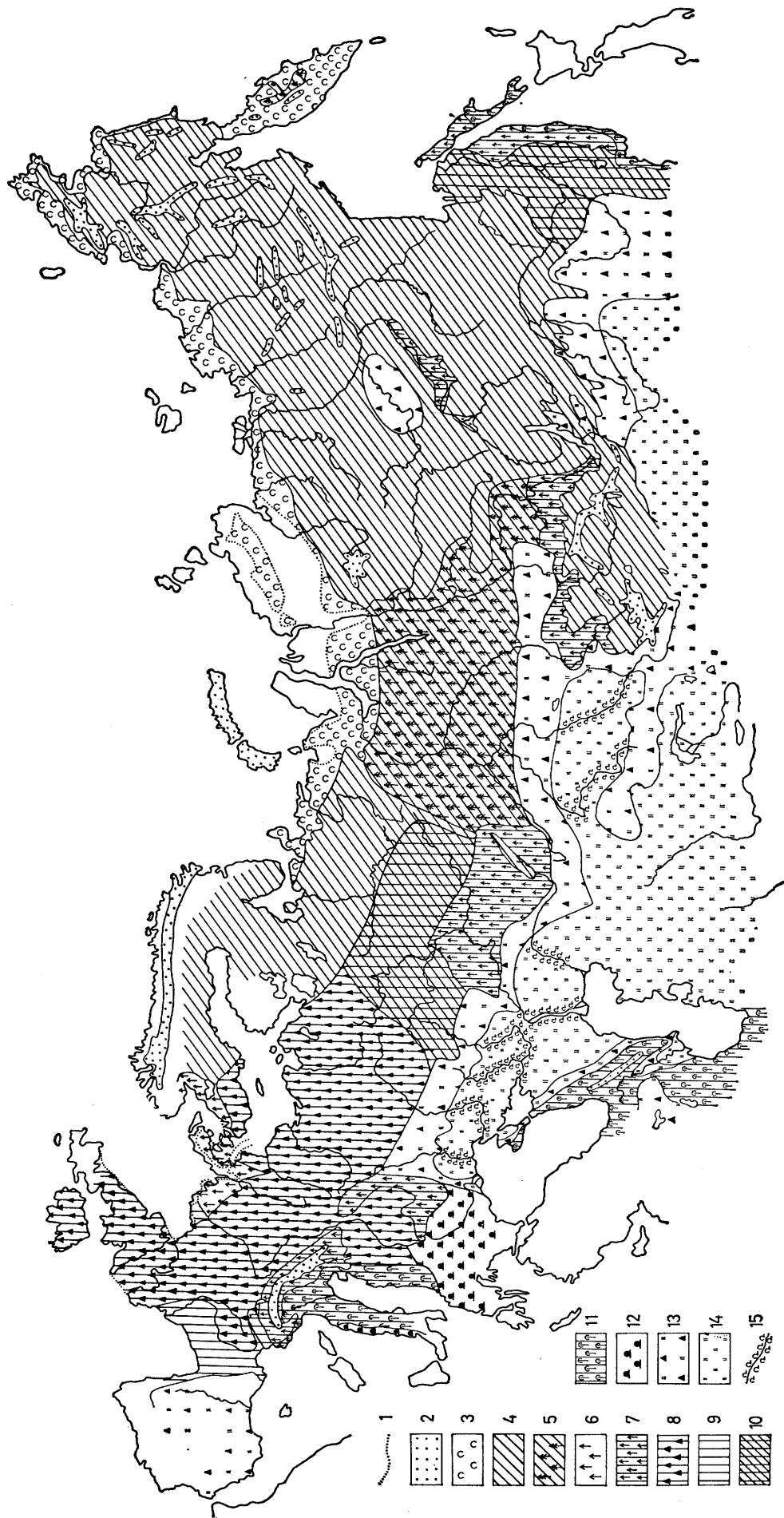




Fig. 5 (opposite page). Plant-geographical conditions at the height of the Weichselian glaciation. (1) Coastlines; (2) glaciers; (3) tundra with steppe elements and arctic steppe vegetation; (4) regions characterized by groves of extremely cold-resistant conifers and deciduous trees within the prevailing steppe vegetation; (5) chiefly hypothetical mixed forests dominated by conifers; (6) hypothetical forests of evergreen broadleaf trees; (7) prevailing loess steppe and some deserts; (8) riverine forests. [From Frenzel (1)]

Fig. 6 (below). Plant-geographical conditions during the Holsteinian interglacial. (1) Coastlines; (2) alpine vegetation; (3) forest tundra and birch forests of Kamchatka; (4) taiga vegetation, chiefly composed of pine, spruce, and larch; (5) forests of spruce, fir, and *Pinus sibirica*; (6) oceanic pine forests; (7) conifer forests, characterized by spruce and fir, with an admixture of thermophilous broadleaf elements; (8) mixed forests of oak, fir, and linden; (9) mixed forests of oak, elm, and linden; (10) forests of pine and spruce with oak, elm, and linden; (11) chiefly forests of broadleaf thermophilous and hygrophilous trees, with Juglandaceae; (12) Mediterranean deciduous and evergreen forests; (13) forest-steppe; (14) steppe and desert; (15) riverine forests. [From Frenzel (2)]



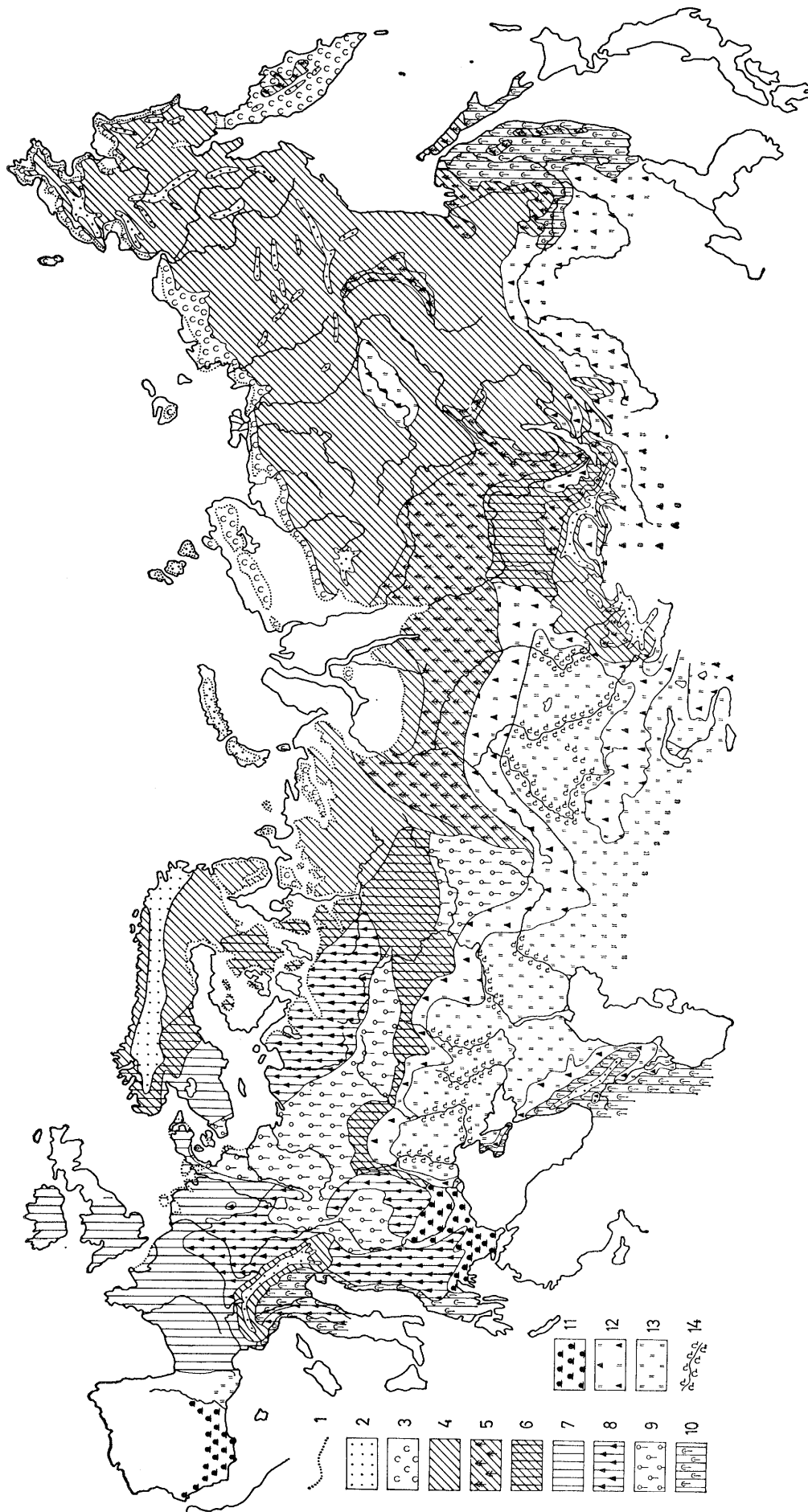


Fig. 7 (above). Plant-geographical conditions during the linden phase of the Eemian interglacial. (1) Coastlines; (2) alpine vegetation; (3) forest tundra and open birch forests of Kamchatka; (4) forests of spruce, pine, and larch; (5) forests of spruce and fir, in some parts with a wealth of *Pinus sibirica*; (6) conifer forests with a small admixture of oak, elm, and linden; (7) mixed forests of oak and hornbeam; (8) linden forests; (9) linden forests, some with oak; (10) forests of hygrophilous and thermophilous deciduous broadleaf trees and conifer forests; (11) Mediterranean oak and pine forests; (12) forest-steppe; (13) steppe and desert; (14) riverine forests. [From Frenzel (1)]

Fig. 8 (opposite page). History of the permafrost area in northern Eurasia. (a) Saalian glaciation; (b) Weichselian glaciation; (c) Eemian interglacial; (d) postglacial. (1) Coastlines; (2) lakes; (3) glaciers; (4) permafrost area during the Saalian, Weichselian, and Eemian; (5) permafrost area during the hypsithermal period of the postglacial; (6, together with 5) recent permafrost area. [From Frenzel (4)]



Europe and in Siberia during the height of glacial times (24). But it seems to me that the relative importance of this ecological group has been exaggerated, since the methods used for analyzing the fossil pollen are not reliable (1). Nevertheless this element within glacial vegetation should not be overlooked. These plants (*Plantago maritima*, *Crambe* cf. *tatarica*, *Cochlearia*, *Zanichellia pedicellata*, *Triglochin* cf. *maritimum*, *Trifolium* cf. *fragiferum*) belong today to the so-called facultative halophytes—that is, plants which are not necessarily limited to soils of high salt concentration. So their existence in the past may only indicate the prevalence of unweathered soils that were continuously reworked by the action of frost and wind. The steppe vegetation, composed of various regional types, was interspersed with small patches of tundra vegetation; moreover, the open vegetation in an area underwent remarkable changes even during a single glacial period (17, 18, 23).

As Figs. 4 and 5 show, no forest belt existed during the height of the last two glaciations. The forest trees were confined, in general, to several small mountainous areas and to the northern border of the Caspian Sea, which spread over the adjacent land during certain phases of the glacial periods. The forested area around the spreading Caspian Sea was much wider during

the initial phases of each glacial period than it was later on. Within these forests or groves only very hardy species seem to have survived times of extreme cold (1, 4, 25).

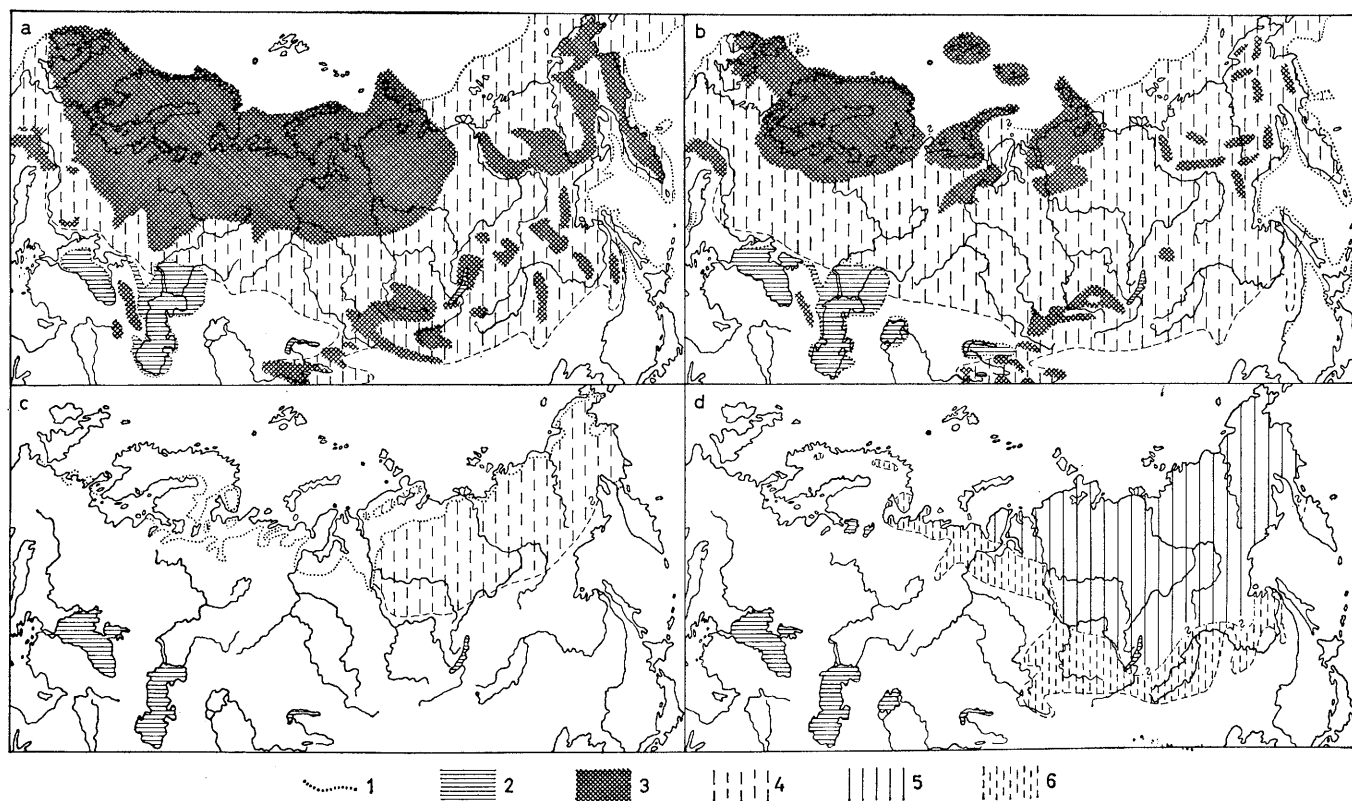
In most areas of northern Eurasia the soil was perennially frozen at the height of the last two glaciations (Fig. 8), thus, at least during the last glaciation, mean annual temperature and mean annual precipitation must have been lower by about 12° to 14°C and at least 300 millimeters, respectively, than present temperature and precipitation (4). Whereas in northern Eurasia glacial periods were characterized by maximum distribution of various steppe communities, interglacials were characterized by forests, which covered the continent from the Atlantic coast to the coasts of the Okhotsk and Japanese seas (Figs. 6 and 7).

The wavelike evolution of interglacial climates makes it necessary, in a study of Pleistocene vegetation, to clearly define those phases of interglacial periods that are to be compared with one another. Here it seems appropriate to study only phases which provided optimum climate for the forest vegetation of zones that now have moderately cold climates: the phase of maximum importance for hornbeam (*Carpinus*) and fir (*Abies*) during the Holsteinian interglacial and the time of greatest development of linden forests (*Tilia platyphyl-*

*los*) during the Eemian interglacial.

Within the first interglacial (the Tiglian) of the Pleistocene, late-Pliocene vegetation types reimmigrated into northern Eurasia. But several typical late-Pliocene genera were either not able to reoccupy their former habitat or had already been annihilated by the first extreme cold of the Pleistocene. (These were *Sequoia*, *Taxodium*, *Glyptostrobus*, *Nyssa*, *Liquidambar*, *Fagus*, *Zelkova*, *Liriodendron*, and several others.) The impoverishment in vegetation so characteristic of the history of the biosphere in the Pleistocene had begun. At the same time, *Tsuga* and many relatively thermophilous plants disappeared from Siberia—an event which led to the establishment of recent Siberian taiga vegetation by the beginning of the Pleistocene. Since that time, this extremely cold-resistant type of forest vegetation has changed very little, though the taiga survived only within very small areas of retreat during the extreme cold of the glacial phases.

Thus, the recent types of forest vegetation in Siberia seem to be much older than the recent types in Europe, where the interglacial phases that provided optimum climate for such vegetation were characterized by special forest communities of their own. One peculiarity in the vegetation of at least the last two interglacial periods was the fact that no belt of tundra vegetation



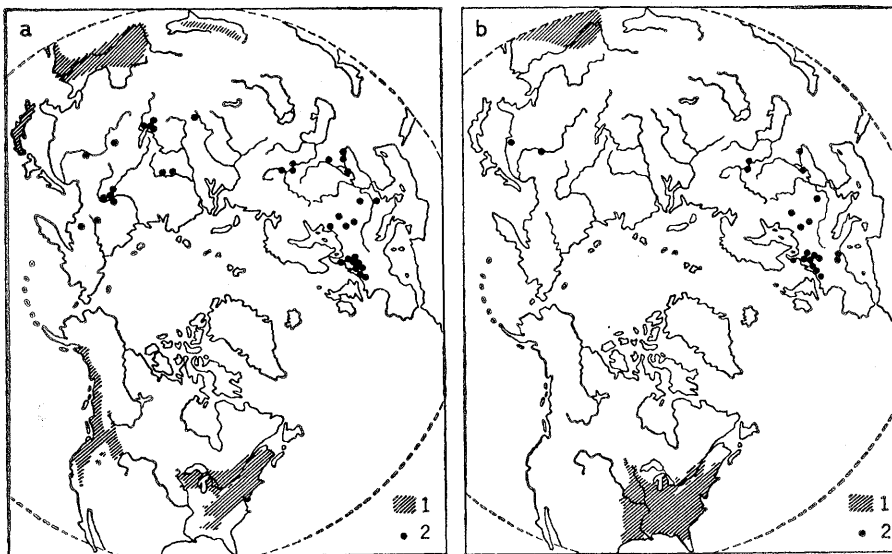


Fig. 9. Recent and Reuverian distribution of (a) *Tsuga* and (b) *Carya*. (1) Recent distribution; (2) finds in sediments of probably late-Pliocene age (Reuverian). [From Frenzel (4)]

then existed in northern Eurasia, earlier belts having been destroyed by vast interglacial transgressions and by the spread of various types of forest vegetation up to the northern coasts of Eurasia. Possibly this special type of vegetation could survive the high-temperature phases of the interglacials as a vegetation belt only in Alaska and Canada (1).

An impoverished Pliocene forest vegetation reimmigrated into Europe during the Tiglian. Such a reimmigration may also have occurred in the Waalian. True Pleistocene types of forest vegetation, devoid of most late-Pliocene genera, were established only during the Cromerian interglacial. Then deciduous forests, chiefly composed of oak and elm, seem to have been widely distributed in Europe. Presumably, there already existed various forest types in different regions of Europe, dominated, for instance, by elm within the oceanic regions but by oak and linden in the more continental parts of central and eastern Europe. Perhaps these oak and elm forests were typical, too, of northern Italy, on the south-facing slopes of the Alps. These forests of broadleaf trees were confined to Europe; in Siberia, forest vegetation of the type found there today covered the vast lowlands of the western regions and the mountains to the east.

In Europe, the various types of vegetation present during the Cromerian interglacial, and their history, strongly resembled the forest communities and their evolution during the Eemian. This similarity has been shown by several

palynological investigations made during the past 5 years. The similarity is so striking that the well-known interglacial beds of Bilshausen (to the southwest of the Harz Mountains in central Germany), which really date from one part of the Cromerian interglacial, were thought, some years ago, to belong to the Eemian (26). But whereas, during the Cromerian, forests chiefly of oak and elm, with only a negligible amount of linden, thrived in western, central, and eastern Europe, forests almost wholly of linden (especially *Tilia platyphyllos*, together with *T. cordata*, *T. tomentosa*, and *Acer tataricum*) seem to have dominated central and eastern Europe during the Eemian (Fig. 7), associated with several other types of forest trees. As may be seen in Fig. 7, at that time, at least, Scandinavia was separated from the continent by a broad inlet. This separation, together with the huge transgression of the north polar sea onto western Siberia, must have strongly influenced the climate of the continent, so that plants which today grow only in the more oceanic regions of Europe could then have grown also in the eastern part of central Europe (Fig. 10).

From this, and from Fig. 7, it may be seen that the forest vegetation of northern Eurasia during the Cromerian and the Eemian interglacials was divided into the European district of broadleaf, deciduous, thermophilous, and hygrophilous forests and the Siberian district of conifer forests. This division does not hold true for the Holsteinian (Fig. 6), since during this

interglacial period conifer forests were characteristic of nearly the whole of northern Eurasia. This might be explained by postulating a severe climate in Europe too, such that no clear-cut ecological differences between Europe and Siberia could have existed. But, as I have stated, the forests during the Holsteinian interglacial immigrated onto the zone of recent tundra vegetation, synchronously with a remarkable transgression of the polar sea, and this immigration was paralleled by an invasion of forests into the area of recent steppe vegetation (Fig. 6). So climate cannot have been more continental in eastern Europe during the Holsteinian than it is today. Moreover this view is strengthened by the past distribution of such thermophilous plants as *Pterocarya* and *Vitis* (Fig. 11). From this it must be argued either that the Holsteinian conifer forests were composed of species different from present-day species [a view that has recently been disproved (27)] or that the strange distribution of conifer forests must have been caused by factors other than climate. I discuss this problem below.

#### Problems of Plant Geography during the Pleistocene

The reconstruction of consecutive steps in the history of vegetation of northern Eurasia during the Pleistocene, as given in Figs. 2–7, needs further interpretation. As I have pointed out, the most characteristic vegetation of the glacial periods is an open vegetation. Paleontological findings indicate that, during the early Pleistocene, this was savanna vegetation. Later, steppe faunas immigrated (28), associated during and subsequent to the Elsterian glaciation with tundra faunas and floras. Thus, different types of open vegetation seem to have followed each other, and the real tundra vegetation is of later origin, at least in Europe. But the oldest types of open vegetation in northern Eurasia (perhaps Praetigian) were related not to recent savannas but to steppe vegetation. Moreover, various types of steppe vegetation seem to have covered northern Eurasia from the Atlantic to the Okhotsk and Japanese seas at the height of at least the two or three last glacial periods, leaving only small patches in which the tundra vegetation could develop. So the history of tundra communities must have been a very complicated one. It might be argued that this special type of vegetation might have

evolved in northern Yakoutia during the earlier parts of the Pleistocene, but no reliable traces of past tundra floras have been found there. On the other hand, during the last two glacial periods, plants typical of recent tundras could have thrived in central Europe in several scattered localities, where soils were relatively moist (17, 18, 23). From this it follows that, at least during extreme glacial times, various types of steppe vegetation characterized most regions of northern Eurasia, interspersed in some localities by patches of tundra vegetation. But though tundra was of merely local importance, plants like *Betula nana*, *Dryas octopetala*, and *Koenigia islandica* could thrive, during these periods, in the southern Carpathians, in the lowlands of Hungary, and to the east of the Alps (18–20, 29). So chances for the spread of the recent arctic-alpine flora must have been very good. Moreover, it must be admitted that we do not know the character of past vegetation on the mountain slopes in most parts of northern Eurasia, where solifluction has destroyed nearly all beds containing plant remains of glacial times. Possibly tundra vegetation could develop there in moist patches much better than it could develop on the dry, loess-covered plains. Since no real tundra belt existed either during glacial times or during the phases of optimum climate of the last two or three interglacial periods, this special type of vegetation must have evolved and been destroyed several times during the Pleistocene. Only at the very beginning of glacial periods, it seems, was tundra vegetation much more widely distributed than it is today, and even then it was interspersed with plants typical of steppe communities.

Most areas of northern Eurasia, which during glacial periods were vast steppes and gradually became covered by thick layers of loess, were covered during the interglacials by various forest communities. The plant-geographical conditions of the Cromerian and the Eemian interglacials were very similar, but differed from those of the Holsteinian, though climate must have favored the growth of thermophilous plants during the Holsteinian also. When one compares the immigration history of *Picea*, *Abies*, *Quercus*, *Ulmus*, *Tilia*, and *Carpinus* during the Holsteinian and Eemian interglacials, it becomes obvious that there were striking differences. At the very beginning of the Holsteinian interglacial, spruce, oak, elm, and linden seem to have immigrated into Eu-

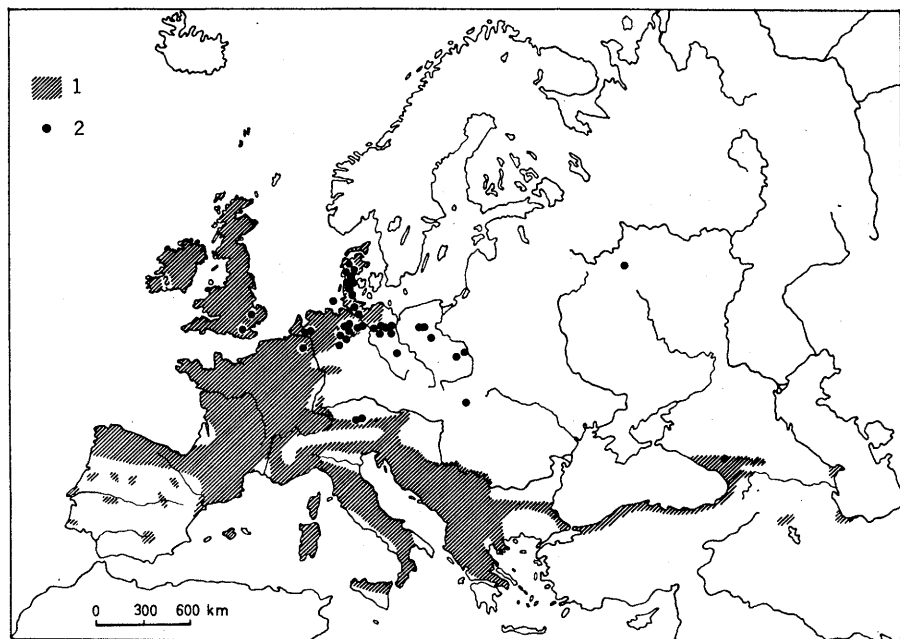


Fig. 10. Recent and past distribution of holly (*Ilex aquifolium*) in Europe. (1) Recent distribution; (2) finds in sediments of the Eemian interglacial. [From Frenzel (1 and 4)]

rope nearly simultaneously from France and from the Carpathians. The existing differences in climate (oceanic as opposed to continental) caused a preponderance of oak and elm in the more oceanic regions and a dominance of spruce to the east of the Elbe. At that time these species could spread almost uninterruptedly over the whole of Europe. Later on they were driven back

by *Carpinus* and *Abies*, presumably coming from the Carpathians.

During the Eemian interglacial, on the contrary, at first chiefly spruce spread over vast regions of Europe, coming from the hilly regions in the middle of Russia. But whereas, during the Holsteinian, *Picea abies* covered nearly all of central, western, and eastern Europe, the first spruce to spread to

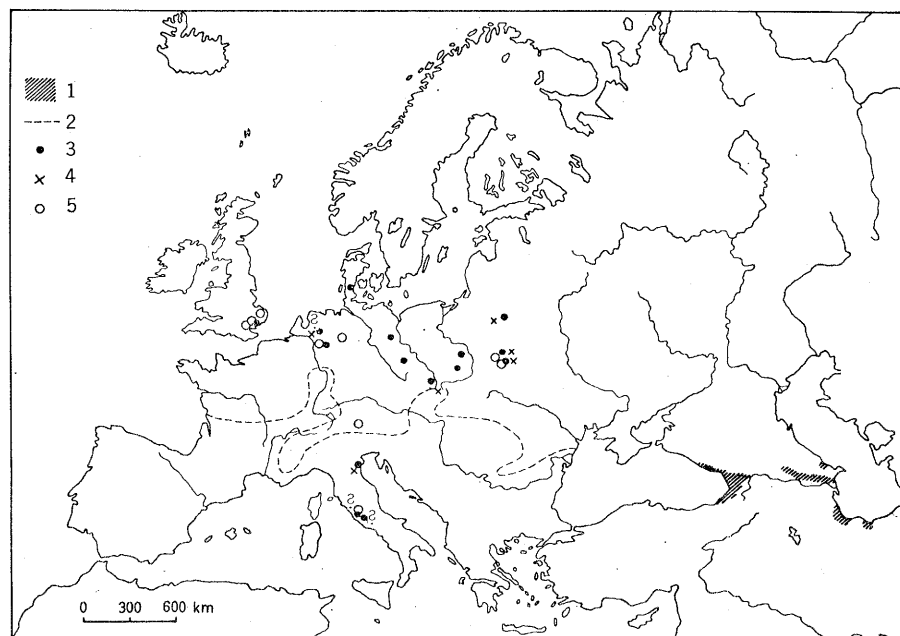


Fig. 11. Recent and Holsteinian distribution of *Pterocarya*, *Carya*, and *Vitis* in Europe. (1) Recent distribution of *Pterocarya*; (2) hypothetical northern limit of spontaneous (recent distribution of *V. silvestris*); (3) finds of *Pterocarya* in sediments of the Holsteinian interglacial; (4) finds of *Carya* in sediments of the Holsteinian interglacial; (5) finds of *V. silvestris* in sediments of the Holsteinian interglacial. [From Frenzel (1 and 4)]

central Europe during the Eemian interglacial was *P. obovata*. Later, a moderation of climate, perhaps combined with severe drought, forced *P. obovata* to retreat but enabled pine, birch, and, to a smaller extent, oak and elm to immigrate. There seem to have been no forests of *P. abies* at this time. When the climate became still warmer and moister, oak and elm and then the shade-loving *Tilia platyphyllos* covered nearly the whole of Europe. It was only at the very end of this interglacial that spruce and fir immigrated into Europe. So, divergences in climate in the early phases of the Holsteinian and Eemian interglacials produced striking differences in European plant-geography during these two periods. (There seem to have been no major differences in climate in the high-temperature phases.) The degree of protection afforded by particular sites and the possibility of reimmigration must have been governing factors in the composition and evolution of forest vegetation (1, 4).

Also of interest is the present-day distribution of various species of linden in northern Eurasia. Forests in which linden is an essential component are widespread in Europe (*Tilia platyphyllos*, *T. cordata*, *T. tomentosa*) and the Far East (*T. amurensis*). But between these areas there are no linden and other thermophilous trees, except in the northern foothills of the Altai Mountains. There *T. sibirica* thrives, together with several herbs and shrubs common in European forests of broadleaf trees (30). Until recently, the period of origin of this divided distribution of linden had not been known, but recent palynological investigations have shown that isolated groves of linden, oak, elm, and alder spread at least during the last three interglacial periods from the Far East or even from the Ural Mountains to the Altai Mountains. So, in the high-temperature phases of the interglacial periods, there must have been fragmentary connections between the broadleaf forests of Europe and of the Far East, by way of southern Siberia. This connection was destroyed during the glacial phases, but each significant moderation of climate caused these plants to migrate anew (1).

As noted above, favorable sites of growth exerted a great influence on the immigration history of interglacial forests. One of the most interesting areas of favorable sites is the Mediterranean region. During glacial periods (Figs. 4 and 5) the northern part of the Mediterranean was in general characterized

by various types of steppe vegetation, in which grasses and *Artemisia* seem to have been dominant (31). This was true not only in the last two glaciations but in much earlier ones as well (32). At these times, layers of loess were deposited in this region, so tree growth must have been restricted to isolated spots where conditions were relatively favorable, and true forests must have disappeared. In contrast, during phases of warm climate the vegetation of the Apennine and Balkan peninsulas strongly resembled those recent thermophilous and hygrophilous forest communities whose distribution is restricted to the Colchis region of Caucasia, where conditions are most favorable for growth. This region is thought to have been one of the essential sites of retreat for Tertiary plant species. The interglacial distribution of forests of warmth- and moisture-loving trees throughout the Mediterranean area [with the exception, perhaps, of the Iberian Peninsula, where forests of pine and evergreen oak seem to have prevailed during the interglacials (33)] is paralleled by the occurrence of *Hippopotamus* during the Pleistocene (Fig. 1).

Thus it appears that thermophilous and hygrophilous trees could survive—perhaps within very small areas of retreat—the cold spells of the Pleistocene in the southernmost parts of the Apennine and Balkan peninsulas. Only at the end of the Eemian, it seems, did the Colchis flora become extinct in Europe, being replaced during postglacial times by recent middle-European deciduous and southern-European evergreen vegetation. Apparently almost the same changes took place in the Colchis itself, where the warmth- and moisture-loving forest vegetation of the lowlands was repeatedly replaced during the Pleistocene by subalpine conifer forests (13, 34). This means that the typical Colchis vegetation of interglacial times often disappeared and retreated to small, strongly isolated, favorable areas, whose history is unknown.

Analogous events governed the evolution of vegetation in the Far East during the Pleistocene (3, 35). So it must be concluded that the forest vegetation of northern Eurasia was not driven to the south during the glacial periods, where it could survive the phases of unfavorable climate as a broad belt, but was almost completely destroyed and replaced by steppe. From this conclusion it follows, furthermore, that nowhere did real pluvial conditions (climates in which precipitation was higher than it is

today) exist in northern Eurasia during glacial phases. Recently it has been argued (36) that pluvial conditions existed during the very earliest glacial phases in modern steppe and desert belts of northern Eurasia, causing huge transgressions of the Caspian Sea (Figs. 4 and 5). But at least during the Weichselian these transgressions lasted for a very long time, from about the beginning of that glaciation to 25,000 years ago, and occurred synchronously with the accumulation of thick layers of loess in adjoining regions of the Ukraine and in the northern part of the Mediterranean region (4). So it seems justifiable to conclude that the glacial transgressions of the Caspian Sea were caused by local conditions of influx and decreased evaporation, not by true pluvial climates.

The facts discussed here show that the history of vegetation in northern Eurasia during the Pleistocene was one of repeated changes between (i) huge steppe areas, governed by extremely cold and dry climates, and (ii) widespread forest whose most characteristic elements, in most parts of Europe and the Far East, were warmth- and moisture-loving trees.

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## Control by Estrogen of Genetic Transcription and Translation

Binding to chromatin and stimulation of nucleolar RNA synthesis are primary events in the early estrogen action.

Terrell H. Hamilton

The physiological effects of estrogen in the mammalian uterus are mediated by increases in the synthesis of RNA and protein (1-3). By 1964 it was clear that an acceleration of synthesis of ribosomal RNA and of ribosomes was an essential feature in the initial or early action of estrogen in its characteristic target organ (4, 5). We also knew, as a result of the experiments of Segal and his co-workers (3), that growth of the estrogen-deficient uterus was induced by treatment *in utero* with RNA extracted from the organ stimulated by the hormone. However, the role of messenger RNA synthesis in this action of estrogen was and still remains uncertain (6, 7). Furthermore, it was also uncertain whether, for early estrogen action, genetic transcription was truly stimulated prior to enhancement of cytoplasmic genetic translation, as expected by the sequence hypothesized: hormone→genome→RNA→pro-

tein. Before 1964 there was no technique for separating the nuclei from the cytoplasmic fraction of the uterus. Since we knew that nearly all of the RNA in the mammalian cell was synthesized in the nucleus and transported to the cytoplasm where most of the cellular RNA resided, it was obvious that isolation of nuclei from the uterus was a prerequisite to studies of estrogen-stimulated RNA synthesis. In 1964 Widnell and Tata (8) developed an excellent technique for isolating intact and enzymically active nuclei from homogenized rat liver. In 1965 Widnell, Tata, and I (9, 10) adapted the technique for application to rat uterus, obtaining a meaningful partition of the nuclear and cytoplasmic RNA and protein in the organ. A series of investigations of the metabolism of RNA and protein *in vivo* and *in vitro* during the course of the action of estrogen in the uterus were carried out first in Tata's laboratory at the National Institute for Medical Research in London, and later in my laboratory at the University of Texas (9-16).

In this article I review the metabolism of RNA and protein in the nuclear and cytoplasmic fractions of the uterus, as a function of time after administration of exogenous 17 $\beta$ -estradiol (1,3,5-estratriene-3,17 $\beta$ -diol) to the ovariectomized adult rat. Variations in the metabolism of RNA and protein in the uterus of the normal rat, from the diestrous to estrous phase of the estrous cycle, mimic in certain particulars the variations observed during early estrogen action. The topics deal with the synthesis of RNA and protein in the nucleus, the binding *in vivo* of tritiated 17 $\beta$ -estradiol to chromatin and the latter's template activity assayed *in vitro*, the transport of RNA from nucleus to cytoplasm, the formation of polyribosomes, and the variation in the incorporation of amino acid by the polyribosomes as assayed in the cell-free system. Although the precise and primary molecular mechanisms involved in early estrogen action remain undiscovered, the broad outlines of the hormone's control of the formation and the activity of the protein-synthesizing apparatus of the organ are clear. The original theory of a genomic site for one of the primary actions of estrogen remains valid, but the inducer theory (17) for the mechanism of action of this hormone strictly according to the Jacob-Monod model for microbial enzyme induction (18) appears in need of revision.

### Metabolism of RNA and Protein

With regard to the variation in concentration of DNA, RNA, and protein, the uterus of the normal rat in estrus contains about twice the amount of RNA and six times the amount of

The author is an associate professor in the department of zoology at the University of Texas, and holds a career development award from the National Institute for General Medical Sciences, U.S. Public Health Service.