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PROBLEMS OF
THE PLEISTOCENE AND ARCTIC

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THE ORIGIN OF THE ARCTIC FLORA.

At the same time as I must apologize for that this seminar will not be as interesting and filled with facts and devoid of major fiction as those preceeding it, I would like to commence with the statement that the flora of the Arctic is the flora of the Pleistocene in those regions of the earth which were affected by the major glaciations. Also, it should be stated that although geologists usually have been able to confirm hypotheses of icefree regions in the middle of the glaciations, these have always first been coined by botanists. This is true for Greenland, it is equally true for Scandinavia and Scotland, perhaps it is only half the truth for Iceland, while although it is also true for North America, geologists are still fighting the idea here. Perhaps this scepticism is caused by the fact that the hypothesis was first advocated for our regions with greater optimism and less documentation than in other countries by Fernald, who always required ten times stronger documentation of others and usually documented his opinions very strongly. But even the best ones among us may be carried away with strong optimism, and those unnecessarily critical will then certainly try to fight the new ideas. In the case of refugia for plants during the glaciations in North America the fight is against windmills, since there is no doubt whatsoever that plants and animals have lived through the Pleistocene in areas very far ~~from~~ north ~~from~~ of the southern limits of the actual glaciations.

We are used to see on maps of the Pleistocene that glaciers did not only cover all the lands in the north but also all the ocean north of the Wyville Thompson ridge. According to these maps the glaciation in the north should have been at least as heavy as that at present in the south. We now know that this was not so. There were even people in northern Norway during the last glaciation - or perhaps even during the second last one, the Komsa culture, and while there are known only two higher plants from the Antarctica, the grass Deschampsia antarctica and the Crucifer~~ae~~ Colobanthus crassifolius, there are about 900 higher plants met with at present in the Arctic, and many of these species have certainly grown in the north throughout the Pleistocene.

Before we go any further, let us define the Arctic as the region where the climate at present is much like what it was just south of the Pleistocene glaciers. We may have some difficulty in delimiting the area by aid of such a definition, because of the fact that we do not know too much about the climate of the past except from deductions from biological and geological observations. Therefore, several more exact definitions have been created. Köppen defined the Arctic as the area north of the *10° C isotherm for the warmest month, Nordenskiöld based his delimitation on the calculations of the points where the average temperature of the warmest month is equal to 9 minus 1/10 of the average temperature of the coldest month. Some people prefer to include in the Arctic all lands north of the southern limits of permafrost patches, or even the southern limits of permafrost. For our purposes the northern limit of trees may seem appropriate, or perhaps still better we could say that the Arctic is the region characterized by tundras in the wide sense of the word. In that way we can avoid to define what we mean with a tree, since even in the tundra there may grow some trees, although they hardly form forests in the usual southern or temperate meaning of the word.

Accepting this rather arbitrary definition, our Arctic will include more land in North America than in Eurasia, since it will include a rim of Alaska and Yukon, a part west of the Hudson's Bay down to the 60° parallel, western Labrador Peninsula to about the 56° degree at Hudson's Bay to a little south of Cape Dalhousie in the east, all the arctic islands and Greenland. In Eurasia, however, it will include the few arctic islands and Iceland, and a rim of northern Scandinavia, Russia, and Siberia. As I mentioned before, this region

inside it will be

has about 900 species of higher plants, belonging to 230 genera and 65 families, but the lower plants known from the same area are roughly estimated to be about 5000 in all, rather less than more. I think it is safe to say that while there will hardly be many species added to the number of higher plants in the Siberio-European Arctic and Greenland, the floristic exploration of the Canadian Arctic is far from being completed and new entities can be expected to be discovered in the future while closer studies of the formerly named species often will result in their being divided or renamed.

There is no flora manual including the entire Arctic, although fairly ~~good~~ complete treatments are available for arctic Siberia, ~~and we are expecting~~ a modern flora by Porsild on the ~~western~~ Canadian Arctic and a still more modern flora of Greenland by Böcher and his collaborators. The Flora Arctica by Ostenfeld and Gelert succumbed died after its first part was published 55 years ago, and since Polunin did not complete his more modern arctic flora before he accepted a position in Bagdahd far away from the cold regions, his attempt will perhaps also be abortive. The regional floras are, however, rather complete so that nobody needs to have any difficulties in determining his arctic plants and discovering if they are new to science or the area in question.

Before going further, some mention should be made of fields of arctic botany other than ~~the floristic one~~. those specially considered in this paper.

I do not know if the ecology or other fields of arctic botany will be considered later in these seminars, so I think I should mention them before going further. Studies on a <u>flora</u> of a region concentrate upon the different kinds of plants inhabiting it, the studies on the <u>vegetation</u> are concerned largely with the question of relative abundance of these various kinds, while their <u>ecology</u> is their relationship to the environment in which they live. The environmental conditions in the Arctic are usually especially rigorous, so that the inhabiting species tend to be few, the individuals reduced in stature, and the ecological relationships frequently critical.

Ecological studies have come well into their own in recent years, so that we now have available numerous and widespread accounts of different arctic vegetation types. Much the same is true of plant sociology, the study of ~~[illegible]~~ the composition of the communities that collectively form vegetation. Unfortunately, none of these studies have been stressed in the Arctic so that we still know very little about such important biological aspects in arctic types as perennation and dispersal mechanisms, propagation except in obvious cases, reaction to the almost continuous summer illumination, and the maturation of fruits and seeds. Perennation has been properly studied only by one Danish botanist working in Greenland, (Sørensen, - -) where he found that many of the plants are able to continue their growth and flowering next summer if interrupted by snow. ~~[illegible]~~ And the reaction to the long days of the summer months has been studied in Greenland, Iceland, and Siberia with amazing results. Despite the cold during the night low-sun time of the day ~~[illegible]~~ day and the low heat during the days, middle of the day the plants studied were able to assimilate almost all the nightless day and formed considerably more sugars than in more southern and warmer regions, and their vitamin content was found to increase substantially. The latter was also true for cabbages cultivated in sheltered places, so the increase is probably directly affected by the continuous illumination and not by inherited factors, although these may also play a certain role. be met with.

In the regions we are used to ~~here~~ in the temperate ~~regions~~ zone the variation of vegetation types is not very obvious in any small area. In the Arctic, however, the vegetation types are very diverse almost everywhere, even where the climate is seemingly comparable, and in spite of the prevailing monotonous dwarfing. Although the youth of the plant communities and of soil ~~[illegible]~~ formation are sometimes supposed to be noticeable in these regions, studies made in Greenland and Iceland on the wood of shrubs or woody perennials from just such youthful communities seem to indicate that they are far from being young. An Ericaceous plant growing in an almost bare soil in a solifluction area in the Icelandic ~~Greenland~~ northwest ~~northeast~~ was found to be almost 500 years old! Also only a glance at the plant associations in the Arctic will be enough to show that these are often mixed and jumbled in a complicating and puzzling way. In the Arctic the "climax" concept does not fit, and perhaps is its lack of an evolutionary background nowhere more evident. Also the fact that only one or two species of grasses or sedges and a few species of mosses and lichens sometimes may cover hundreds of square ~~miles~~ kilometers in the Arctic does not make it easy to study phenomena like succession and dispersal there, and the complications of frost-heaving and solifluction, snowdrift and snowmelt phenomena, and the protection by snowcover even in very small niches all make the work of the ecologist and sociologist a very tedious one.

approaches of the floristic phytogeography

Let us then again enter the flora and forget about the vegetation of the Arctic. As I mentioned before, there are about 900 species of higher plants known to grow uncultivated in the arctic regions. Out of these about 1/3 has been introduced by man during his colonization of the Northlands, so that only about 600 species are really indigenous within this tremendously wide area. More than twice this number is met with in the Gaspé Peninsula, and four times the number is typical of the flora of the British Isles.

You should not be interpreted these words so that 600 species of higher plants could be collected all over the Arctic. ~~regions~~. Only a fraction of this number is met with ~~all over the~~ almost everywhere in the region, from north to south, east to west, in North America as well as in Eurasia. ~~Between~~ Perhaps around 200 ~~and 250~~ species are circumpolar in the rough sense of the word, but only about 200 are high-arctic and several of the others are also met with south of the Arctic, sometimes very far south. But although circumpolar, these species are not without great gaps in their areas, so that in no place can they all be gathered without extensive travelling.

Greenland is the largest country in the Arctic, and it is also better known botanically than any other part of this region. It has a little more than 450 species, though hardly more than 300 really indigenous. But if the country is divided into three equally large areas on each coast, each of these areas has only about 175 species of higher plants, irrespective if they are lying in the far north or in the far south. All the Canadian Arctic Archipelago does not have more than 330 species, of which only a few may be introduced, while in Iceland which has the most livable climate of all the Arctic, there are 540 species growing wild, but only 387 originally indigenous. In the most northern lands the species number is lower so that while in Spitzbergen there are 143 species, there are only 85 species known from Peary Land, and in Franz Joseph Land there have been collected altogether 36 species of higher plants despite of intense searches by several scientists during a period of fifty years. If the climate of these high-arctic islands were a little more amiable it would probably be a paradise to taxonomy students, who could learn the entire flora in some few hours or days for the most.

Endemics are plants restricted to more or less defined areas and not met with elsewhere. [For example, there are some species of plants known to grow only in the Gaspé Peninsula or around the estuaries of the St. Lawrence River.] It is generally accepted, though probably not ~~completely~~ always correct, that the frequency of endemism in a flora is an indication of its age, since long time isolation will affect the speciation processes stronger than does shorttime isolation. Studies in the Arctic have revealed that in any particular area, like e.g. Greenland or Iceland, (Böcher et al.; l.c.) L. & L. 1956 there are only about 4-5% endemic species, if the apomictic genera are excluded from the calculation, and from this the conclusion has been drawn that endemism is rare in the Arctic and, thus, the arctic flora must be young. This is, however, only one of many common fallacies. It is true, that in any small area in the Arctic there is only a low frequency of endemism, [which may or may not be indicative of a relatively young flora in these regions.] But if the arctic flora is taken as a whole, it is very rich in endemism since more than 75% of its species do not grow outside the arctic regions except a few ~~secondarily~~ on some high mountains a little south of these regions where they certainly are secondary. It is, therefore, evident, that although endemism has had difficulties in evolving in any small area in the [illegible] Arctic, the great majority of the species, and even genera, of the higher plants in this region have been confined to the cold north for a very long period of time.

Studies on the distribution of several plants [illegible] clearly show that a substantial number of the arctic plants has had an area considerably wider than at present ~~pr~~ sometimes before or during the Pleistocene glaciations, or at least before the [illegible] two last glaciations. Some species are known ~~at present~~ only from widely isolated localities in northernmost Scandinavia, Siberia, Alaska, and northeast Greenland, as in (to mention) one well-known example from the genus Rumex, (Love 1943) and others may ~~now~~ be represented by different varieties or subspecies in Alaska, southern Greenland, Iceland, northern and southern Scandinavia, and Russia as well as in eastern Siberia. There are species confined to northeastern Greenland and Spitzbergen in the Atlantic region and to the arctic islands north of Alaska and Siberia in ~~the~~ - should we say - the Pacific region, and several taxa are known to grow in central east- and west-Greenland separated by the present glacier, and agian in northern Scandinavia and northern Alaska. Several such examples have been investigated in great detail, especially by Scandinavian botanists working in Greenland, Spitzbergen and northernmost Scandinavia, and they have given indications as to the dispersal routes and age of some of the main elements in these floras. On basis of such studies on the present distribution of the highern plants in Greenland, Sörensen ( ) has come to the conclusion that

90% of the Greenland flora can be divided into six different groups according to their present distribution and their probable origin and age in the flora. These groups are:

I. Comparatively recent immigrants - 20%.

These are plants which have a smaller closed area in Greenland and which at the same time show an "oblique" distribution, i.e. their distribution shows different northern ~~and~~ southern limits on the east and the west coast. None of these species seems to have an isolated occurrence outside their closed areas. Sörensen divides the recent immigrants into four subdivisions, or the southeastern recent immigrants, the northeastern recent immigrants, the southwestern recent immigrants and the northwestern recent immigrants. The southeastern ~~group~~ group is ~~supposed to~~ composed of about 20 species which are supposed to have come from Iceland late in the Pleistocene and have survived the last glaciation in Greenland. Recent studies on the Icelandic flora support this suggestion very strongly, since just these and geographically related plants have been shown, by aid of paleobotanical evidence~~s~~, to have come to Iceland from Great Britain and southwestern Europe not earlier than at the end of the second last interglacial and certainly prior to the last interglacial. The northeastern group includes some few species with a restricted area in the northeast, and they are supposed to have dispersed from Spitzbergen and Siberia at much the same time as the last group came from Iceland. The southwestern group ~~have their~~ has its main distribution in southwestern Greenland and show~~s~~ a symmetrical condition to the southeastern immigrants; they are all American species unknown from Europe except Iceland, and only one grass is also met with in a few places in the Scottish mountains. And the ~~northeastern group~~ northwestern group is only met with in the Thule region or in western Peary Land, and must have come lately from the American high-arctic regions.

II. Immigrants of an oceanic warm period - 30%.

A very large group of the southern species in Greenland shows a peculiar distribution, having a southern closed area and isolated occurrences farther north. This group seems to be fairly old in the country but its area has been considerably wider sometimes in the past. They all grow on slopes, but in their northern localities they are restricted to southfacing slopes of basaltic or calcareous mountains, especially at the inner parts of the fjords. These plants may be supposed to be older in the country than the first group, but during the last interglacial or perhaps even as late as during the postglacial optimum they have dispersed farther north and then been able to stay in the most favourable places.

III. The boreal steppe plants - 10%.

These are plants entirely confined to the continental parts of Greenland, especially to dry places in the interior of the long and warm fjords. It seems apparent that these plants are relicts of a much warmer climate in Greenland, and for reasons we cannot discuss in detail it is supposed that they have survived here during the entire Pleistocene. Most of these plants are small, some of them annual, others grasses related to prairie grasses or even prairie sedges.

IV. The arctic desert plants - 5%.

These are species closely related to the last group and at least equally old in the flora, though they are distinctly arctic with a northern distribution. In addition, some of these species are also met with in dry localities in the inner parts of some southern fjords, where they prefer northern slopes, and are supposed to be relicts there from a more severe climate.

V. <u>The ancient cold plants</u> - 15%.

This group comprises a great number of circum-Greenlandic plants which are certainly very old members of the Greenland flora. This statement is inferred from the fact that besides having a continuous distribution to the north they are distinguished by having isolated occurrences to the south but then only on the highest summits where they seem to be relicts of a colder period. Especially in this group are many of the circumpolar arctic plants which outside Greenland show disjunctions in their area indicative of their high age.

VI. <u>The ubiquists</u> - 10%.

These are widely distributed Greenland plants, ~~with a southern limit~~ without a southern limit but limited to the north on both sides of the country by a fairly sharp boundary in the high-arctic regions. These species grow in many kinds of different habitats and at different exposures and are thought to be old in the country.

VII. The remainder ~~-~~ 10%, are endemic plants, halophytes, water plants, etc. which ~~have~~ are insufficiently known or may even have been introduced by the Greenland-Icelanders, who lived in Greenland from year 985 to somewhat after 1400. The~~se~~y may have been introduced either from Iceland or America, or both.

At the beginning of the botanical investigations of the Greenland flora it was regarded as a fact that all the Greenland plants must have dispersed from other countries after the end of the Pleistocene. In the 1880's, however, Warming came to the conclusion that a great part of the flora must have survived the Pleistocene in the country, and at present we know for sure that this theory is correct. There can be no doubt that the great majority of the indigenous

Greenland plants have grown close to the areas they still occupy also prior to the last glaciation, and many of them have been there also during the former glaciations. It would carry us too far to give a review of the building up of these theories or their background - this would need at least one long extra seminar - and I hope you will try to accept them without explanation. But your good arguments against them will be welcomed in the discussion.

It is now regarded as certain that the plants grouped in the III-VIth groups by Sörensen are Greenland representatives ~~ofth~~ of the old Arctic flora, while the first two groups may include rather recent immigrants also from extra-arctic regions in Europe and America. Recent in this connection means either early post-glacial or perhaps more correctly during the last or ~~second last~~ third glaciation or second or third interglacial, and more and more facts seem to point in the direction that only very few of them can be postglacial. But although many of the present species now grow in wide areas in Greenland, it is regarded as most likely that they have survived the glaciations only in a few restricted areas there. The botanical and geological evidences seem to assign the position of refuges for plants and animals to the regions in or around Peary Land in the far north, to continental areas around Scoresbysund and Myggbukta, the Disko region, and the coastal areas in southwestern Greenland, as well as to the continental shelf outside the southern parts of the country.

It does not seem unlikely that the hardiest of the Greenland plants which at present occur at the highest altitudes on nunataks, might have survived the Ice Age in Greenland, but the fact is, that a large number of the species which must have survived the glaciations there are rather tender lowland species which in no way correspond to the notion of high-arctic elements. Because of this fact, Gelting assumed that in between the glaciers there must have been sheltered and continental lowland areas which may have harboured such plants and animals. In these areas there must have been forests of birch, elder, willows, and

Has [illegible] E-W [illegible] in — flora.

mountain ash, and on the forest floor the more tender plants got the necessary protection against the cold. Some of these species are not met with in the American Arctic but seem to be of a Eurasiatic origin.

According to Gelting and Sörensen there are botanical evidences available to support the hypothesis that the more recent elements in the Greenland flora have dispersed from other regions during the ~~next last~~ third glaciation~~s~~, and these evidences are in accordance with Icelandic evidences as I mentioned before. The last glaciation was, again according to these two Danish botanists and to the geologists Wegmann and Lauge Koch, by far more heavy in Greenland than was the ~~next last one~~ third one. During the ~~next last~~ third ~~glaciation~~ Ice Age the centre of glaciation in Greenland was south of Scoresbysund in the highest massifs of the country, while the whole of northern Greenland north of a line extending almost from Scoresbysund in the east to Sukkertoppen in the west was, roughly, free of ice. Gelting, who is a firm believer in the Wegener hypothesis of continental drift as is Sörensen and many of the Greenland geologists, supposes that at the time of the ~~second last~~ third glaciation the North Atlantic was only a narrow belt between Scandinavia and Greenland, reminding perhaps of the Red Sea of the present times. The ice shield is supposed to have divided the early Pleistocene flora into a northern division, isolated north of the ice, and a southern division, whose place of survival is less essential in this connection. The former, in particular, is of interest for our present day flora of northern Greenland. A number of arctic-continental species may have had or acquired a continuous distribution area from arctic North America via North Greenland to Siberia, and as to the more hygrophytic species Gelting postulates a regular zone of crossing immediately north of the ice shield where they have profited by the nival and rather continental climate.

The northwards advance of the ice during the last and greatest glaciation in Greenland extinguished large parts of the early Pleistocene flora, but the present peculiarly discontinuous distribution of many species shows, that refuges were left in certain places.

Sörensen, who certainly is one of the very few botanists with a complete knowledge of the Greenland flora, is of the opinion, that this is the only theory, or should we rather say hypothesis, which satisfactorily explains the origin of the Greenland flora and its two main elements, separated in history and ecology: the northern old element and the younger southern element. Some of the species of the latter element are still advancing, while the high-arctic plants seem to be unable to advance southwards, at least at present, probably because they cannot survive a certain amount of summer heat and less light. The old and high-arctic element is remarkably stable all over the high-arctic regions and consists of about 200 species met with in refuges all over the now icefree area in the far north, while the younger and southern element is still changing and much more local in the real Arctic and with evident connections to southern regions even in the lowlands.

After these lengthy details which may have confused you at the same time as it may have helped you to see how little is really known about the history of the arctic flora, we may mention two other kinds of approaches which have given very similar results as the plantgeographical studies. The first of these is the study of the frequency of polyploids, the second one involves studies of the so-called life-forms.

The chromosomes are the bearers of almost all the genetical substance of the living beings, and it has been known for more than half a century that their number is constant within each species in the strict meaning of that term.

Sometimes it occurs, however, that their number increases, and when it becomes only a multiple of the previous one, differences in ploidy are said to be met with. A plant with 7 chromosomes in the sex cells, 14 in the soma cells, is said to be a diploid, that with 28 chromosomes in the soma cells is a tetraploid, one with 42 chromosomes a hexaploid, one with 56 chromosomes an octoploid, and so on, and all numbers above the diploid one are said to be polyploid.

It would carry us too far from the subject to discuss how polyploids are formed, but new polyploids have got all the essential characteristics of a new species, at the same time as their tolerances have been altered. It is known from several studies on different polyploids that their hardiness increases as compared to the diploids. Statistical investigations have clearly demonstrated that at the same time as the number of species in a flora decreases from south to north, the frequency of their polyploids increases significantly up to a certain limit. Old and relict species and genera show a higher frequency or even degree of polyploidy than do other plants, probably because the increased number of genes widens their tolerances and makes them therefore more fit for survival in climates and conditions the diploids might be unable to stand.

It has been found that in the southern and younger element in the Greenland and subarctic flora the frequency of polyploids is between 65 and 70%. This is true also for subarctic areas in Siberia, Russia, Scandinavia, Iceland, and the Canadian northlands, but small variations occur from place to place. The frequency increases successively from the about 30% of polyploids occurring in the warm temperate countries unaffected by the glaciations to the about 70% in the subarctic regions, and there are all reasons to believe that the almost linear increase in frequency indicates successive selection by the same climatic factors. The only jump observed so far - and it is observed in the eastern as well as the western parts of the Arctic - comes where the high-arctic flora replaces the subarctic and low-arctic ones. There fairly suddenly the frequency of polyploids among the higher plants changes from about 65-70% up to 80 - 85%. This latter frequency then is fairly stable and characteristic for the flora of widely separated areas with very different number of species in the high-arctic, from Peary Land and Franz Joseph Land south to Devon Island and eastern Greenland north of Scoresbysund.

Several conclusions may be drawn from this fact, but the one of interest to us in this connection is, that this jump must indicate that the high-arctic flora has been isolated from the more southern one for a considerable period of time, and that it has been produced by conditions far more severe than those prevailing at present.

The so-called life-form classes were defined by Raunkiaer on basis of the position of the hibernating buds in relation to the surface of the ground. Thus, trees more than eight meters heigh are mega- and mesophanerophytes (MM), trees and shrubs between two and eight ~~and~~ meters are microphanerophytes (M), and shrubs between 30 cm and two meters are nanophanerophytes (N). Undershrubs or herbs whose perennating buds are raised into the air but not more than 30 cm above the surface are chamaephytes (Ch). Hemicryptophytes (H) are plants whose buds are formed in the surface of the soil, geophytes (G) have deeply buried buds, while therophytes (Th) are annual plants. Studying the frequency of these and some other life forms, Raunkiaer and his students were able to classify different kinds of phytoclimates, and they could also demonstrate that certain changes occurred in the frequency of the different classes from south to north. The phanerophytes disappeared and the number of therophytes decreased. But although it ~~was~~ could be expected that the best protected geophytes and hemicryptophytes would become more dominant in the Arctic than elsewhere, this is not so. The most extreme regions of the

~~Gentiana tenella~~
Lomatogonium tenellum,
Euphrasia latifolia
Koenigia islandica.

Arctic are characterized by having a higher frequency of chamaephytes than any other parts of the world, so that 1/3 of these plants ~~are chamaephytes.~~ belong to this life-form class. Hemicryptophytes are, however, not rare, and ~~geophytes~~ about 1/10 of the high-arctic flora consists of geophytes, while only three annuals, one of them biennial, are able to grow from seed to seed during the four to five weeks of above-freezing temperatures during the summer days in the high-arctic regions.

It has a certain interest in this connection that recent investigations by Mølholm-Hansen have definitely demonstrated that the different life form classes are not equally old. The earliest life forms within the higher plants were the trees, which originated in the early Cretaceous Period. The microphanerophytes evolved mainly in the Paleocene, while the nanophanerophytes and hemicryptophytes are known first from the Eocene and Miocene. The youngest life forms are the Therophytes and Chamaephytes which developed in the last part of the Tertiary and culminated in the earliest part of the Quaternary Period. Mølholm-Hansen has been able to show that while most of the therophytes are plants of southern origin or have originated in the warmer parts of the world, the chamaephytes evolved in the Arctic, where they still predominate.

After all these details we can at last come to the conclusion as to the origin of the present flora of the Arctic regions. The real arctic element, or 200 odd plants, is the remnant of a flora, which developed in the north when the climate there was much more amiable than it became later and is at present. ~~This flora probably includes~~ Originally this flora probably included ten times higher number than at present, but after it was surprised by the ice preventing its retreat southwards it diminished slowly but certainly during the successive glaciations. During the glaciations and at the interglacials this flora had some possibilities of an east-west, or west-east movement, but although a northwards dispersal still is possible, the limited tolerances to summer temperatures and short days prevent this real arctic flora from dispersing southwards, although some few species have been able to do so during the cold periods of the Pleistocene. The more southern or subarctic-lowarctic element, however, consists mainly of species which have either come rather recently from more southern regions where they are still represented, or developed lately from the temperate floras south of the arctic regions. The real arctic plants are the same all over the arctic regions although their frequency may vary, while the subarctic-lowarctic species ~~element~~ show~~s~~ much closer relations to the floras just south of each region than ~~the~~ to species east or west of their areas ~~do to each other~~. The arctic element in Greenland is the same as the arctic element in the Siberian islands, while the subarctic element in the Siberian islands is Siberian, that in Greenland definitely American rather than Icelandic-European.

At least I would like to emphasize that the botany of the Arctic outside Greenland and Siberia is not too well known at present, although just this part of the biology may be a better basis for solving many of our problems of the ~~present~~ past and present than other sciences, because of the difficulty of the plants to move to far away places. It is pity that still the only really good arctic botanical institutions are in Russia and Denmark or even in Greenland, while splendid institutions for arctic geography and zoology are at McGill and other places in North America too. But we must hope that it is only a question of time when such investigations will also start here in a bigger scale, since the problems of American Arctic botany are more than sufficient for hundreds of students for a long period of years.

Typed December 1, 1971.

Áskell Löve:

PLANT EVOLUTION AND CONTINENTAL DRIFT

It is an old observation that a large-scale scientific advance depends primarily on finding the naturalistic explanation of some natural process or set of facts. Usually what is important is the material basis of the process; once that has been discovered, the explanation becomes evident. Of course, scientific advance depends also on the [illegible] discovery of new facts. But such discoveries of fact, however novel and exciting, are important mainly because they set people puzzling after new explanations of old processes, or on to the trail of a new and unexpected process to be explained.

Historical biogeography is no exception to this observation. Although half a century ago some of its proponents had realized discovered, that its foundations must be [illegible] connected with the processes of evolution and with explanations of the geological mechanisms, with natural selection by climatical factors at its center, it was hardly a science at all, but just a series of speculations, weighed down by superstitions as that of the stability of the oceans and the lability of the species, and leavened by a few tentatives of scientific study of distribution areas past and present. Yet today it seems to be on an almost meteoric orbit towards becoming recognized as the most central and most fundamental of all the evolutionary sciences. If we ask how this spectacular progress has been achieved, the answer is simply: through the discovery of the material basis of heredity as the foundation of the two main processes of evolution, and through the new understanding of the dependence of evolution on geological facts and their recently explained theoretical basis.

Let us for a moment pause to summarize the basic ideas of biogeography which dominated half a century ago and still are the main substance of available textbooks. The proponents of this approach had accepted the Darwinian belief in natural selection as the strongest factor in evolution and proposed that slow climatic change has been most important in the evolution of species and the principal known cause of their present distribution. It was claimed that the main lines of dispersal in later geological epochs had been radial from Holarctic centers of dispersal. It was believed that geographical changes required to explain the present distribution of land biota had not been extensive and for the most part had not affected the permanence of the oceans as defined by the continental shelf. Biogeographers believed that the theories of alternations of moist and uniform, with arid and zonal climates, were in accord with the course of evolution of land biota, when interpreted with due allowance for the probable gaps in the record. But although numerous hypothetical land bridges in temperate and tropical regions had been advocated by earlier biogeographers, their colleagues some five decades ago found these to be improbable and unnecessary to explain geographical distributions, though many such ideas still survive. On the contrary, it was frequently pointed out that the then known facts distinctly indicated a general permanance of the continental outlines during the later epochs of geological time, though usually with a proviso for probable gaps in our knowledge. Mentioning of the cytogenetical approach to the material basis of evolution was usually avoided, at the same time as the shaky background of the hypothesis of oceanic stability was tacitly bypassed.

Some change in biogeographical thinking became observable in the early 1940's, when the American Stanley Cain and the Russian Eugene Wulff hinted at the importance of evolutionary cytogenetics as one of the main pillars of scientific biogeography, though without realizing that this would inevitably lead to the replacement of the common belief in the lability of species. They also observed that the geological basis of this science must be regarded as shaky, and mentioned the possibility of continental drift, although time was apparently not yet ripe for switching from the old superstition of the permanence of the oceans.

During the past decade or so a revolution in biogeographical thinking has been emerging, from two sides. In the field of cytogenetics, it has been possible to demonstrate that the process of evolution is not single, and that whereas adaptation is a simple, fast and reversible process based on gene mutations, genetic recombination, and natural selection, it does not lead to the isolation of species, which is achieved through the distinct process of speciation. That accomplishment, however, is irreversible and slow and connected with changes in the structure or number of chromosomes. Older evolutionary speculations based on the neo-Darwinian acceptance only of the adaptation process had been a doubtful basis for biogeographical deductions of climatic changes as mirrored in biotic dispersals, whereas the new explanation based on the acceptance of the almost immutable species as contrary to the easily adapted race seemed to be more in accord with the observed biogeographical facts. This development had been anticipated by the great geneticist Goldschmidt in the early 1940's, although still almost all evolutionists prefer to ignore this important observation.

From the geological side, the change in approach has also been slow, although it has been evident to many for at least six decades that the oceans are not permanent and that the lands on the earth drift like icefloes on a lake in the spring, carrying with them the various biota of the globe. The idea of climatic variations of great sizes has been slowly replaced by the conviction of the relative permanence of climatic zones. Instead of thinking of varying climates invading the lands and affecting their biota, has come the observation of the lands floating into these zones of variable weather, and ideas of dispersal of plants into unfavorable areas have been replaced by the hypothesis that they are being forced into such zones by the drifting continents, and either have to adapt, disperse against the drift to avoid the deteriorating environment, or plainly succumb. In reality, such a fundamental reversal of basic ideas is making most textbooks and older theoretical explanations in biogeography irrelevant, at the same time as it is likely to set scientists onto the trail of innumerable new and old observations to be explained on basis of the new processes.

It is my intention to try to relate the new ideas as they pertain to plant evolution and plant dispersal, with an emphasis on the latter. The processes and tempo of evolution will, however, be mentioned in passing, though these processes and the new geological basis for evolution and dispersal can hardly be properly treated in a long textbook and still less in a short evening lecture.

Observation of possibilities of socalled continental drift were made by Francis Bacon in 1620, and I expect that somebody soon will demonstrate that the ancient Greeks also had gotten this idea, proving as the Eccliastes says, that "there is no new thing nothing new under the sun". Actually, the American geologists F. B. Taylor and H. B. Baker presented the idea in 1908 and 1911 respectively in interesting articles read by few. It was, however, the German meteorologist Alfred Wegener, later professor of meteorology and geophysics in Graz in Austria, who deserves the credit for having launched the idea so forcefully in two articles in 1912 and a small book in 1915 that it had to be taken seriously, although most geologists ignored it for two generations. There were, however, a few who understood its importance, and perhaps a decade ago time had arrived to let the theory take its place as the basic explanation of most geological phenomena on earth and, consequently, of many biological conditions as well.

Although the geophysical process of continental drift is now accepted by scientists as a reality of the past which continues into the present, most biogeographers and evolutionists still seem to prefer to base their imagination on hypotheses still current in available textbooks that refer to past and present angiosperm distribution as being the result of polar origins and southward migration, to wide polar shifts and concomitant climatic changes, to massive trans-oceanic landbridges, and to long-distance dispersal. Nevertheless, a few have already observed that what actually remains as an alternative to the old model is that continental drift must have been the major factor in dictating the present distributional patterns of angiosperms, and of other organisms whose life histories are tied to those of higher plants. Some have even begun to realize that this geological explanation not only ought to revolutionize all thinking in the fields of historical biogeography, but that it also requires that we revise almost every one of our contemporary ideas on evolutionary history.

Wegener based his ideas of continental drift mainly on the similarities between South America and Africa. Although this still is accepted by all geophysicists as a very good demonstration of what actually has happened, the theory has been greatly revised and the dating proposed by Wegener has also been corrected by aid of more sophisticated methods than were available to him. Most geophysicists seem to agree that all the present continents were once joined in a single supercontinent, Pangaea. There is a reason to believe that Pangaea remained a single, irregularly-formed landmass for a long period of time and it then was balanced and situated around the South Pole with its central part, the present Sahara, at the Pole. This assumption is based on the evidence for continental glaciation on the Tassili Plateau in eastern Algeria in the late Ordovicium about 350 million years ago, and supported by the much more conclusive evidence of the

Permo-Carboniferous glaciation. Recent discoveries of certain Triassic reptiles in Antarctica convincingly demonstrate that the continents were grouped into a single Pangaea as recently as 200 million years ago. Nobody has ventured a guess how long this equilibrium has existed, but it was disrupted about 200 million years ago, according to recent estimates by the American geophysicist Dietz, who bases his reconstructions on the new idea of global tectonics and the hypothesis of sea-floor spreading, which seems to be thoroughly supported by paleomagnetic data.

The concept of plate tectonics supposes that the outer surface of the earth has a strong lithosphere about 100 km thick as an average but probably thinner at the rift zones and thickening towards the trenches. This lithosphere is believed to be divided into a number of rigid plates that are margined by trenches, which are areas where the sialic continental crust is overriding the thinner crust of the ocean floor, ridges, where movements force the impinging continents to move away from the rifts, and megashears, which are big fractures between plates where crust is neither added nor destroyed. Plate tectonics may be envisioned as an extension of earlier concepts of sea-floor spreading in that it accepts the thesis of sea-floor spreading while adding that these giant conveyor-belts may themselves also be moving. It assumes that the crustal plates are largely interlocked on the earth's upper shell so that most motions are accomodated globally. This presumably arises because there are few plates that are rectilinear in shape and consist of an opposing rift and trench connected by opposing megashears. In general, the crustal plates appear to be interlocked into two plate systems, one of which is the Indian Ocean - Tethyan system and the other being the Atlantic - Pacific system, the first taking up northward motion and the second accomodating westward motion, with a resulting northwesterly spiral motion. Perhaps the lack of ideal plates is not too surprising, for it is impossible to subdivide the surface of a globe into spherical rectangles.

When the irregularly formed Pangaea was in an equilibrium around the South Pole, its outermost peninsulas reached northwards into the southern subtropical zone. This resulted in a well-zoned climate from temperate to tropical near the humid coasts, whereas inland a dry desert of fantastic dimensions may have predominated, centered around the coldest area on earth.

Opinion among geophysical advocates of drift differs as to whether there were formerly one universal continent of Pangaea as proposed by Baker and Wegener, or two separate continents of Laurasia (North America and Eurasia) and Gondwana (all the southern continents plus the subcontinent of India) as favored by Du Toit and several others. The Canadian geophysicist Tuzo Wilson has recently supposed that Laurasia and Gondwana were originally separate geological entities, which collided in the late Paleozoic by moving toward a common trench in an ancient North Atlantic ocean to form Pangaea and then subsequently parted once again along approximately the same geosuture with the formation of a new rift in the Triassic. The hypothesis that Gondwana and Laurasia were originally separate entities is supported by their remarkable equivalence of area, suggesting that they may have been born by differentiation from opposite hemispheres. Perhaps they originally were stable caps at each Pole, then moved for a while, united, and stabilized for a long period at the South Pole, before the movement started that is still going on? It has sometimes been suggested that the movement of continents has been a long-continued process of separation and reassembly, but other evidence is said to indicate that there was no significant scattering of the continental nuclei prior to the last and present great drift episode. Pending agreement among geophysicists, which hopefully will soon be reached, it is possible to leave the far past to their speculation, and to begin our checking of evolutionary influence of the present drift only after the last and present period of drifting commenced with the initial breakup of the South Polar Pangaea in the Triassic about 200 million years ago.

It is anybody's guess why Pangaea commenced to disintegrate into Laurasia and Gondwana and still smaller plates, and many learned speculations have been ventured during the past decade. But although even the story of this drift of the entire landmass and some differential drifting of the individual plates still is insecure in detail and too long for being exactly related here, there is no doubt that with the plates went the biota on and around their coasts. They had evolved slowly for millions of years under very stable conditions, but were now forced to react against a movement that carried them northward either into and later out of the tropical zone or over the decreasingly temperate and cold zones where inland Pangaea had been, at least sometimes at a speed of about 2 degrees latitude per million years.

Our imagination knows next to nothing about the situation of the continental mass when chemical evolution started on the earth, and all the eons of evolution of the prokaryonts remain in the dark of biological prehistory, since not even the slightest signs of such primitive life have been identified. Studies of the oldest known rocks, which are at least 3600 million years old, indicate that between roughly 3500 and 2500 million years ago some weathering processes comparable to those at present became operative. The atmosphere most likely contained abundant nitrogen, variable amounts of water which was extremely scarce over and in the inland desert, and some carbondioxid. There is no way of knowing quantitatively the precise conditions on the surface of the ancient earth, but it does seem possible, that initially at least some methane was present in the atmosphere, and some hydrogen and some ammonia were dissolved in the primitive oceans. In distribution of the temperature, total pressure, partial pressures of minor atmospheric constituents, the total land mass, and volcanic activity was not vastly different from what it is now. Probably at the time sediments were laid down in the Swaziland system of southern Africa some 3100 million years ago, and certainly by the time the

Bitter Springs sediments in Australia were formed some 1000 million years ago, physical conditions where these rocks were formed were very similar to those at present. Probably the most critical differences between the early Precambrian and the Phanerozoic environments were in atmospheric conditions. In the early Precambrian free oxygen had most likely not accumulated in the atmosphere; by the Phanerozoic the atmosphere was oxydizing.

It has been speculated that very primitive prokaryonts were formed almost 4000 million years ago, and it is reasonable to suggest that this has been in the chemical broth of some protected bays where the Pangaean continent reached the warmer parts of the world, or during one of the earlier periods of drift. These primitive biota evolved slowly under anaerobic conditions until about 2700 million years ago, when aerobic conditions developed and made possible the evolution of the bluegreen algae and aerobic bacteria. That change in the air was caused by prokaryotic photosynthesis which released oxygen into the atmosphere. Roughly 1000 million years ago the first eukaryonts were created, but not until about 600 million years ago came real but very primitive plants, animals and fungi. They lived near the perifery of the Pangaean continent and near occasional water holes and possible fjords further inland. Soon ferns, fern-allies, and seedferns developed and covered the earth with veritable forests. It is perceivable and indeed likely that Pangaea had already settled for its long rest at the southern end of the earth and that conditions were reasonably stable in the regions where life evolved up to that of the seedferns and even gymnosperms.

We can leave speculations as to the evolution of animals at this time to the zoologists, it would be unfair to steal even a part of their evolutionary dream, although animals are secondary to plants, which they eat. However, when Pangaea began to disintegrate about 200 million years ago and divided into Laurasia and Gondwana, the gymnosperms had become well developed on Gondwanaland as shown by the present distribution of the podocarps and some related groups which still constitute the majority of the gymnosperms. But no angiosperms could have been contemporary with this continental configuration, and present interrelationships of angiosperm floras seem to negate any diffusion of these highest evolved of plants throughout even Gondwanaland alone.

On the basis of much more evidence than I am able to present in a brief discussion, we may conclude that the angiosperms originated in the Triassic to Jurassic Period roughly 150 million years ago as a strictly monophyletic taxon. It probably evolved from a pteridosperm-like ancestor, most likely in the general area of the newly formed Laurasia which now extends from southeastern Asia into Malesia, which was situated just north of the then recently formed Tethys Sea but south of the Tropics. In a comparatively short time, measurable in only a few tens of millions of years, the angiosperms had extended their range northward into warm temperate Asia and southeastward into the New Guinean and eastern Australian region. After establishment and initial diversification in this area, they spread over the rest of the world's land surfaces, which were much closer to each other but otherwise not vastly different in the middle and late Cretaceous Period than they are today. Most if not all these Cretaceous or Tertiary angiosperms spread in various directions in aggregations, or floras, though some seem to have been dispersed long-distance, probably also over stepping-stone islands or land-bridges or, perhaps most likely, through the agency of now vanished tectonic plates.

It ought to be emphasized that during the early evolution of the angiosperms, the lands where they originated moved from the southern subtropical and temperate zone into the southern Tropics. It is evident that this movement has increased considerably the variation in environment and climate where these plants grew, and the combined influence of these changes and the evolutionarily very strongly stimulating general tropical conditions likely not only triggered the origin of angiosperms but also greatly affected the scale and tempo of their initial evolution.

Before expanding on the possible routes of dispersal of the primitive angiosperms from the Malayan region into all corners of the globe, it may be worth while to discuss somewhat the evolutionary processes as we know them and mention some of the putative primitive characters of angiosperms as represented in surviving families and genera. We can begin with the statement that there are known at least about 150.000 species of higher plants, although some estimates give numbers that are 200.000 species higher. In addition, ten times more species are likely to have become extinct. All this variability is the result of evolution during only about 150 million years.

Evolution is based on the processes of genetics, which at the level of the socalled gene pool, which is identical to the biological species, is a process of adaptation caused by gene mutations, which increase the basis of variability, gene recombinations, which shape the variability, and natural selection, which decides about the survival of variability. If this were all the process, evolution would have stopped at the level of the first gene pool, because the interfertility of all individuals at this level prevents the differentiation into entities closed from miscibility with other such entities. Therefore, nature has invented another mechanism, that of speciation, which isolates gene pools from each other. In the eukaryonts this is accomplished by changing the chromosomes morphologically or numerically to create new lines of evolution that are reproductively isolated from all earlier lines. Selection again helps to decimate such combinations and make them increasingly distinct, and it is also selection and extermination of intermediates which seem to be the main factor in creating new genera, new families, and new taxa at any higher levels.

The nature of the two main processes of evolution, which we call adaptation and speciation, is such, that it tells us much about the genic creation of variability of all kinds within the species, and also about the limits between species, which are based on the chromosomes and their ability or inability to pair at meiosis. But our present cytogenetical methods can only give us some indications about relationships through the number and morphology of chromosomes at levels above that of a species and genus, because beyond that no biological categories are able to cross. Therefore, botanists have invented a complicated network of hypothetical primitiveness of numerous morphological characters on basis of which they construct a system of advancing evolutionary lines. Admittedly, this is a very insecure basis for building a skyscraper of such enormous dimensions as is the system of plants and history of their development and dispersal, but it remains the best we have available. Hopefully, some day some ingenious cytogeneticist may replace this with a more truly evolutionary scheme, although we are so satisfied with the present method that we do not believe his results will be very different.

Although other hypotheses of angiosperm evolution have been proposed, most botanists familiar with this kind of work seem to agree that the most likely explanation of the origin of angiosperms is the socalled strobiloid hypothesis, which assumes that the higher plants have evolved from fern-like plants with a strobilus, or a cone-like cluster of flowers and that the primitive angiosperm flower has numerous, free perianth parts, stamens, and carpels spirally arranged on a conical or rounded receptacle. Proponents of this hypothesis have fixed on a certain cluster of extant species as retaining, to one degree or another, some of the characters of the strobiloid flower. There are, of course, other concepts of primitiveness in angiosperms, some calling upon hypotheses of polyphylesis or origin from several lines of descent, but for our purpose the monophyletic strobiloid hypothesis must suffice.

The presumably most primitive group of higher plants as far as the strobiloid hypothesis is concerned, includes less than 60 families of the perhaps 500 families of angiosperms that exist today, with about 500 genera and some 12000 species, and they are arranged into 14 orders. One character of considerable importance that is rarely mentioned in support of the primitiveness of these orders and families is the fact that they include presently a high frequency of primarily and especially secondary polyploids, a characteristic indicating a high age, because the polyploid condition has a very strong selective value.

Since I consider names merely as tools of the trade, of little consequence to basic theory, I will try to use them as sparingly as possible, especially since most of the taxa concerned are familiar only to those few botanists, who have had an opportunity to visit and work in the Pacific and Malayan regions. It can be mentioned, however, that among these taxa are familiar families as the Magnoliaceae, Annonaceae, Lauraceae, Ranunculaceae, Berberidaceae, Papaveraceae, and Nymphaeaceae, though they are not necessarily the families most significant to the present problem.

One of the characters that the adherents to the strobiloid hypothesis considers primitive is the absence of true vessels in the conducting tissue of the xylem. In earlier groups of vascular plants, such as the ferns, the fern-allies, and the gymnosperms, the conducting tissue in the xylem, with a few exceptions, is composed of tracheids only. True vessel-elements undoubtedly evolved from tracheids. If there exist any angiosperms without true vessels, they are certainly primitive in respect to their xylem. In fact, we know that more than 100 species of extant angiosperms retain such primitively vesselless wood, and they are all met with in the Pacific area and mainly in eastern Asia.

Another character that is peculiar to angiosperms, is the type of sieve tube elements in the phloem. A typical angiosperm sieve tube element is modified into sieve plates at the ends and accompanied by socalled companion cells, which occur in no other vascular plants. If there should occur angiosperms with a gymnospermous type of phloem, - that is, sieve cells with scattered sieve areas and without companion cells, - we would have to consider them primitive in this respect. Only one such family is known, composed of two species and occurring in a limited area in Queensland.

Dicotyledonous pollen demonstrates a very significant evolutionary innovation in that it is characteristically tricolpate, with three germinal apertures or some modifications of this condition. Monocolpate pollen is characteristic of the pteridosperms and of such gymnospermous groups as the Cycadales and Bennettitales, and it also occurs in some monocotyledons. The tricolpate pollen grain is not known in other seed plants; it certainly is novel to the dicotyledons, and hence we may safely infer that it denotes a derived or advanced condition. But in the dicotyledons monocolpate pollen occurs only in 25 - 30 families that may conveniently be referred to the subclass Magnoliidae, which includes mainly tropical Pacific families but also some to which belong some familiar boreal plants, as the Magnoliaceae, Piperaceae, Lauraceae, and the Nymphaeaceae. The Magnoliaceae has a truly strobiloid flower as is emphasized in all taxonomical textbooks. As a rule, the perianth-segments, stamens, and carpels are spiralled on an elongate, conical receptacle. The more significant characters that indicate primitiveness in the Magnoliaceae, however, refer to the monocolpate pollen, the unspecialized stamen, and the comparatively primitive wood. Although high chromosome numbers are an advanced character, they are also an indicator of a high age, and the Magnoliaceae are characterized by high and secondary basic numbers on which polyploidy again has been built, so that although the extant species may not be very old themselves, they derive from an ancient evolutionary line also in this respect. In distribution, the Magnoliaceae are typical of several of our primitive extant angiosperms, having a great center of diversity in eastern Asia from Japan to the Himalayas and New Guinea, and a second center, with greatly reduced morphological diversity, in eastern North America and southward into tropical America.

This discussion of primitiveness must suffice. Since most of the families exhibiting the primitive strobiloid characters occur in the present Malayan region, it is reasonable to conclude, that the first angiosperms were formed in this region at the northern and eastern coasts of the Tethys Sea when they were situated in the southern subtropical zone, and that their original diversification occurred mainly when these lands drifted northwards through the Tropics.

For those taxa of the early angiosperms that dispersed slowly and as parts of a flora, which usually evolved into comparatively advanced forms as they moved into new terrain, the following seem to have been the few major dispersal routes, before Laurasia and Gondwanaland split into smaller plates or before these plates drifted far apart:

One was on the southern coastland of Laurasia, which was the northern coasts of the Tethys Sea. It reached all the way to the western coasts of the Laurasian continent which later became the western coasts of North America, where the plants continued northwards to reach the southern shores of Alaska and the later Beringia, but for some unknown reason they were not able to cross Alaska onto the northern shore of the continent. Remnants of this southern dispersal are, for instance, met with in the London clay, in the socalled Wilcox flora in Mississippi and in the Goshen flora in Oregon, the close relationships of which becomes easily understood on basis of this explanation. Parts of this dispersal group later covered the southern and perhaps central parts of the western lands that were to become North America and western Eurasia and still other elements later developed into the very special vegetation of the Mediterranean climates on the northern shore of the Tethys from India to California when they became trapped by the dry climates of this south shore of the continent by the drift into these climates.

Another arm of dispersal went northward on the eastern Laurasian coast. Some of these elements, or perhaps rather taxa derived from them, were able to reach the northern shores of Laurasia from the eastern direction westward to what later became northern Greenland and arctic Canada and cover it with as lush a vegetation as climatical changes permitted in the warm temperate to subtropical zone in which these northcoasts then were situated.

Still another route for the early angiosperms was westward along the coasts of the Tethys and then skirting along insular chains to Madagascar and Africa. And a fourth route was southward into western and central Australia, becoming highly adapted to dry conditions, and also southward along eastern Australia and along the New Caledonia - New Zealand insular chain into the West Antarctic Archipelago and, perhaps by aid of insular stepping stones or a vanished plate, from there into South America.

In the early Eocene, the northern shores of Laurasia, which later were to form the arctic lands, had by aid of the spiral movement of the tectonic plates reached north of the tropical zone and moved into a region of slight but increasing seasonal changes. The flora that had reached these parts of the globe was still much Malayan, as shown by the clearly tropical composition of the Greenland flora in the late Cretaceous or very early Eocene, although natural selection certainly had not allowed all the original species to survive or even reach this part of the world. However, the rate of evolution of new entities by the ordinary processes of adaptation and speciation had decreased with the drift into less equable climates, and a more harsh natural selection took place and favored characteristics that had not been outstanding before. One of these was the deciduous habit of trees, which greatly favored survival even in the severest of winters, and it was accompanied by an intense fall coloring of the leaves just before they are shed. It is likely that this evolution took place in a large bay into the northern part of Laurasia which has been called Northbay, or Sinus borealis, because the oldest remnants of this deciduous flora have been collected from the coasts of this bay from the earliest parts of the Tertiary about 60 million years ago.

It is of fundamental interest to emphasize that at the end of the Cretaceous and in the early Eocene the northern shores of central Laurasia, which presently are in the arctic regions, were situated in the comfortable coastal climate around the 40th parallel. This made it possible for the deciduous flora to evolve into what we prefer to call the nemoral flora, which nowhere is more typical than in central Virginia, central Japan, and central and southeastern Europe. It is a flora of deciduous forests with some element of conifers, the famous fall coloring, and the herbs of spring and summer which nowhere else are as delightful. This nemoral flora dominated the northern landscape of these southern latitudes, as shown by numerous studies from the now northernmost of lands and especially from Spitsbergen. This flora has been termed Arcto-Tertiary because of its occurrence in the northlands during this early period, although it always has remained tender and adapted to the climates and daylengths around the 40th parallel. It seems likely that the continent has since rotated somewhat clockwise, because in Alaska there occurred at this time a somewhat different and more warmth-loving flora closer related to the Malayan flora, an indication that the dispersal westward and northward over this route never reached the northern shores. However, the geological and plant record from the northlands provides an unequivocal evidence that these lands were then actually situated near the 40th parallel, or at least 40 degrees further south than at present, and that the flora had become genetically so impoverished that its evolutionary rate had greatly diminished, except for some minor selective effects. The majority of its species had become so genetically restricted to these environments that if the land would continue to drift into other climates, the flora must either succumb or retreat southward at the same pace as the lands would move northward, in order to stay at the latitude and climate to which it had adapted.

Indeed, the northward drift continued with the speed of one to two degrees latitude per million years, as documented in the paleobotanical layers. The climate on the eastern shore of Laurasia continued to be humid and temperate, and the forming of the socalled Angaran plate in easternmost Siberia opened up a temperate waterway on the shores of which the nemoral plants could escape back east when the climate of the northern bay became too severe. On the westcoast of Laurasia, which was to become the westcoast of North America, mountains had risen and formed a climate too unfavorable for most of the nemoral plants. However, at about the same time the North Atlantic rift had progressed from both directions and created situations favorable for a southward dispersal of the nemoral plants on the westcoast of the rift down to the Scoresbysund area of Greenland, where Scotland also was situated. When the plates separated at this point, volcanism commenced and formed the northwestern part of Iceland in the Miocene about 15 - 20 million years ago which for some time remained as a bridge to central Europe. The humid and temperate climate of the south coast of this bridge was favorable for an eastward dispersal of the tender nemoral plants, at the same time as their majority got an easy passage southward on the coast west of Greenland during the gradual northward drift of the land. Paleobotanical evidence from Iceland supports this explanation, since it shows that in the Miocene the tender nemoral forests with dominating beech, maple and Fraser-fir and with the pleasant herb flora covered the coastal plains and river valleys. The inner parts of this then actively built up basalt plateau, however, seem to have been deserts of dry lava, similar to the present Craters of the Moon in Idaho.

The North Atlantic widened during Miocene and Pliocene and the lands of Eurasia and North America reached almost their present position before the Pleistocene colds set in. The nemoral plants dispersed gradually down the coast at the same pace as the lands moved northward, until they reached their present area from southern Ontario to the mountains of the Carolinas, where it again could mix with some of the species or at least genera of the flora from which it originated although these had first selected to disperse westward near the northern shores of the Tethys instead northwards and westward on the northern shores of Laurasia.

Allow me to digress briefly to consider the role of evolutionary processes in stabilizing mature floras, because the three nemoral vegetations have long puzzled phytogeographers. It is a fact well-known since Humboldt that in areas of climatical similarity, the physiognomy of the vegetation tends to become alike. Numerous attempts have been made to utilize various characteristics of vegetation and relate these to present regional, local or even microclimates, and it has often been concluded that environmental similarity can produce growth form similarity no matter what the evolutionary history of the flora in question. In addition to the intensely fall coloring deciduous forests of eastern Asia, eastern North America, and southeastern Europe, the usual examples mentioned in support of these conclusions are the woody evergreen sclerophyllous species of the mediterranean climate type in southern Australia, central Chile, South Africa, California and southern Eurasia, and the divaricate microphyllous flora of New Zealand.

Non-geneticists have frequently claimed these cases as results of socalled convergent evolution, which is a doubtful concept sometimes used to hide our inability to find an acceptable genetical solution of a less complicated kind. The mediterranean type may require an explanation of its own, since it is represented in isolated regions in both hemispheres, and the unique New Zealand flora is likely the result of isolation and selection directed by local environments of the past and no later replenishing by dispersal from elsewhere. The three nemoral floras, however, are simply three parts of populations that evolved under a strong environmental stress that restricted their genetical adaptability close to the point of no return just before geological changes made it possible for them to escape in three directions at the same pace as the lands went into other climatical zones. Their similarity is clearly genetical and not caused by their present climates except as these are identical with the Tertiary climate that selected them. They are similar not because of any convergent evolution but simply because they had become evolutionarily rigid before they dispersed towards the three areas which they presently shower each fall with the same intense fall colors in eastern Asia, eastern North America, and southeastern Europe.

When the lands of the nemoral flora floated northwards and forced the tender trees and plants to disperse south to maintain their latitude, some of the plants of the original nemoral were able to stay and adapt to the new conditions. This first happened to the conifers, which are a typical component of the nemoral and even Malayan flora, and they formed a zone north of the deciduous forests together with a number of hardy herbs. When the lands went north of the tolerance limits also of these trees, the conifer zone tapered out and was replaced by the now arctic plants, which could survive even the coldest conditions unprotected by forests, when the conifers left them alone. It is my opinion that they had preadapted earlier near the seashores or in the hills within the nemoral vegetation, some perhaps as long ago as the deciduous character of the nemoral trees themselves. Their evolution was completed in the Pliocene about 5 million years ago, save for the very severe selection by the Pleistocene glaciations, which trapped many of them in the then very much colder northlands. Before that, the arctic socalled cryophytes or cold-plants probably included about 1500 species of higher plants of mainly circumpolar distribution, but during the Pleistocene their number was drastically reduced and also their individual areas.

Mentioning a reduction in the number of biological species in areas of climatical stress brings us to the question of the rate of evolution in higher plants. Such a discussion requires the statement that a biological species must be reproductively isolated from other such species, since that sets it apart from the interfertile subspecies, which some taxonomists still prefer to furnish with a species name. The rate of the evolution of subspecific categories may be extremely high, as documented among the cultivated plants, and they can easily revert to their original condition if the non-biological factors that isolated them and affected their development disappear. Whereas the rate of evolution of the biological species is considerably lower at the same time as that kind of evolution is absolutely irreversible.

It is my opinion that only about 150.000 good biological species of higher plants are presently met with on the earth, although some estimates are considerably higher. It is my guess that ten times as many biological species have succumbed to selection during the evolution of the higher plants since it commenced 150 million years ago. That would mean that a new species has been created as an average once every century.

Naturally, the rate of evolution is considerably higher in warm than in cold regions, whereas the rate of extinction is immensely higher in areas of environmental stress. This may be the reason for the fact, that in Iceland, which during the past million or so years has enjoyed the somewhat oscillating climates on the border of the Arctic and the temperate zone, only a single polyploid species has been formed during the past half a million years, though many more have become extinct. In the Scandinavian countries with a much more moderate climate, a dozen good biological species seem to have been formed during the about 12.000 years since the last glaciation, which is a rate of one species per 1000 years.

Although human influence on evolutionary processes are mainly those of selection resulting in subspecific variations, we are aware of some good biological species which have been created thanks to man's transportation of plants to regions where they met with relatives with whom they could hybridize to form new alloploids. The best example of this kind is the grass species Spartina anglica, which was formed a century ago from sterile hybrids of the European S. maritima and the introduced American S. alterniflora in the Channel zone of western Europe. Also, at least two well-defined alloploid species of the composite genus Tragopogon have recently been formed from introduced populations in western North America. That only shows that this rate could be greatly increased by a mixture of floras composed of gradually evolved related species. Such a condition must have developed several times during the great dispersals of the past, adding considerably to the frequency of alloploids that still might be observable and useful in locating such zones or pockets, one of which is likely situated in the southeastern United States.

It is apparent that the replacement of the imaginary stability of the oceans and the assumed lability of the species with the more logical concept of the stable and conservative biological species and the theory of continental drift as the main pillars of biogeography requires that we change all of our basic concepts of dispersal and history of the floras of the world. However, the impact of this fundamental change is also considerable on the evolutionary history of many other life processes which hitherto have been explained on basis of aggressive dispersal into constant climates of immovable continents, because dispersal is apparently rarely aggressive into inferior environments. One such phenomenon which I have had ample opportunities to investigate on two continents, is that of the frequency of polyploids, which long has been known to increase with an increase in latitude and altitude. Earlier explanations assumed that this was, for the continents, caused by differential dispersability of diploids and polyploids and, for the arctic islands, the result of selection by the severe climates of the Pleistocene. Although both these explanations still may carry some grain of truth, the theory of continental drift might seem to require an explanation that discards all active dispersal into cold or otherwise stressed regions but is instead based on the selective effect on a tender flora of a climate that becomes increasingly severe when the land and its plants drift into more northern latitudes. But that is a story which we may perhaps better ponder upon at another time.

The unveiling of the story of the evolution of this planet and its biota certainly confirms the old idea of scientists as puzzle-solvers, because this is what we actually are and want to be. Science can be a dull profession when it consists solely of fact-gathering, and it gets its meaning first when the hypothetico-deductive method is employed by one who likes to speculate. We are not overly disturbed that so many of the pieces in the center of the puzzle are absent, and some of them, indeed, may always remain lost. Nevertheless we can reconstruct the shape of these pieces from what is known about the pieces next to them. As the puzzle radiates from the center, the missing pieces become fewer and fewer until at the perifery the puzzle is complete. In our present puzzle, the perifery represents the existing biota and the present-day land configurations.

In today's search for relevant questions worthy of the efforts of those, who are not prisoners of temporal expedience, the questions of evolution and continental drift should have a high priority. The present can be understood and appreciated only in terms of the past. The position of northern Laurasia a hundred million years ago may not seem important to the man on the street, but it is important to those who want to understand the present. In some degree that position is interrelated to the distribution of animals and plants, to the evolutionary trends of biota from prokaryonts to man, and ultimately also to the wisdom with which the laws of evolution are going to be managed so that life can both be conserved on earth and be successfully adjusted as a basis of humanization of man himself.

Seminar

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POLYPLOIDY AND DISTRIBUTION

Chromosome number investigations started the year 1882, when the German botanist Strasburger and the French botanist Guignard published observations which seemed to indicate that a species of plants is characterized by a single chromosome number which occurs in all its somatic cells. Twenty-five years and several hundred studies later, it was shown, by the German botanist Roth, that in the genus Rumex chromosome numbers which are multiples of a single basic number form a series from one species to another. About that time, numerous embryologists and cytologists in various parts of America had also started to count chromosomes in plants, but the center of such investigations remained in northern Europe, where the Danish geneticist Winge summarized, in 1917, the then existing knowledge concerning chromosome numbers and came to the conclusion that a comparative study of this subject would result in important contributions to systematics and phylogeny. Around that time, the German cytologist Tischler published the first review of known chromosome number, and his chromosome list was later followed by several others that made closer comparisons of groups from various regions possible. About half a decade later, the Swedish botanist Täckholm, who made a classical cytological and embryological study of the remarkably complicated genus Rosa, pointed out that the high-polyploid species of this genus are more northern in their distribution than are diploids and lower polyploids. Although that was the first and most basic observation on the relation between chromosomes and distribution, its significance was neglected until the Danish botanist Hagerup, in 1928, pointed out that in the heath family there is a distinct correlation between polyploidy and extreme climates, as demonstrated by the temperate diploid <u>Arctostaphylos diversifolia</u>, <u>Clethra arborea</u>, <u>Empetrum nigrum</u>, and <u>Kalmia latifolia</u>,as contrasted to the northern tetraploid species <u>Arctostaphylos uva-ursi</u>, <u>Clethra alnifolia</u>, <u>Empetrum hermaphroditum</u>, and <u>Kalmia glauca</u>. In 1931, Hagerup added to these observations material from other families from Timbuktu in northern Africa to Greenland in the north and stated, that in cases of intrageneric polyploidy, species "with the higher chromosome numbers are always the ones growing further north, and thus more exposed to extremes of temperature". He also pointed out that one could presume that an increase in the frequency of polyploids could be observed within the floras as a whole with an increase in the extremeness of the climate. That assumption was the beginning of considerable investigations and discussions about the geobotanical significance of polyploidy which still are going on among some groups of scientists. Until recently, considerable arguments were presented against this hypothesis, but they are calming down with the acceptance of this as a fact, whereas some of us are still discussing the possible explanation of this phenomenon of correlation of cytological and geobotanical characteristics.

The historical development of this idea has included studies in various parts of the world, some intensive and well planned, others less sophisticated, and a review of these discussions could furnish an interesting demonstration of faulty logics and strong emotions, which seem to be no less prominent among scientists than they are among poets, philosophers and politicians.

However, I will try to avoid spending too much time by relating the sequence of these observations and discussions, but instead try to tell about the results and evaluate various efforts towards their explanation.

When Hagerup proposed his hypothesis in 1931, only a handful observations on a few genera could be used in its support. It was, however, the German cytological encyclopedist Tischler who not only invented a method to test the idea but also did just that by calculating the frequency of polyploids of the cytologically known species in the European floras of Sicily, Schleswig-Holstein, and Iceland. Since his results, published in 1934, seemed to support the hypothesis very nicely, despite the limited number of observations and the simple statistics employed, numerous others followed suit. Chromosome counting has since multiplied so that at present there are more than 6000 numbers published every year from every corner of the globe. Our present knowledge of the frequency of polyploids in Europe and other areas of the northern hemisphere and also in a few areas in the southern hemisphere is summarized in the Tables which I have distributed to the audience. Let us look at them a little closer.

Even a quick look at Table A, which shows our knowledge from Atlantic Africa and Europe, clearly supports the generalization that the frequency of polyploids in any given flora increases with an increase in latitude. This will be even more convincing if the data are subjected to statistics of any kind, simple or sophisticated. Although the phenomenon is far from being as simple as it may look, evidence from various parts of the northern hemisphere and also from the southern hemisphere is clearly in support of the generalization. Without going into details, that led to this conclusion, I would like to emphasize that the frequency of polyploids in the angiosperms of the floristically rich Tropics seems to be between 20 and 25%, and it is similar in the socalled Subtropics, which also are characterized by a flora very rich in species.

In the hot and dry deserts, which are characterized by a considerably poorer flora, the frequency of polyploids increases to about 36 - 38%, but it decreases to about 34 - 35% in the again enriched floras of the Mediterranean climates. From there on, northwards as well as southwards, the gradual reduction in the species number of any given flora is followed by a gradual increase in the frequency of polyploids, up to the drastic 85 - 86% of polyploids in the cold deserts of the high-arctic regions and on Maquarie Island in the Antarctic Ocean.

If we look at the F part of the Table, which concerns mountain floras, the situation is similar though not as extreme. The difference between the lowlands and highlands is greatest when tropical mountains are compared with tropical lowlands, whereas in the high latitudes of for instance Iceland the difference is slight or insignificant. This can also be supposed to be connected with the considerable reduction in the number of species from the tropical lowlands to the highlands, and the insignificant reduction from arctic lowlands to the highlands, to mention but one parallel phenomenon.

As long as the calculations of the frequency of polyploids in various floras were based on a low number of chromosome numbers that were perhaps sometimes determined by cytologists little skilled in taxonomy or on material of doubtful origin from other areas than under study, there was some reason for concern as to the correctness of the data and the accuracy of the calculations. When Tischler did this the first time, in the middle thirties, even the Scandinavian floras were cytologically little known. However, this changed rapidly when a new generation took over after the publication of a critical chromosome list of the Scandinavian countries in 1942, so that presently about 30% of the about 160.000 good biological species of the world are cytologically known, the Scandinavian floras and some others are known more than 90%, and the flora of Iceland and of Mount Washington in New Hampshire are completely known from this point of view. To doubt the correctness of the data now is, therefore, unreasonable and indeed unwise. Since we must accept this as a geobotanical fact, our next step must be to seek an explanation which is acceptable and applicable to the entire problem.

Although proposals made earlier in order to explain away the factual observations of the increase of polyploids with an increase in latitude and altitude are only of an amusement value at present, I would like to mention a few of these, in order to help my listeners to avoid accepting such fallacies when meeting them in some of our textbooks. Since the frequency of polyploids in the monocots, especially the grasses and sedges, is significantly higher than that of the dicots, the Danish geneticist Westergaard proposed that the observed increase from south to north could be caused by the known increase in the frequency of monocots with an increase in latitude. This was swallowed by some, whereas a statistical test based on floras of areas of comparable size at different latitudes of the same longitude in Europe revealed that although the frequency of monocots increased considerably, the frequency of polyploid dicots and monocots also increased independently. So this could not be the explanation.

Another attempt to explain the observations away pointed out that vegetative reproduction or apomixis are more frequent in the northlands than in more equitable regions, and since apomixis was supposed to be connected with polyploidy, the Swedish geneticist Gustafsson and the Californian geneticist Stebbins suggested, that this could be the sole or at least main reason for the increase in the frequency of polyploids in arctic regions. When statistically tested, this hypothesis was also found to be doubtful, since vegetative reproduction actually is independent of high chromosome numbers in most genera. So it was soon agreed that even this suggestion could not explain the facts away.

Several scientists have pointed out that the composition of floras change from low to high altitudes and latitudes, and since polyploidy is not equally frequent in all families, the change in the combination of these groups could be the main cause of the increase in the frequency of polyploids. Instead of swallowing this, we decided to test it by aid of s study of the frequency of polyploids in the different families and orders occurring within the floras of four areas of comparable size in Europe, ranging from Hungary in the south, over the Danish island of Zealand and Pite Lappmark in northern Sweden to the Sassen quarter of arctic Spitsbergen. The results showed very clearly, with and without sophisticated statistical treatments, that in every family the frequency of polyploids increased with an increase in latitude, though a few families reached only 50% of polyploids in Spitsbergen and some others 100% already in Zealand. Even families which are known to include some of the most hardy species of arctic diploids showed a distinct increase in the frequency of polyploids from south to north. So even this attempt at explaining the observations away must be regarded as a mistake.

It was proposed by the Swedish geneticist Gustafsson and later widely dispersed by the American geneticist Stebbins that the high frequency of polyploids in arctic regions must be strongly influenced by the increased frequency of perennials, which these and other authors claimed to be polyploid in a higher degree than the annuals. It is true that annuals are extremely rare in arctic floras, but statistical studies on the frequency of polyploids within annual species at different latitudes in Europe revealed that also this was a fallacy, because as long as annuals are met with in these floras, their frequency of polyploids clearly increases with the latitude.

Both Gustafsson and Stebbins have emphasized very strongly that the increased frequancy of polyploids in arctic and alpine climates must first and foremost be caused by changes in the socalled biological spectrum. The biological spectrum is a phenomenon of accepted ecological and geobotanical significance which was proposed by the Danish botanist Raunkiær early this century in connection with his observation that all plants are easily classifiable into some socalled life-forms based on the adaptation of the plant to survive the unfavorable season, especially with regard to the placement of their winter buds. The percentages of these life-forms in a flora constitute its biological spectrum, which varies with certain climatical conditions and characterizes the great climatical plant formations of the world. The Raunkiær system is rather detailed, but for our purpose, which was the testing of the Gustafsson claim, we found it to be sufficient to distinguish between the life-form of the phanerophytes, or trees and bushes more than 30 cm high, chamaephytes, or undershrubs with their buds above the soil but lower than 30 cm, hemicryptophytes, which have their buds in the surface of the soil, geophytes, with deeply buried buds, hydro- and helophytes, or water plants whose perennating buds are situated under water, and therophytes or annuals, which survive the unfavorable season as seeds. I may add that forests are, naturally, dominated by phanerophytes, deserts are characterized by bushes, chamaephytes and therophytes, the grasslands are dominated by hemicryptophytes, whereas most arctic and alpine vegetation is typically composed of chamaephytes.

We selected four small and floristically well known European regions as a basis for our test of the claim by Gustafsson that the increase in the frequency of polyploids with latitude should be caused mainly by the change in the biological spectrum. These regions reached from central Czechoslovakia, with 52% polyploids, to arctic Spitsbergen, with 80% polyploids, and the number of species in these floras varied between 900 in the southernmost region and 90 in the northernmost one. By aid of various more or less sophisticated statistical treatments it could be demonstrated that the frequency of polyploids increased from south to north within everyone of the six life-form classes included in these floras, though the increase did not reach 100% in the Arctic for the chamaephytes, hemicryptophytes, and therophytes. Comparisons were also made between Spitsbergen and the more southern regions based on the assumption that only the biological spectra had changed rather than the frequency of polyploids within each of them, but the differences between expected and observed frequencies were so great that a statistical treatment was meaningless, giving a p-value of much less than 0.0001. This showed that changes in the biological spectrum are completely independent of alterations in the frequency of polyploids with an increase in latitude, although some writers still continue to repeat this fallacy 20 years after it was statistically refuted. The biological spectrum and the frequency of polyploids are apparently equally important indicators of environmental conditions of floras, though probably more past than present.

The earliest students of the frequency of polyploids in northern regions, like the Danish botanist Hagerup, the Swedish geneticist Müntzing, and the German cytologist Tischler, suggested that this high frequency might be the result of that cold shocks had produced these polyploids in situ and that they then could survive because polyploids were hardier than diploids and more resistant to wet and frozen soils. These suggestions were logical results of then available knowledge of the artificial production of polyploids and of their assumed physiological characteristics as indicated by preliminary experiments. At our present stage of knowledge, however, we realize that although cold treatments can produce meiotic disturbances that may result in polyploidy, this has happened very rarely in the Arctic, since almost all northern polyploid species have an area of distribution which indicates an age considerably beyond that of the Pleistocene colds. Actually, it would be contrary to all other knowledge of the laws of evolution if the plants reacted against adverse conditions by becoming polyploid. That they certainly do not do. Instead, natural selection forms ecotypes which through recombination of old genes get the ability to invade new areas and climb altitudes and latitudes, within the tolerance limit of the species. But since polyploid populations have wider tolerances than the diploids, as we will see later, they have a better chance to such an ecotypic adjustment to adverse conditions than do the diploids.

Physiological investigations, which still must be regarded much too few to be conclusive, seem to indicate that although natural polyploids are hardier than their diploid relatives thanks to several physiological characteristics which favor their survival under adverse conditions, experimental polyploids are not necessarily better adapted to extreme conditions until they have been selected and bred for adverse environments. Polyploidy per se does not necessarily make the plant physiologically superior in any kind of climate, though it clearly increases the variability of every physiologically important characteristics, as was demonstrated three decades ago by the Hungarian physiological geneticist Györffy but never tested again by later authors.

Some polyploids are apparently hardier than their diploid relatives, others have gained a new life-form that makes it easier for them to survive under adverse conditions, still others have changed from the annual to the perennial habit that allows them to grow more slowly in the short but intense summer of the northlands. Some become more resistant to wet soils, others change from short-day reactions to day-neutral or from day-neutral to long-day conditions so they can enjoy the nightless days of high latitudes, whereas still others become less susceptible to the short summers by becoming apomictic or by acquiring other kinds of vegetative reproduction. With other words, polyploidy affects various characteristics which all may be of a strong survival value in the cold regions of the world, be they high latitudes or high altitudes. These characteristics also seem to be of importance when high age of a plant group results in a low speciation rate and a high rate of selection pressure, since the few presently surviving pteridophytes are highly polyploid - but that is another story which we may perhaps discuss later.

This seems to complicate the explanation to the degree that might result in the claim that no single explanation could be offered for the phenomenon of the increased frequency of polyploids with an increase in latitude and altitude. Fortunately, however, there is a simple genetical explanation that is applicable to all these cases and many more. It was originally proposed by the German geneticist Melchers, who later turned molecular but remained ingenious. He pointed out, that even within the least variable polyploids which are termed autoploids, hardiness, or any other of the characteristics mentioned earlier as possibly affected by polyploidy, is at least caused by two and frequently many genes or gene pairs, even at the diploid stage. In order to simplify the example, Melchers assumed that hardiness is affected only by two pairs of genes, F and f, and H and h. The gene F increases hardiness with 1°C and is completely dominant, whereas the gene H decreases hardiness with 1°C. The original diploids with ffhh are hardy only at 0°C, plants with Ffhh survive at -1°C, those with FFhh can withstand -2°C, FFHh can take only -1°C frost, and FFHH are hardy only at 0°C. It is selfevident that near the cold limits of this diploid species, selection soon will eliminate all but the individuals hardy at -2°C, or those with the genetical constitution FFhh.

When such a population becomes polyploid, the selective adaptability of the tetraploids will be very different. In the first generation, the strict autoploid ffffhhhh and FFFFHHHH will show no difference in hardiness from their tender diploid ancestors, the tetraploid ffffHHHH individuals will be less hardy than any of the diploids (+4°C), whereas the tetraploid FFFFhhhh will be considerably hardier (-4°C). But when the population is sexually reproduced so its genes can mix at random before the environment selects from it the most favorable combinations, it can rapidly change into a group of individuals everyone of which will withstand more cold than any of its diploid ancestors. Ultimately, the polyploid population will become hardy in twice as low temperature as the most hardy diploids and be able to disperse into areas far too severe for survival of any diploid population. It is worth to notice that this demonstrates that it is utterly important to select heterozygous diploid material when breeding by aid of polyploidy, a rule that many have sinned against with catastrophic results. But that is for the plant breeders to ponder and discuss.

The same genetical explanation may be used for every other character of selective value or of importance for what we call tolerance, be it morphological or physiological, and it alone accounts effectively for every phenomenon connected with polyploidy. A theory is the more impressive the greater the simplicity of its premises, the more different kinds of things it relates, and the more extended its area of applicability. This explanation of the genetical basis of the superiority of polyploids is one of these biological theories of universal content which even count for observations that nobody ever thought could be properly understood.

The genetical theory of the superiority of polyploids certainly accounts for their hardiness and other characteristics which make it possible for them to survive under adverse conditions. But although it explains why these plants are presently able to survive in the northlands and highlands, it does not tell us much about the history of these plants or about how they were able to reach their present areas. The frequency of polyploids in a flora may, it is true, indicate the severity of the present climate, but if we compare the floras of lands of similar climatical severity on the continents and on the arctic islands, it is obvious that the latter are characterized by a considerably higher frequency of polyploids. Rather than assume that this is caused by differences in oceanity, as some colleagues have proposed, it seems more logical to postulate that this indicates that this frequency could be used also as a measure of the climatical severity of the past, since the island floras have not been replenished after they were decimated by the glaciations of the Pleistocene, as far as our present understanding goes.

It is a well-known fact that the Pleistocene glaciations wiped out all vegetation from large areas on the Eurasiatic and American continents, so they had to be revegetated from the south or from the few coastal in north refugia where near arctic forests, some hardy plants had survived. It has been suggested, mainly by the Californian geneticist Stebbins, that the gradual increase which now can be observed in the frequency of polyploids from the areas south of the ice border north to the arctic coast, should be the result of the greater dispersability of polyploids than diploids. or of the superiority of the former when invading areas newly laid bare. This hypothesis can neither be supported or refuted on basis of available evidence, though it may contain a grain of truth. Geobotanists have, however, pointed out that every species of the unglaciated temperate regions has actually had plenty of time to disperse to the northlands since the ice-cover disappeared, so the explanation of the gradual increase in the frequency of polyploids within these regions is likely to be more complex. As to the oceanic islands, however, their very high frequency of polyploids certainly is connected with the fact that this flora is the remnant of a much larger pre-Pleistocene flora, which was drastically reduced where it was trapped for survival or capitulation in icefree refugia throughout all the glaciations, without ever having had an opportunity to replenish from elsewhere except in a very limited scale.

The first students of the frequency of polyploids observed that in the Arctic as well as on high mountains this frequency was considerably higher than in more equitable regions. It was but natural to them, without our present knowledge of geobotany of the northlands, to assume that cold shocks on the meiotic divisions had caused this high frequency by creating these polyploids in situ. This is refuted by the wide and peculiar distribution of polyploids in the arctic lands, and in the North Atlantic area, for instance, only a single polyploid species, an apomictic Alchemilla, seems to have been formed since the onset of the Pleistocene. Although the frequency of polyploids is highest under extreme conditions, polyploids seem to be formed in a similarly low frequency in all climates. They are considerably more numerous in the most equitable climates, since 20% of 40.000 species of a tropical flora is 8000 polyploids, whereas 80% of 40 species of an arctic flora is only 50 polyploids.

Studies on the frequency of polyploids connected with investigations on the geobotany of the plants concerned have revealed that most species of present angiosperms are old and established taxa which have actually survived uplift and erosion of mountain chains and the drift of the continents over considerable distances of latitude and longitude. Indirect evidence indicates that when the southern rim of the Laurasian continent formed the northern shore of the Tethys Sea, the coastal mountains were covered by an alpine flora which had a relatively low frequency of polyploids, though distinctly higher than the lowland plants. Remnants of this alpine flora are presently known from the Rocky Mountains, Caucasus, and the Mediterranean, and they all are characterized by a frequency of polyploids close to 50%, so there is perhaps a reason to believe that this was the frequency within the flora already when it became stabilized long ago. The alpine floras of southern or temperate mountains with arctic relationships, however, demonstrate a frequency of polyploids between 60 and 70% wherever they have been studied in regions to which they may have dispersed during the Pleistocene glaciations where appropriate land connections were available.

On the northern shores of Laurasia, which then were situated around the 40th parallel of northern latitude in a humid and warm-temperate climate north of the northern coastal mountains, there evolved a flora which we know reasonably well so we can still estimate its frequency of polyploids to about 40%. This flora, which mistakenly has been named the arcto-tertiary flora because its fossil remnants now are known from the Arctic, was clearly adapted to a mild and coastal climate and a length of day typical of medium latitudes, though it also included numerous non-forest species of coastal rims and mountains, which were, most likely, predominantly chamaephytes. Wheh the continent split and formed the North Atlantic and drifted in a kind of a spiral northwards and westwards, most of the plants of the tender forests, which we prefer to call the nemoral vegetation rather than arcto-tertiary flora, dispersed southwards so that they could stay at the 40th parallel when the land drifted northwards, to form the present nemorals of eastern North America, eastern Asia, western Europe and western North America. Since the most constant of these nemorals, that of Asia and eastern North America, still are characterized by about 40% of polyploids and the European one a little more, there seems reason to believe that the original nemoral has been made up of about 40% polyploids.

Some of the species of the original nemoral, especially those of mountains and coastal areas, were apparently able to adjust to the gradually increasing severity of the climate when their localities drifted into the more adverse climates, and so could also the conifers which previously had been mixed with the hardwoods of the nemoral. The conifers formed the new northern boreal forest; though they themselves are diploid, they shelter a vegetation that demonstrates about 50% polyploids. Still other plants could continue to stay in their old localities when the climate became even too harsh for the hardy conifers and their communities and so formed the arctic flora. We have no reason to doubt that this first arctic flora was predominantly polyploid, though it is likely that its frequency of polyploids has later increased considerably through selection favoring the genetically more adaptable plants with high chromosome numbers when they were trapped by the certainly severe climates of the Pleistocene Arctic.

This must carry us to a conclusion, which I suppose most of my audience has already drawn. Differences in the distribution of polyploids, and then also in the frequency of polyploids in different regions and in plant groups of different age, are a function of the increased genetical variability of polyploids as compared with diploids, thus enhancing their survival ability under extreme conditions of any kind. These differences have, however, nothing to do with the rate of creation of polyploids, which may be different in different plant groups, but does not vary conceivably with climatical or other environmental conditions. The highest number of polyploids is in the Tropics where selection pressure at the level of species seems to be very low and where the frequency of polyploids is also very low, but this frequency increases with an increase in the severity of the environment and the organically with the reduction of the number of species, reaching the highest value in high latitudes and altitudes where the number of species is very low. That observation allows us to claim that the frequency of polyploids is also a function of the reduction in species number with an increase in the adversity of the habitat, or that relatively fewer polyploids than diploids are eliminated when a flora extends into more severe conditions that force a reduction in its number of species. That such a reduction takes place from lower to higher latitudes is evident to every observer. The richest floristic regions of the Tropics seem to include over 40.000 species of vascular plants, whereas the poorest lands of the Arctic and Antarctic are inhabited by 40 species or less. Similarly, the tropical African flora of about 13.000 species decreases to less than 100 taxa near the summit of Kilimandjaro.

The frequency of polyploids in any given flora does not necessarily reflect the present conditions of the severity of the climate in which it lives, but rather the adversity of the conditions in the past, when the flora was put under the most heavy stress. But the evident selective superiority of polyploids is, in whatever way we look at it, a distinct function of their increased genetical variability.

Although we tend to look upon the frequency of polyploids as a geobotanical tool, we should not forget that this is only a secondary function of the phenomenon of polyploidy. The condition itself is one of the most effective methods of the creation of reproductive isolation which is the basic characteristics of the good biological species, and as such polyploidy is an evolutionary process of utmost importance. But that is perhaps another story for discussion in another connection.

Lecture

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Speciation and the evolution of the ecosystem.

Although species and ecosystems have been on earth since long before man arrived on the scene, it is only lately that others than a few specialists have become aware of the fact that man, like every other living being, is an integral part of an important system that is called ecosystem, and that if this system is disturbed, its reactions may affect the human community itself in no less serious degree than they will hit its other components. These components are the species, which modern biologists since Lamarck and Darwin believe are the basic units of evolution, although the perhaps most important part of their evolutionary processes are intimately connected with their living and dead environment, or their ecosystem.

Ecology is the most important science concerned with the ecosystem, although evolutionary taxonomy is the main pillar on which it rests. As a matter of fact, biology started with taxonomy, and it may well be said to be as old as human thought. In a sense, taxonomy is considerably older than the mammals, because it may perhaps be regarded as having originated with reacting organisms, since even the lowest of biota respond differently to a varied environment and effectively order their own world.

It is but reasonable to expect that such an ancient and universal activity, vital to the most primitive tribes and the most advanced scientists alike, should have developed into a precise and undisputed technique. It may, therefore, be astonishing that it still is not uncommon for different students of the same material to arrive at altogether different classifications, and these may at times seem to be evaluated more by the reputation of their authors than on their approximation to reality. One of the reasons for this is probably the fact that even truly observational science has not yet reached more than a fraction of the biota of the world, and very many of those who work in the field of taxonomy are still confined to the basic ideas of pre-Darwinian thinking. Because of several seemingly unsurmountable difficulties, empirical studies still predominate with their inevitable tendency towards authoritarianism.

Taxonomists, especially those working with plants, frequently claim that species are of such a great diversity that they cannot be defined or classified on basis of the same concept. It is my feeling that this is the result of their education which, knowingly or unknowingly, frequently tends to ignore or perhaps even deny evolution at a level other than the historical; and genetically trained plant taxonomists are a rare breed.

Before proceeding further, we ought perhaps to mention some of the principal theories of biological classification. Looking over the entire field, the still widespread inability to agree upon the basis of this science seems to be caused by the fact that the many conflicting endeavors of various taxonomists are the results of an adherence to one of four basic theories of taxonomy. Three of these go back to the pre-Darwinian period while one is based on the evolutionary concept. These four theories are essentialism, nominalism, empiricism, and evolutionary (classification.)

realism

Essentialism is a philosophy which considers it the task of pure knowledge to discover the hidden nature (or form or essence) of things. When applied to organic diversity, it believes that all members of a taxon share the same essential nature; they conform to the same type. This is why essentialist ideology is also referred to as typology (which, naturally, has nothing to do with the socalled taxonomic type, which is a method of expediency in nomenclature). Classification of organic diversity consists, from the point of view of the essentialist, in assigning the variability of nature to a fixed number of basic types at various levels. Variation is considered a trivial and irrelevant phenomenon. Essentialism has a long history in philosophy and it dominated biological classification from Aristotle to Linnaeus. It still is not rare among certain groups of botanists, who seem to be unaware of the fact that this philosophy, which might have seemed defensible as long as the creationist dogma prevailed, is a strangely inappropriate concept to a modern biologist.

Nominalism is the philosophy that claims that only individuals exist in nature, or, as the American botanist Bessey put it a generation ago, all groupings and all classes are only artefacts of the human mind since universals do not exist. To a nominalist, such things as birds or flowers are not real but only names invented by man and arbitrarily attached by him to groups of individuals considered to be similar. I have the feeling that the basic fallacy of this concept is its misinterpretation of the causal affiliation between similarity and relationship. Nominalism arose in opposition to essentialism. It played a considerable role during the eighteenth century among the French opponents of Linnaeus, faded out towards the end of that century, to rise again in the presently belligerent school of socalled pheneticists, who deliberately set out to construct taxa on the basis of calculated overall similarity as fed to computers. It seems to be strongly supported through the inability of most taxonomy teachers to avoid the few and otherwise good textbooks in taxonomy of plants which have recently been published by this school, especially in England, because neutral or quite modern textbooks in the field are not available. Nominalism frequently leads to a classification close to that of the evolutionary concept, though it has a number of serious weaknesses the greatest of which is the certainly false claim that groups in nature are the product of the computer or the human mind, rather than of evolution. But it certainly is useful when applied to groups with immature classifications, like bacteria and certain lower forms of life. Though modern nominalists may perhaps misuse the computers in favor of their philosophy, this should not be regarded as negative for computer techniques, which certainly are among the very best techniques for any kind of taxonomy and scientific work and will always remain useful for modern taxonomy and museum and retrieval techniques.

Empiricism came into existence during the century between Linnaeus and Darwin, which was a period of transition. Deductive principles, whether based on essentialism or nominalism, were increasingly rejected, and taxonomists based their taxa on the totality of characters to an increasing extent. This was started by Adanson, but a strongly empirical philosophy characterized virtually all the leading taxonomists of this period. The term "natural" acquired a new meaning, signifying a classification unbiassed by a priori considerations and based on a weighing of totality of characteristics. By their uncommitted labor, the empiricists prepared the way for coming developments. If there was anything wrong with their approach, it was that they could not supply a reason for the existence of natural groups. This was, of course, precisely the deficiency that was repaired by the theory of evolution.

The theory of evolutionary classification, first proposed by Lamarck and Darwin, delimits taxa on the basis of two considerations - common ancestry and subsequent divergence. Implicit in such a system is the idea of biological relationship. With the acceptance of the theory of evolution, this implicit postulate actually becomes explicit, and the question asked by the comparative method, which is basic to nominalism and empiricism, must become similarly altered, because behind common resemblances we must reach for common ancestry. The result of this is a phylogenetic classification, or a grouping intended to express evolutionary descent and relationships, and for this classification the definition and delimitation of at least the main categories is evidently important. When the great evolutionary significance of the category of species at last had been established, the replacement of the essentialism and nominalism concepts, which in the living world had become a misconception, might seem to have become a necessity, because an evolutionary approach requires an evolutionary concept. As a matter of fact, such a concept was defined already by De Candolle in 1813, when he required as a main characteristics of a species that it should possess a reproductive barrier towards other species.

The comparative method in conjunction with the theory of evolution actually requires a new procedure which is best termed differential analysis. This seeks to clarify the major question about the causes of differences between the members of a related group and also between the related groups themselves. This, in fact, is the modern method of cytogenetics, making analyses after hybridization and studying the mechanism of cell division. It is firmly associated with studies of the interrelationships and total pattern of each system of detectable components and the history of evolutionary divergence and its causes. It goes without saying that this treatment requires an exact definition of its basic categories, since it sees in them important evolutionary steps which are repeated endlessly by all kinds of organisms. It is from this approach that we have been able to conclude not only that the category of species is a biological phenomenon of utmost significance, but also that the ability of this category to be sympatric to other related taxa of the same group without mixing coincides with the stage of evolution when a major genetical system becomes closed and loses its ability to interbreed and fuse with other such systems. It is true that good species are sometimes able to hybridize, but if they are biologically sound, then their inherent barriers are likely to disturb the processes of interbreeding so radically that they effectively prevent miscibility. It is miscibility, not crossability, which is evolutionarily important. These genetical observations have added strength to the evolutionary ideas of classification at, and especially below the generic level. As a result the idea of the species as the most important step in the evolution of barriers to genetical miscibility has been much clarified. However, by what looks like the irony of fate, at the same time the hope for a cytogenetical background for a phylogenetic system of plant classification has faded away, because even cytological observations seem to be of a secondary and insecure value above the level of genus. This means the scanty paleological evidence still remains the safest basis for general phylogenetic considerations, though to it are being added in recent years considerable genetical evidence collected through chemotaxonomical investigations. The idea of the species, on the contrary, has been transformed into what we prefer to term the biological or evolutionary species concept. It emerged gradually and has been defined and redefined by many during the past century, but its most simple and clear definition was proposed by the zoologist Mayr in 1940 when he claimed that the species is "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". The avoidance of all reference to morphological characters is significant as is the often overlooked fact that to be a different species is not a matter of difference but of distinction.

Another important discovery made by the aid of the cytogenetical approach is that races within a species - be they classified as subspecies, varieties, ecotypes, demes or something else - are genetically open population systems with at least a potential ability for effective interbreeding that will certainly remove their distinctive identity by mixing whenever they can hybridize freely. They are Mendelian populations, which may differ in as little as a single gene, though more frequently they deviate in a number of hereditary traits, either visible and thus useful to the taxonomist, or invisible and determining physiological characters that can only be studied experimentally. Studies on numerous animals and plants have revealed that the differential traits of subspecific units are connected with all kinds of genetical distinctions, like a number of single gene mutations, multiple alleles, and, perhaps most frequently, a group of genes or polygenes. The development of these subspecific or intraspecific traits has been shown to have progressed through the three basic processes of neo-Darwinian evolution: gene mutations, genetic recombination, and natural selection. This discovery may seem to explain the futility of using morphological characters as a basis for definitions of species; but when such traits have become fixed by reproductive isolation and changed or added to by further evolution, they become most useful tools in distinguishing the genetically closed gene pools of the reproductively isolated species systems.

The dynamism of the processes of subspeciation varies widely, and it is closely connected with the stability of the ecosystem to which the species belongs. Actually, very little is known about the different modes of subspecific evolution in different kinds of ecosystems, though it has been suggested that subtropical and arid ecosystems permit more selective changes at this level than do ecosystems in more stable tropical and temperate areas; but in the very unstable arctic and alpine ecosystems such changes are frequently very rapid so the same plant community in various valleys may be characterized by different varieties or formae of several species, especially when these are diploid or only occasional outbreeders, or both.

The processes of speciation have been thoroughly studied in laboratories and experiments by geneticists, as amply reviewed in classical works by Dobzhansky and Clausen. From these studies it cannot be emphasized too strongly that the population is ultimately the key to most evolutionary problems, though it has also become evident that the ecosystem itself, or the competition and balance between the species that constitute the ecosystem, is extremely important when it comes to allowing natural selection to make changes at any taxonomic level. At this level, the studies are still very incomplete, but it seems likely that concerted efforts combining the methods of cytogenetics, genecology and, above all, plant sociology and modern ecosystem approach will soon solve the riddle of the apparently almost unbelievably slow subspecific evolution of extremely rigid species of stabilized ecosystems.

According to a still generally accepted paralogism, which originated with Darwin, the same processes as cause subspecific and morphological variability also lead to speciation and the evolution of genera and families. This could mean that subspecies are incipient species, as believed by Darwin, who postulated the gradual change of one species into another by aid of additive changes of populations into geographical varieties, through major geographical races up to the species level. However, there seem to be ample reasons to believe that the genically determined processes that cause intraspecific variability do not necessarily lead to speciation, or to the reproductive isolation of the genetically closed systems we name species.

They seem rather to be a kind of a blind alley carrying the species no further than to subspecific development and increased adaptation to diverse ecological conditions within the limits of each ecosystem, though at the same time they form the paramount gene pool which determines the success of species and higher categories and of the ecosystem itself. As repeatedly pointed out be geneticists, a subspecies is an incipient species only insofar as an emergence of reproductive isolation between such genetic systems may give it a specific status, since reproductive isolation alone constitutes the effective closing of the breeding system at this level, actually or potentially. Our present knowledge does not exclude the possibility that such a barrier to reproduction could be formed by genetic changes of a similar kind and occurring parallel to those causing subspeciation, if it affects some kinds of sterility genes, though we know of no safe example indicating that such genes have accumulated into a distinct and unsurmountable reproductive isolation. In at least almost all cases so far studied there seems to be no observable correlation between the processes of subspeciation, or the genetic changes which make races and subspecies visibly and physiologically distinct, and the mechanisms which produce distinct reproductive isolation by means of hybrid sterility and inviability. It is another matter that certain of the processes of speciation, like chromosomal rearrangements that result in partial sterility, begin already within the species and may proceed parallel to the subspeciation processes and even stimulate them by aid of the formation of irreversible gene blocks.

The processes leading to reproductive isolation are the processes of speciation in the strict sense. As defined by geneticists, this term includes all those differences which prevent two populations from exchanging genes through the formation of fertile or, perhaps, partially sterile hybrids, actually or potentially. This kind of isolation ought not to be confused with isolation caused by marked differences in occurrance in space, in ecological preferences, in seasons of flowering, or in pollination mechanisms, since the latter are of a different nature and comparable to spatial or social isolation between human beings. Extensive cytogenetical research has shown that reproductive isolation is brought into being either by changes in the linear genetical arrangement within the chromosomes, or simply by changes in their number. The former process has fittingly been named gradual speciation, whereas the latter has been termed abrupt speciation. In present molecular terms, gradual speciation is caused by a rearrangement of DNA, and abrupt speciation results from an increase in DNA, whereas they are most simply explained in cytological terms as caused by chromosomal rearrangement and polyploidy respectively.

The processes of gradual speciation are complex and wear many guises, but they are always due to a variety of changes that lead to hybrid inviability, sterility and, finally, incompatibility, without affecting the chromosome number. As far as is known, they are caused by inversion, segmental interchange, and other chromosomal rearrangements which prevent or interrupt chromosome pairing in hybrids. It is apparent that these changes tend to be additive. Inversions occur within every plant and animal species so far closely studied, sometimes in considerable number, and it looks, at least in some plants, as if many of these soon will be rejected because of some kind of selective inferiority. But if they survive and show a selective neutrality or superiority, then they are slowly joined by aid of hybridization, whereas new alterations within the same chromosome add to their effect on chromosome pairing until this has reached the degree of an effective barrier to gene exchange. These changes are, naturally, irreversible at all stages. Natural selection seems to perfect the reproductive isolation of types differing in the linear arrangement of the chromosomes more quickly in sympatric populations where hybridization is frequent than in allopatric races where exchange of chromosomes is prevented by geographical isolation, probably because hybridization results in more chromosome breakage and reorganization. This perhaps indicates that though the effects of geographical isolation on the processes of subspeciation are considerable, its effects on the processes of speciation may be negligible, contrary to common belief; and that effective speciation always begins sympatrically. It goes without saying that geographical isolation, preventing gene exchange and collecting and keeping independently produced chromosomal rearrangements, must inevitably, in the long run, result in speciation, as indicated by the floras of many long isolated islands. But the speed of this kind of evolution seems to be considerably slower than often surmised, and extinction of intermediates may be more effective in producing apparent distinction than the development of the real reproductive barriers themselves.

Without going further into details of our still much too great ignorance of the development of gradual isolation in plants, we can conclude that gradual and additive chromosomal rearrangements supported by hybridization and guided by natural selection seem to form by far the most important process by which reproductive isolation is being built up in most plant groups. Taxonomists of all schools have recognized this kind of isolation by means of morphological discontinuities, which are soon created by the ordinary processes of subspeciation and extinction of intermediates, and also by the fact that taxa having reached reproductive isolation are able to occur sympatrically without mixing. Nevertheless, it ought to be emphasized that gradual speciation is a slow and erratic process with irregular manifestation; it is in great need of considerably more attention by plant biosystematists having the ingenuity, patience and facilities to design and carry out suitable experiments with appropriate material.

The other process of speciation is the abrupt and instantaneous creation of a very effective barrier to reproductive miscibility by means of changes in the number of chromosomes. This may happen by alterations in the basic number through certain kinds of segmental interchanges or by a loss of a chromosomes pair.

In the families Cyperaceae and Juncaceae and in certain lower plants and insects this can also happen by the very special and still too little understood process of agmatoploidy, in which an increase in chromosome number occurs without an increase in chromosome matter, because the chromosomes of these organisms are polycentric and can be broken into several pieces that still function. Most frequently, however, the abrupt creation of a reproductive barrier is connected with polyploidy, or the duplication of an entire chromosome set of an individual. This process is considerably less complex than gradual speciation and so it has been observed intensely and in greater detail, especially in the cultivated plants of which the majority has evolved abruptly from their wild relatives for which man has little use.

Polyploids are of different kinds, and of different ages, and they have been produced in a very low frequency in all kinds of climates since times immemorial. Since their genetical constitution makes them selectively superior to their relatives, they live longer than these, and so their number has slowly increased. It has been calculated that within the dicots there are about 30% polyploids, within the monocots about 50% and in the ferns more than 90%, and whatever the reason for the difference between the dicots and the monocots is, there can be no doubt that the high frequency of polyploid ferns is caused by that they are dying out, first the diploids, later the polyploids. The most successful of polyploids have been formed from very sterile and rare hybrids between remotely related species, whereas some are direct duplications of the chromosome number of a single and purebred individual, and the majority has evolved from only partially sterile hybrids between recently separated gradual species. But all polyploids have in common that they have become very effectively separated from their diploid relatives by aid of the strongest barrier to miscibility that we know of. To claim that a good species is characterized by a single chromosome number and that differences in chromosome number cannot occur within a well-defined species is, therefore, not a matter of dogmatism, as sometimes has been said, but of pure and unadulterated logic.

I could go into details in order to demonstrate the simplicity of the complex processes of subspeciation and speciation as explained by the theory of evolution, but this must suffice. It is true, that perhaps the majority of plant taxonomists still are more than skeptic of the importance of the theory of evolution as the basis for biological classification. But we have nothing as simple and effective to explain the endless variability of life which in every form evolves its variability at the gene pool level and then conserves the best gene combinations by aid of the reproductive barriers that characterizes the species.

This ought to have reviewed the methods with which species evolve, but these very important processes would be meaningless if the new races or species were not allowed to survive and multiply. That part of the process is intimately connected with the science of ecology, and I hope you will forgive me if I say that I feel as if I were carrying coal to Newcastle when discussing this at the University of Minnesota, because few academic institutions have contributed more deeply to the philosophy of the ecosystem.

Although ecology is one of the most important sciences of evolution, it was ignored by scientists for a long time, during which the essentialist and nominalist points of view dominated all thinking in biological classification. When it at last started less than one and one half century ago, its development was slow and erratic so we may perhaps claim it to be only slightly older than this century.

In this connection, it must necessarily be realized that the method of approach to any scientific problem is of marked importance, and will have great effects on the type of discovery made. Or, to put the matter the other way round, the method of approach is itself largely ruled by the kind of answer one anticipates; it is, actually, also a kind of a question. In addition, time and the advance of knowledge in each particular field are likely to change the question in such a way that, when one method has provided the main crop of answers that it could be expected to yield, then it is time to ask another kind of question by adopting a new approach.

This is just what has happened to the field of ecology, where the original and basic approach is inevitably descriptive, because biologists set out to describe as fully and accurately as possible the variety of ecological systems and the phenomena which they display. This approach is designed to answer the question about what are the facts. That basic phase of ecology was, inevitably, founded on the essentialism philosophy, according to which morphological characteristics are regarded as entities distinguishable by complete and equally important discontinuities and characterized by qualities of similar significance as are stones and chemicals. A good deal of ecological work still belongs to this phase of approach.

The descriptive phase is inevitably supplemented by the comparative. This first centered around the question of more advanced grouping, because we need to know what pattern an aggregate of biota has in common, and what distinct types are at various levels of characterization. This leads to various kinds of classifications and approaches, from the relatively simple studies of large communities still practiced by anglosaxon ecologists, to the sophisticated analyses made by the European and Soviet schools of plant sociologists. The result of this approach was the acceptance of the concepts of succession and climax and also of the ideas of the biome and the vegetation as a complex organism. These basic concepts and ideas were, however, vaguely conceived and their circumscription was clearly based on the nominalistic philosophy of holism, as is obvious in the works of the great Clements of America and Braun-Blanquet of Europe. Nevertheless, it was the important work based on this approach and these concepts that led to the acceptance of the theory of evolution of the ecosystem, which was first presented by the English ecologist Tansley a generation ago in an American journal and then thoroughly ignored or included in the nominalistic terminology. The philosophy of the ecosystem is based on the grouping of the complex of organisms together with the entire physical factors forming what we call the environment or the habitat factors in the widest sense, past and present. Though the organism, or the species, may claim our primary interest, when we are trying to think fundamentally, we cannot separate them from their special environment, with which they form one physical system, and although we may have discovered the processes of evolution by studying only the individual organism and its populations, they are tethered to their ecosystem and are unable to evolve except in harmony with it.

The comparative method in conjunction with the theory of evolution requires a new procedure, an approach which is best termed differential analysis. This seeks to clarify the major question about the causes of differences between members of a related system and also between the related systems themselves. This, in fact, is the modern method of making analyses by aid of historical and rock geology, pedology, climatology, meteorology and other phases of physical geography, and also by aid of evolutionary taxonomy of higher and lower plants and animals, cytogenetics, chemistry, mathematics, agronomy of all kinds, human sociology and related sciences, and numerous other methods of evolutionary studies. It is firmly associated with studies of the interrelationships and total pattern of each system of detectable components and the history of evolutionary divergence and its causes. It is from this approach that we have been able to conclude that the category of the ecosystem is the basic unit of living nature on the face of the earth. Our natural human prejudices force us to consider the organisms as the most important parts of these systems, but certainly the inorganic factors are also parts, since there could be no systems without them, and there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and inorganic. Ecosystems are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom. The entire method of science is to isolate systems mentally for the purpose of study, so that the series of isolates we make become the actual objects of our investigation, whether the isolate be a solar system, a planet, a climatic region, a community of living beings, a species, an individual organism, an organic molecule, or an atom. Actually, the systems we isolate mentally are not only included as parts of larger ones, but they also overlap, interlock, and interact with one another. The isolation is partly artificial, but it is the only possible way in which we can proceed.

Because ecology in all its phases has long been based on indifference to the evolving ecosystem and its complexities, it may seem unwise to try to change it into studies of the much wider field of the ecosystem. Whatever our philosophy, ecology and sociology will remain important methods of study of the biotic part of the ecosystems themselves. When accepting this evolutionary concept, we need to create a new and wider approach, which will allow close cooperation between all methods of importance for the understanding of the evolution and characteristics of the system. This most important of new evolutionary approaches I would like to name ecosystematics.

Since ecosystems still are studied mainly without the concerted effort they require, our knowledge of their evolution is fragmentary. It is evident, however, that the ideas of succession and climax of the biome philosophers are correct only in part, because one system changes into another through a successive invasion of new organic members during times of disturbance and changes in the inorganic components. A homeostatic ecosystem, or should we rather say a balanced or stabilized ecosystem or an ecosystem in equilibrium or climax, is extremely conservative, and it seems to be characterized by a constant number of species and a constant number of individuals of each species. If one species leaves, it will either be replaced by another, usually unrelated species, or its space will be invaded by some of the old species which then increase their own number and gradually change the balance of the system until a new homeostasis is reached. This conclusion has been arrived at from studies of birds of Californian islands and in Florida, but also from observations on plant communities in the arctic and boreal zones. It has also become evident from an almost endless number of observations of the results of disturbances through human activities of uncontrolled exploitation, the use of pesticides, and, peculiarly enough, unwise conservation based on insufficient understanding of the ecosystem to be protected.

The conservative nature of the ecosystem is perhaps most strongly indicated in the socalled nemoral vegetation, which was formed in the early Tertiary on the northern rim of the Laurasian continent when it was situated near the 40th parallel. When the continent drifted northwards and split where the North Atlantic now is, the nemoral ecosystem dispersed against the drift in order to remain at the same latitude, which at present is situated in eastern North America, eastern Asia, western Europe, and western North America. Climatical and geological conditions apparently disturbed the homeostasis of this ecosystem in Europe and, especially, western North America and allowed it to be invaded and almost erased, whereas in eastern America and eastern Asia it still is identical as to physiognomy, societies, genera, and even species and subspecies.

At the same time as the nemoral ecosystem strived to stay at the same latitude and in the same climate, a part of the old vegetation became zonated where the climatical conditions became new, thus forming the boreal conifer forests and, above all, the arctic flora, which evolved from the hardy coastal and highland components of the old nemoral, when the continent with their old habitats drifted into regions of short summers without nights. This is, however, another story which is intimately connected with the apparent necessity of rewriting every textbook in evolutionary geobotany and biogeography because of the fundamental changes in approach that are required because of the ultimate acceptance of the universal biological importance of the theory of continental drift and the evolutionary conservatism of the species and, above all, the ecosystem itself.

Man is an integral part of the ecosystem, but he is also the animal which has disturbed it most violently. Agriculture is a somewhat controlled disturbance of the ecosystem, since it requires that large parts of the soil be laid bare and recovered with plants and animals useful to man. Through other activities man has eradicated animals and plants, either intentionally, as when dangerous beasts, agricultural pests, or human diseases have been reduced or wiped out, or accidentally, as when the great auk, the mammoth, and numerous other biota have disappeared through his indirect action. We recognize the need of controlling pests and diseases by aid of various chemicals, but since this also influences the ecosystem as a whole, studies need to be made of the hazards of all controlling and conservational activities to wildlife, in the widest meaning of the word, because sometimes a bitter experience has shown that an important but thoughtless eradication has resulted in tenfold disaster before the ecosystem again could reach homeostasis.

The commonest homeostatic ecosystem consists basically of a forest, though there are regions where the establishment of forests is climatically impossible; the balanced ecosystem there is some form of scrub, grassland or tundra. An ecosystem in equilibrium always has the effect of moderating the excesses of climate. Under forest, for example, extremes of light and temperature are reduced, changes of the humidity of the atmosphere are levelled out, and the movement of air is subdued. The forest shelters the soil and the plants and animals living in it, and their survival depends upon it.

If the green mantle of vegetation is destroyed or reduced, the physical forces of the weather have nothing to resist them. They strike the earth at full power and in time destroy the structure of the soil which then crumbles and blows away. When man, even by careful farming, interferes with the homeostatic ecosystem, he is bound to lessen its effectiveness as a barrier against the severity of the weather. The extent to which he can do this without causing more harm than good to evolution depends chiefly on how severe the climate is, and the limits of his activities can be determined beforehand only through proper research, which usually is not available.

Originally, no doubt, man himself was a part of the natural ecosystem, and still human society with all its complexities is but an integral part of the ecosystem of ecosystems. Primitive man, being rather a rare specimen, had little permanent effect on his surroundings. The larger plant-eating animals are better equipped than man to live on vegetation, and man cannot compete in efficiency with meateating animals like wolves or large cats. Indeed, he was likely to find himself an occasional item on their menus. He does not breed so prolifically as many of the smaller animals, so if he was the prey of man-hunting creatures or suffered disease or exposure, his chances of being wiped out of the ecosystem were considerable. However, he was compensated for these inadequacies by his superior intelligence. He invented tools. He learnt how to harvest parts of plants which he could digest, and to help evolution in producing other edible plants. Above all, he discovered fire, which perhaps is the most significant feat in his history. So man kept alive and changed the homeostasis of the ecosystem in his favor in part by inventiveness, for by instinct alone he would have succumbed to selection. But this often involved him in new problems of his own making. Fire, for instance, is much easier to start than to put out, so that its damage to the ecosystem could be out of all proportions to its advantages. Thus, even before he had become an agriculturalist or industrialist, man played a considerable part in influencing the ecosystem, though we can only recon how great this was by archeological investigation.

When early man selected certain plants for food, for medicines, or poisons, he could well have reduced their abundance. In Africa trees used for dugout canoes have been wiped out for miles from navigable water, and in North America primitive man exterminated numerous big mammals. On the other hand, the influence of man may also favor plants and animals, which he wishes to use so he helps to thrust them into the ecosystem or change their frequency, as for instance grass for grazing his animals, or the animals themselves. The removal of trees by fire or axe favors grasses and herbs and, at least in temperate climates, the grazing which results may produce a permanent sward which will become available for a still more advanced artificial ecosystem of cultivated grain crops.

We all realize that the present has developed through an unbroken evolutionary sequence from the past; and the concentrated impact of man on the natural ecosystem has reached an unprecedented intensity because of the universal population explosion. We need greater production from the land, so we add to it more of the essential nutrients in the form of fertilizers. Weeds compete with our crops for these nutrients, so we apply weedkillers. Our crops are attacked by insects, so we spray insecticides. For each problem there is a separate, isolated answer. We act as if we were not aware that we are dealing with an ecosystem in which everything that happens has repercussions on other things. For example, we decide weeds are a bad thing and set out to eliminate them as if they were a universal enemy of mankind. But there are times and places when the vegetation we call weeds has an important and helpful role to play even on our farms. Weeds in a grassland are sought after by stock and the instinct of the animals has been shown to be sound, for the weeds contain trace elements essential for their health and ours. Weeds in an arable field may protect the soil against wind and water.

I will be the last one to require a ban on antibiotics, pesticides and insecticides because I realize their importance in controlling diseases and pests and, thus, lengthen our lives. But it is a most blatant example of irresponsibility when powerful insecticides are used to kill a whole range of living beings in order to destroy a single pest, because many insects play an important part in the production of food. In this we see how particular, ill-conceived intervention in natural processes can set off chain reactions of far reaching character in the homeostatic ecosystem. We are only partially aware of the destructive effects of these ecological ripples because research on this is left without funds when we make sport trips out into the universe as a kind of opium for the people.

Since we seem to have come to the stage of understanding rather than only acknowledging the importance of the evolution of the ecosystem, perhaps an academic question would be appropriate. We have many departments where descriptive and somewhat synthetic ecology is being performed and where plants and animals are studied from various points of view. But we have no place where we can train sincere and well prepared young graduate students in the deep and cooperative research in the most important field of evolutionary ecosystematics. This could best be done in a good and solid postgraduate department, or institute, or at least a program of ecosystematics, which ought to consist of first-class research workers in every field of importance for its united approach to all phases of the evolving ecosystem, basic as well as applied. Such a department would not only add greatly to our understanding of the laws behind the ecosystem and its evolutionary changes, but educate well-rounded ecosystematists who could become advisers to governments, industries, farmers, roadbuilders and you name them, or work as ombudsmän to help protect our ecosystem from those who ought to be its friends. Above all, the applied phase of ecosystematics could help make the science of agronomy grow into the very best possible helper of agriculture, because for those who produce our food and conserve and improve our ecosystems only the very best is good enough.

When ecosystematics has exposed the evolutionary principles behind the healthy ecosystem, time will be ripe for a universal management of it for the best of all men. It is likely that ecosystematists then will be regarded as the most important specialists for the planning of all kinds of human activities, and we will be able to prevent destruction of our resources and environment as those that we in our ignorance allow today. But it is also likely that we then will be able to make efforts to improve the ecosystem in order to ameliorate the life of man and his companions on earth so that these organic compounds of the universe do not only enjoy the best of conditions but also produce the optimal amount of all kinds of matter that will be beneficial for the ecosystem as a whole.

This will have to be the beginning of the end. I would like to emphasize that a theory is the more impressive the greater the simplicity of its premises is, the more different kinds of things it relates, and the more extended its area of applicability. Therefore, the deep impression of the modern theory of evolution. It was originally set up as an explanation of the variability of organisms, whereas now it includes most of the systems of the universe and, particularly, is the only basis on which we can successfully plan our future.

In his philosophical work on "Creative evolution", the great French philosopher Henri Bergson postulated a theory of time and duration in which the reality of life and evolution was contingent on a movement through what he called "cinematographically perceptible states of change", in which past merges with present. In his view, life is a constantly redefined process of change, evolution and metamorphosis in which each stage is drastically modified by the preceeding stage. I prefer to conclude with that explanation the full richness and complexity of which we are just beginning to understand by aid of studies of the evolving species and, above all, the evolving ecosystem of ecosystems.


The world – Atlantic –
Polar view


SEAL EDGE WITH WARM IRON.
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Continental Drift


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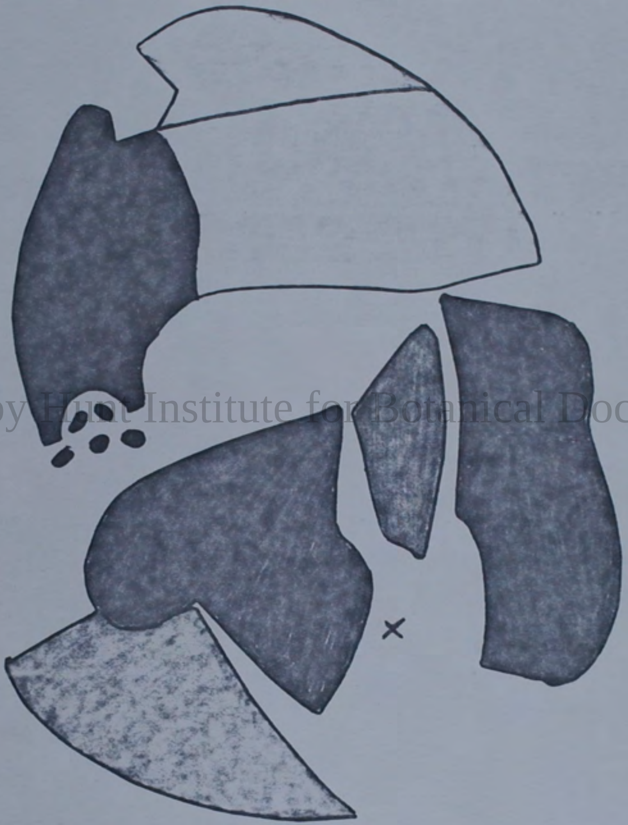
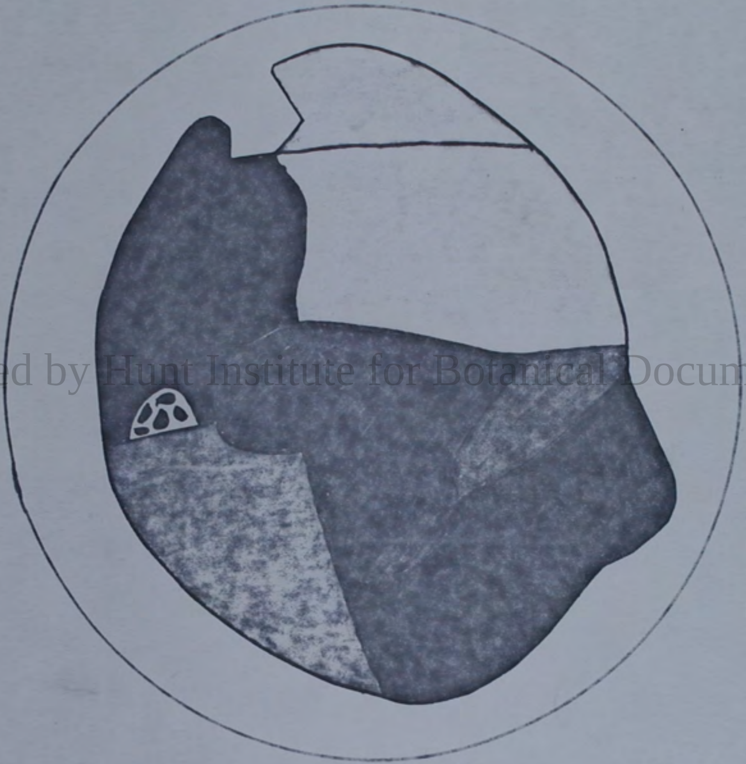


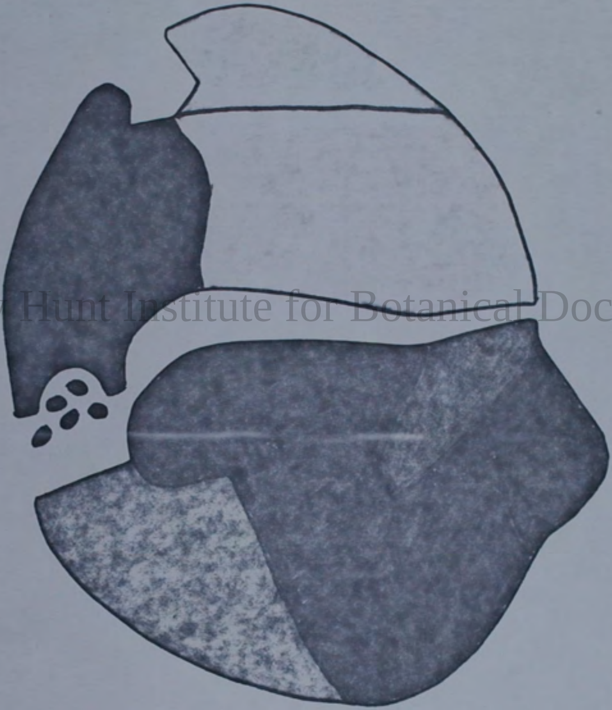
MIDDLE JURASSIC

150 MILLION YEARS AGO



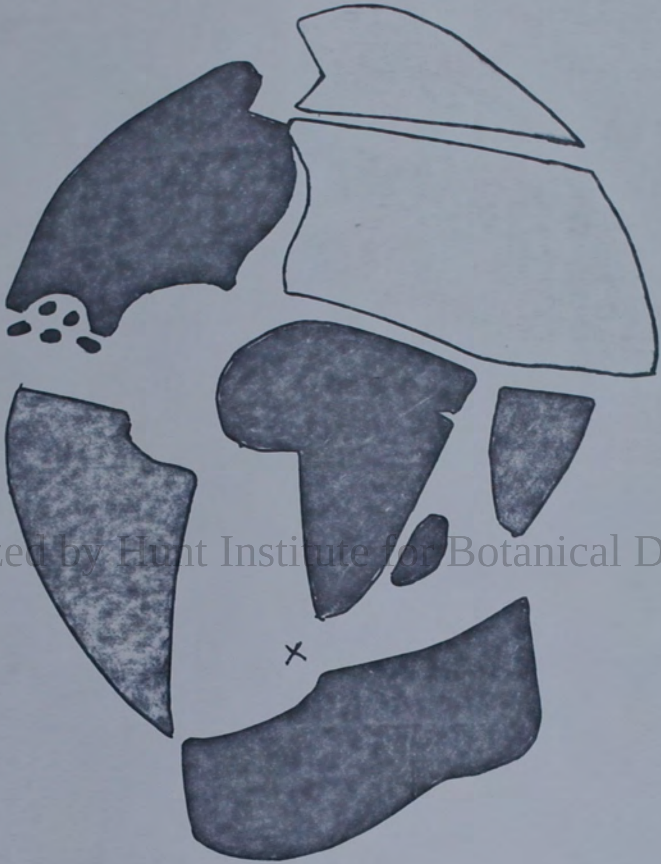
EARLY TRIASSIC

200 MILLION YEARS AGO



LATE TRIASSIC

190 MILLION YEARS AGO



EOCENE

50 MILLION YEARS AGO

MIOCENE

15 MILLION YEARS AGO