LILLOA
REVISTA DE BOTÁNICA

PLANT MIGRATIONS AND VEGETATIONAL HISTORY

OF THE SOUTHERN APPALACHIAN REGION (1)

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RESUMEN

Migraciones de plantas e Historia de la vegetación de la región Apalachiana del sur. — El autor intenta, por primera vez, una relación cronológica de las diferentes migraciones vegetales, que han dado como resultado la presente flora característica de las regiones montañosas de los Apalaches del sur. Estudia los grupos de flora y migraciones de plantas que parecen haber participado en la evolución de la flora moderna de los Apalaches del sur, y que son los siguientes :

1º La flora paleozoica antigua, compuesta principalmente de Pteridófitas y Pteridospermas, fué modificada, durante la revolución de los Apalaches, por la exterminación y evolución de formas, a la primitiva vegetación mesozoica.

2º La región de los Apalaches casi plana, fué invadida en los primeros tiempos cretácicos, por el nuevo desarrollo y esparcimiento rápido de las Angiospermas, que entonces eran tropicales en su distribución.

3º Al terminarse la era mesozoica, el levantamiento, ocasionó la migración de estas formas tropicales hacia las llanuras de la costa que recientemente habían surgido, dejando sin embargo, numerosas colonias, vestigios en los Apalaches.

4º Las montañas elevadas nuevas fueron ocupadas por los bosques arctoterciarios, que en aquel entonces eran de extensión circumboreal, pero que ahora están limitados a unas pequeñas regiones geográficamente muy separadas.

5º En la última era cenozoica, los climas que se hacían más fríos, causaron la segregación de la flora arctoterciaria originalmente homogénea, en un bosque conífero en el norte y un bosque perecedero en el sur.

(1) Contribution nº 4 from the Herbarium of West Virginia University.

6º La glaciación pleistocena causó la migración hacia las montañas del sur de muchas formas del norte.

7º El retiro del hielo, permitió la migración de los bosques de coníferas hacia el norte, reocupando su área original, pero dejando un extenso residuo en las regiones de los Apalaches del sur más altas y frías.

Observa que el trabajo individual de muchos botánicos será requerido para llenar los huecos y suplir evidencias para modificar la hipótesis aquí discutida.

The existing vegetation of an area can only be thoroughly understood from an investigation of the history of repeated migrations of successive floristic elements which have reached the region from various directions and at various times. Unfortunately, this history, rendered exceedingly complex through the disappearance of ancient and the evolution of modern forms, has left behind but few clues as to the course of its development. Nevertheless, through a careful evaluation and comparison or various kinds of evidence, it is possible to derive certain deductions which may be woven together to form a historical back ground that satisfactorily accounts for present conditions, at least in some instances.

THE LINES OF EVIDENCE

Conclusions as to pre-existing stages of vegetational distribution and migrations must, of necessity, be reached through studies that begin with present conditions and are extended backward in the reverse order from that in which the migrations occurred.

Relict colonies. — Explanations of the more recent plant movements may be sought in the study of isolated colonies of species existing far beyond the continuous range of distribution of any of them. Kearney (1) suggests that these may be either the relicts of a withdrawing flora or the vanguard of an advan-

(1) KEARNEY, *The Lower Austral Element in the Flora of the Southern Appalachian Region. Science,* ser. 2. 12 : 830-842. 1900.

cing one. As Gleason notes (1), isolated stations of a single species are of little value in this study. Nevertheless, when several or many species which grow together in one area, should also be observed together in another remote section outside the normal range, there can be offerred but one plausible explanation, that these colonies were at some time in the past connected by a nearly continuous distribution. Thus the present distribution of relict colonies may be more or les co-extensive with the past extent of the flora of which they were a part. Needless to say, the full extent is probably seldom indicated, since the relict colonies may have completely disappeared over parts of the earlier range. Climatic changes which cause the advance or retreat of one species generally have like effects upon its associates. Hence, « whole floras migrate together, the hardiest and most mobile species first, the others in their train. They establish successional series in the region which they enter, and build up new associations in the new territory. These are analogous to the associations of their original range, but differ in the absence of the slower moving species and in the presence of laggards from the retreating flora » (2).

Ancient climates. — The study of relict colonies in turn points to still earlier floras and migrations. Since the relicts of these earlier movements have been almost or completely erased, information concerning them must be sought elsewhere. An important source of additional evidence is afforded through a study of past climates as recorded in geological formations, leading to inferences as to the types of vegetation developed during the various epochs. The most striking climatic changes occurring in recent geologic times have been the succession of glacial and interglacial periods which must have left a great impress upon the nature and location of the vegetation, despite the fact that the glaciation did not actually enter the southern Appalachian region.

(1) Gleason, *The Vegetational History of the Middle West. Ann. Ass. Amer. Geog.*, 12 : 39-85. 1923.

(2) Gleason, *l. c.*, 50.

Climates of more remote ages likewise influenced had development of floras but our knowledge of such results becomes and their importance as affecting present-day vegetation reduced as progressively more ancient periods are reached.

Fossils. — In still more remote geologic periods, vegetational history may be deduced from the study of fossil plants. However, since the Appalachian region has been constantly above water since the close of the Paleozoic, the fossil record is broken off sharp with the Permian and no evidence is preserved for the long stretch of Mesozoic time. While a fairly satisfactory picture of carboniferous plant life is available, this has only a very indirect bearing upon the development of modern floras.

Other evidences. — In connection with his study of the distribution of plants and animals from a hypothetical center located in the southeastern United States, Adams (1) formulated certain criteria which he believed useful for determining the center of migration. These points, omitting n° **10**, which applies to the migration of birds, are as follows;

1. Location of the greatest differentiation of a type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms.
4. Location of maximum size of individuals.
5. Location of greatest productiveness and its relative stability.
6. Continuity and convergence of lines of dispersal.
7. Location of least dependence on a restricted habitat.
8. Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal.
9. Direction indicated by biogeographical affinities.

(1) ADAMS, *Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull.*, 3 : 115-131. 1902.

PRESENT CONDITIONS

Climate. — Present-day climatic conditions within the mid-Appalachian area are well illustrated by temperature and rainfall records for West Virginia, a State which may be regarded as in the heart of the region. Table I gives the average temperature and precipitation of the State as a whole since 1891, when official recordations were begun. Because of great variations in altitude, ranging from 272 feet at Harper's Ferry to 4860 feet above sea level on Spruce Knob, there occur significant differences in the temperature of different points. The lowest temperature recorded in the State since 1891 was 37° F., at Lewisburg in 1917. The highest in the same period was 112° F., at Moorefield in 1930 (1).

TABLE I

Average Temperature and Precipitation for West Virginia

	Temperature			Precipitation (inches)	
	Mean.	Max.	Min.	Aver.	Snow.
Jan.....	32.5	83	—34	3.63	8.1
Feb.....	33.1	86	—35	3.11	8.6
Mar.....	42.4	94	—18	3.97	5.9
Apr.....	51.7	101	— 4	3.51	1.9
May.....	61.7	105	14	3.97	T
Jun.....	69.6	109	27	4.32	—
Jul.....	73.1	112	31	4.58	—
Aug.	71.7	112	30	4.08	—
Sep.....	66.5	107	22	2.93	T
Oct.....	54.6	102	8	2.81	0.3
Nov.	43.2	88	—14	2.77	2.2
Dec.....	34.6	83	—37	3.36	6.3

(1) *United State Department of Agriculture, Climatological Data,* various volumes, especially for 1930, 1933, 1936.

Some idea of the variations of temperature between different regions of the State may be had by comparing the maxima and minima at Bayard, one of the coldest places in the State, with those at Huntington, one of the warmest. In addition, the figures for Moorefield well illustrate the great range in temperature likely to occur in a valley between high mountain ranges, where the effect of coldair drainage may be noted (Table II).

TABLE II

Maximum and Minimum Temperatures, 1930

	Bayard		Huntington		Moorefield	
	High	Low	High	Low	High	Low
Jan.....	65	— 7	72	1	80	—11
Feb.....	68	—10	80	6	81	— 4
Mar.	67	5	76	15	74	15
Apr.....	88	23	92	30	98	23
May.	88	27	92	40	96	34
Jun.....	88	27	105	42	99	29
Jul.	94	34	108	53	109	41
Aug.....	95	30	107	48	112	39
Sep.....	90	32	98	44	106	39
Oct.....	77	8	85	24	86	13
Nov.....	73	—14	78	8	74	— 1
Dec.....	50	—12	59	14	57	— 5

Nor is rainfall at all uniform over the area. It reaches its greatest amount on the western slopes of the mountains, where the high ridges intercept the rain clouds, and its lowest amount in the intermontane valleys just east of the Alleghenies. The accompanying table (Table III) gives a comparison of several stations at the western edge of the mountains with stations located just east of the Alleghenies.

Farther south the same conditions exist. Table IV shows comparative temperature records for two stations in the same latitude, Memphis being located at a low elevation in Tennessee and Highlands, North Carolina, being 3850 feet above sea level.

TABLE III

Precipitation at stations east and west of the Alleghenies

(Summary)

	Stations east of the alleghenies			Stations west of the alleghenies		
	Brandywine	Upper Tract	Moorefield	Pickens	Princeton	Holcomb
Jan.....	2.61	2.55	2.26	6.68	5.49	4.93
Feb.....	1.79	1.69	2.62	5.07	4.12	3.27
Mar.	3.74	2.54	2.58	5.68	6.32	5.17
Apr.....	3.12	2.47	2.41	5.04	5.72	4.15
May.....	3.03	3.18	3.79	5.30	5.24	4.68
Jun.....	3.37	4.19	3.94	6.11	7.18	5.00
Jul.	3.82	3.80	3.84	6.37	6.11	4.86
Aug.....	3.29	3.75	3.67	5.11	5.26	4.90
Sep.....	2.66	2.32	2.63	3.93	3.92	4.06
Oct.....	1.93	2.20	1.95	4.07	3.64	4.05
Nov.	1.31	1.53	1.84	3.85	3.57	3.15
Dec.....	1.70	2.21	2.29	5.20	4.40	3.78
Ann.....	32.37	32.43	33.82	62.51	60.97	52.00

TABLE IV

Temperature records for Memphis, Tenn., and Highlands, N. C.

(Summary)

	Memphis			Highlands		
	Mean	Highest	Lowest	Mean	Highest	Lowest
Jan.....	41.0	79	—8	34.4	65	—14
Feb.....	43.6	80	—9	35.4	67	—19
Mar.....	52.6	87	15	42.0	75	— 7
Apr.....	61.8	90	27	49.6	81	15
May.	70.4	97	40	57.9	84	26
Jun.....	78.0	100	50	64.2	87	32
Jul.	80.8	104	58	66.5	87	39
Aug.....	79.6	102	53	65.7	85	40
Sep.....	73.4	99	39	60.6	84	27
Oct.....	63.0	92	28	52.3	79	15
Nov.....	51.6	82	16	42.5	72	3
Dec.....	43.0	76	2	35.1	69	—10

Precipitation records may be compared in a similar manner. Highlands, on the western slopes of the southern Blue Ridge, has an annual rainfall double that of Asheville, North Carolina. in the valley between the Great Smoky Mountains and the Blue Ridge, as shown in Table V.

TABLE V

Precipitation Records at Highlands and Asheville, N. C.

(Summary)

	Highlands Mean	Asheville Mean		Highlands Mean	Asheville Mean
Jan.....	6.77	2.60	Aug.	7.57	4.59
Feb.....	7.91	2.63	Sep.....	5.94	2.99
Mar.	8.03	3.64	Oct.....	6.34	3.04
Apr.....	6.70	3.09	Nov.	5.20	1.72
May.....	4.88	3.48	Dec.....	7.91	3.09
Jun.....	7.22	4.29	Ann.....	82.75	39.86
Jul.	8.28	4.70			

Plants formations. — Before the coming of the white man, the area was almost entirely covered by forests, consisting principally of deciduous trees, but also including an extensive belt of evergreens along the high ridges of the Alleghenies. Classified according to the Life Zones of Merriam (1), the principal species belong to the Upper Austral, Alleghenian, and Canadian Zones, with a sprinkling of species from the Lower Austral and the Hudsonian, in the lower and higher elevations, respectively.

The conspicuous species of the deciduous forests are mainly trees of the Upper Austral and Alleghenian Zones. Along the river valleys the principal species are *Populus deltoides, Betula nigra, Castanea pumila, Ulmus americana, U. fulva, Celtis occidentalis, Morus rubra, Sassafras officinale, Liquidambar Styraciflua, Platanus occidentalis, Cercis canadensis, Tilia heterophyl-*

(1) MERRIAM, *Life Zones and Crop Zones of the United State, Bull.* 10, U. S. D. A. 1898.

la, Nyssa sylvatica, Oxydendrum arboreum, Diospyros virginiana, Fraxinus americana, F. pennsylvanica and a great array of herbaceous species. On drier uplands with poorer soils, the dominants include such Alleghenian types as *Hicoria ovata, H. glabra, Castanea dentata, Quercus alba* and *Q. montana.* On richer uplands the principal woody species are *Juglans nigra, Fagus grandifolia, Magnolia acuminata, M. Fraseri, Liriodendron Tulipifera, Hamamelis virginiana, Acer saccharum* and *Rhododendron maximum* (1).

At higher elevations, the cold, wind- swept ridges of the Appalachians are clothed by the coniferous forests characteristic of the Canadian Life Zone. Woody members of the Canadian forest found in the southern Appalachian region include *Tsuga canadensis, Pinus resinosa, Picea rubra, Abies balsamea, Betula lutea, Amelanchier oligocarpa, Pyrus americana, Prunus pennsylvanica, Acer spicatum, A. pennsylvanicum, Viburnum alnifolium* and *Sambucus racemosa.* On the forest floor may be found such herbaceous plants as *Clintonia borealis, Streptopus roseus, Maianthemum canadense, Trillium undulatum, Chrysosplenium americanum, Oxalis acetosella, Cornus canadensis, Chiogenes hispidula,* and *Linnaea americana.* On exposed summits there may even be found such Hudsonian types as *Betula papyrifera, Ribes prostratum, Rubus strigosus, Potentilla tridentata* and *Aralia hispida* (2).

PLANT MIGRATIONS

The region of the Appalachian highlands has been constantly above water since the close of the Permian, and the southern half lies wholly outside the limits of the Pleistocene glaciation. Hence the present flora is the result of plant migrations that have been going on for an enormously long period of time.

(1) See HARLOW *Textbook of Dendrology,* 1937.

(2) See MILLSPAUGH, *The Living Flora of West Virginia. W. Va. Geol. Surv.* V (A). 1913 ; also, STRAUSBAUGH AND CORE, *Some Additions to the Millspaugh check-list of West Virginia Spermatophytes. Proc. W. Va. Acad. Sci.,* 4 : 38-48. 1930.

Paleozoic floras. — The Pennsylvanian and Permian floras were extraordinarily rich in species of Pteridophytes and Pteridosperms. This flora can be partly reconstructed from the fossils of those ages but its migrations are unknown. It is estimated that more than 3,000 species have been described, most of which « are conpicuous for their almost world-wide distribution and their luxuriance and abundance, along with a dense and varied undergrowth ». The most characteristic representatives, both in number and size, were species of *Lepidodendron* and *Sigillaria*, some of which grew to over 100 feet in height. Another remarkable group, composed of species of *Calamites* and related genera, resembled superficially the cane-brakes and bamboo thickets of today. There were many true ferns *(Alethopteris, Pseudopecopteris,* and others), as well as many other fern-like plants which bore seeds *(Sphenopteris, Archaeopteris, Aneimites,* etc.). An absence of growth rings indicated also an absence of seasons until towards the close of the Pennsylvanian. The climax forests were developed mainly in low-lying, swampy ground and their partially decayed remains constitute the source of the world's most valuable coal beds (1).

The Coming of the Angiosperms. — At the close of the Permian, the Appalachian Revolution, culminating in the elevation of the Appalachian Mountains, produced conditions extremely unfavorable to the ancient march-loving flora and resulted in the extinction of innumerable types (2). During the long ages of Triassic and Jurassic times, the region was again base-leveled and the Coastal Plain, as known today, entirely submerged. Into this peneplained region came the advance hosts of the newly evolved Angiosperms, representatives of prevailingly tropical groups ranging far to the north as a responce to the mild climate of the time. These plants belonged to families, tribes, genera and sections today « shared by the Americas with tropical and subtropical Africa, tropical and subtropical

(1) Pirsson & Schuchert, *A Textbook of Geology.* Part II. *Historical Geology.*, p. 373-388. 1924.

(2) Pirsson & Schuchert, *l. c.*, p. 426, 427.

Asia, and Australia but for the most part unknown in temperate Europe and largely unrepresented in temperate Asia », including such genera as *Xyris, Eriocaulon, Hypoxis, Drosera, Galactia, Pontederia, Lygodium, Schizaea, Stenophyllus* and *Podostemon.* The present-day ranges of these tropical groups « closely coincide with the existing continental and insular remnants of hypothetical Gondwana, the great equatorial land which ... is supposed ... to have stretched from Australia and peninsular India to Africa and South America » (1).

Origin of the coastal plain flora. — At the close of the Mesozoic and throughout the early Cenozoic the peneplained Appalachian region was again uplifted at intervals, resulting in « the consequent deep dissection of the extensive plateau and its inevitable conversion from a low Cretaceous plain with retarded drainage into a vast upland mesophytic area, ready for occupation by the abundant mesophytic types of the climax forest which could now freely mingle between Asia, northwestern America, eastern North America and Europe » and forcing the members of the old Mesozoic groups, « by drainage of the area and by invasion by the horde of actively colonizing mesophytic types, to abandon their once congenial but now uncongenial haunts on the Appalachian area and to move out to the newly available xerophytic and hydrophytic habitats, chiefly on the Coastal Plain.... where the acid savannahs, bogs, shallow pools and dry sands » supplied the environment in which they could still survive (2).

In favorable habitats on the now uplifted peneplain, however, Kearney (3) thinks some Cretaceous species were able to maintain themselves and so have survived as relict colonies. « It may be conceived that while some individuals maintained themselves in well-sheltered situations and were not forced to a change of abode, others escaped the changing environment by

(1) Fernald, *Specific Segregations and Identities in Some Floras of Eastern North America and the Old World. Rhodora,* 33: 25-63. 1931.

(2) Fernald, *l. c.*, 50, 51.

(3) Kearney, *l. c.*

a gradual retreat into the... lowlands. The individuals which remained in the mountains were the direct ancestors of the present Appalachian species, while those which migrated and later accustomed themselves in the Coastal Plain... gave rise to the Austro-riparian species that attract our attention today because of their close resemblance to Appalachian forms ».

Fernald (1) recently published extensive lists of species which occur chiefly on the Coastal Plain, but which are also represented by colonies on the Appalachians. Included in his list of these plants, the most ancient elements of the present Appalachian flora, are *Panicum meridionale, Parnassia asarifolia, Galax aphylla, Lechea racemulosa, Viola Stoneana, Sabatia campanulata, Stachys hyssopifolia, Chelone Cuthbertii, Houstonia tenuifolia, Aster gracilis, Silphium atropurpureum, Carex Collinsii, Trillium pusillum, Iris prismatica, Asarum virginicum, Rhexia mariana, Kalmia caroliniana, Gratiola viscidula, Gerardia setacea, Vernonia glauca, Solidago yadkinensis, Aster grandiflorus, Coreopsis verticillata, Orontium aquaticum, Cleistes divaricata, Asarum arifolium, Sarracenia flava, Monotropsis odorata, Lobelia Nuttalli, Eupatorium album, Liatris graminifolia, Woodwardia areolata, Aristida virgata, Lechea minor, Ascyrum stans, Bartonia paniculata, Gratiola pilosa, Viburnum scabrellum, Scleria oligantha, Xyris torta, Juncus diffusissimus, Hexalectris spicata, Castanea pumila, Phoradendron flavescens, Desmodium laevigatum, Clitoria mariana, Phyllanthus carolinianus, Rhus Toxicodendron, Obolaria virginica, Ilex opaca, Bignonia capreolata, Diodia teres, Elephantopus carolinianus, Liatris squarrosa, Chrysopsis mariana, Solidago erecta, Gnaphalium purpureum, Helianthus atrorubens, Bidens laevis* and many others.

This relationship between the flora of the Coastal Plain and the Appalachian Mountains has been recognized by many botanists. As long ago as 1879 Redfield, describing an ascent of the Blue Ridges in North Carolina, said: « The botanists returned from it laden with plants, and it was curious to see among them so many of the species which are associated with

(1) Fernald, *Local Plants of the Inner Coastal Plain of Southeastern Virginia, Rhodora*, 39 : 321-366, 379-415, 433-459, 465-491. 1937.

the sandy barrens and swamps of southern New Jersey » (1).

It is, of course, to be conjectured that these species of the Coastal Plain may have moved into the ancient uplands, rather than that the migration has occurred in the opposite direction. After enumerating several Coastal Plain species found in the East Tennessee mountains, Kearney asks: « What are we to infer from the presence of these Austro-riparian plants among the flora of northern origin that chiefly cover these mountains ? Possibly they are the advance-guard of an invading army. Much more probably, however, they are the lingering survivals of a more southern flora, once widely distributed over the southern Appalachian region » (2).

Pennell thinks some migrations may have ocurred in both directions. While « *Amianthium, Xerophyllum* and *Helonias* have all the expected features of ancient genera, few species, small or widely disrupted ranges », in regard to « *Calopogon* and *Cleistes,* genera with the highly modified floral structure of the Orchidaceae and seeds fitted by their minute size for carriage to long distances by wind, we can but ask whether these may not have passed inland from the lowland to the highland, at a relativery recent time » (3).

Pennell, however, is almost alone in suggesting this interpretation. Small says, of *Cleistes divaricata :* « After the seas which deposited the Coastal Plain strata retreated, this plant spread to the seacost, but still maintained a foothold in the mountains » ; (4) and elsewhere, « *Cleistes* is perhaps a very ancient type. Its altitudinal range indicates a migration from the ancient highlands where it still maintains a foothold » (5). E. Lucy Braun, considering the possibility of migration of certain species either from or the Coastal Plain, concludes that their presence « on undissected remnants of the plateau or on monadnoks and their wide separation from the general area of their ranges,

(1) Redfield, *Bull. Torr. Bot. Club,* 6 : 335. 1879.

(2) Kearney, *l. c.*

(3) Pennell, *Scrop. E. Temp. N. Amer.*, 588, 589. 1935.

(4) Small, *Manual Flora,* S. E. U. S., p. 375. 1933.

(5) Small, *Addisonia,* 18 : 39.

points to the relic interpretation » (1). Fernald states, concerning *Cleistes divaricata,* that « its scarcity on the Coastal Plain north of Florida... does not suggest that it has recently been invading the mountains from these weak and scattered Coastal stations » (2). Harshberger also believed that some of the endemic Coastal Plain plants may have been derived from ancestral species inhabiting the crests of the Alleghenies (3). Stone states that the flora of Garrett County, Maryland, is much like the pine barrens of New Jersey « and is quite likely a remnat of an early primitive flora » (4).

Camp is doubtfull if either of these explanations is the correct one. He believes that the evolution of the present Coastal Plain species took place in the ancient highlands slightly to the southeast of the Appalachian Mountains, in what is now the piedmont region, or in some other region. Then, « During the climatic changes and orogeny of the Tertiary, two easy avenues of migration were open. One was into the mountain systems to the northwest undergoing a cycle of secondary elevations ; the other was to the coastal plain. Both of these migrations evidently took place » (5). Not only is there no evidence to support Camp's theory but it seems entirely unnecessary to explain the relationships existing between the coastal plain plants and the relict colonies in the mountains. Certainly there would have been nothing to prevent the widespread distribution of the ancient types throughout the Appalachians long before the elevation of the coastal plain, so there is no need to postulate that the migrations into the coastal plain and the mountains took place at the same time.

The ocurrence of numerous species near or about the Great Lakes, chiefly Lake Michigan, that occur also in the Appala-

(1) BRAUN, *Some Relationships of the Flora of the Cumberland Plateau and Cumberland Mountains in Kentucky. Rhodora,* 39 : 193-208. 1937. See also her, Notes on *Kentucky Plants. Castanea,* 1 : 41-45. 1936.

(2) FERNALD, *l. c.,* 487. 1937.

(3) HARSHBERGER, *Proc. Acad. Nat. Sci. Phila.,* 1904 : 607.

(4) BARTONIA, nº 5 : 16. 1912.

(5) CAMP, *The genus Leiophyllum. Bull. Torr. Bot. Club,* 65 : 99-104. 1938.

chians and on the Coastal Plain suggets that the migration from the ancient upland center may have also taken place towards the northwest and west, as well as to the east.

The arctotertiary flora.— The new flora which came crowding into the rising Appalachians early in the Cenozoic was composed of representatives of groups which were widespread over the northern hemisphere in the late Mesozoic and early Cenozoic, due to the land bridges connecting northeastern Asia, North America, northeastern America and Europe which permitted ready migration. This group, commonly designated the arctotertiary flora, having crowded the old tropical forms off the uplifted Appalachian area into the newly emerged Coastal Plain, has given rise to the present characteristic flora of the southern highlands. Through its great antiquity it has been reduced to geographically segregated remnants in the northern hemisphere, particularly in eastern and central Asia and eastern North America, the resemblance of whose floras was first noted long ago in Asa Gray's classic paper (1). Among such ancient genera may be listed *Arisaema, Symplocarpus, Chamaelirium, Aletris, Saururus, Menispermun, Magnolia, Zanthoxylum, Podophyllum, Caulophyllum, Diphylleia, Jeffersonia, Maclura, Laportea, Penthorum, Hamamelis, Liquidambar, Fothergilla, Hydrangea, Buckleya, Panax, Shortia, Phryma* and *Triosteum.* Hooker says: « This generic identity, however, gives but a faint idea of the close relationship between East American and East Asiatic... floras, for there is further specific identity in about 230 cases, and very close representation in upwards of 350; and what is most curious is that there are not a few very singular genera of which only two species are known, one from east Asia, the other in east America » (2).

Waxing enthusiastic over the fact that many of the plants preserved in the geologic record are still alive today in the southern Appalachians, Guppy describes the possible experiences

(1) Gray, *The Flora of Japan. Scientific Papers,* 2: 125-141. (1859) 1889.

(2) Hooker, *The Distribution of North American Flora. Am. Nat.,* 13 : 155-170. 1879.

of a student as follows: « In the woods around him were growing the Liquidambar, the Sassafras, and many other shrubs and trees that had flourished in the Mesozoic ages in the spot where he was standing. Their remains crowded the Cretaceous deposits exhibited in the cliffs nearby. Specimens of the past and present were in his hands. Though the difference in kind was very slight... the difference in time, meassured in human lives, amounted to eternity. It is a story of perpetuity, rather than of change... He begins with the cosmopolitanism of such types in the Cretaceous age and he ends with their more restricted distribution and somewhat greater specialization now... Those old genera become the genera of today; and the genera of today, though the genera of a thousand ages, are but as yesterday in the history of flowering plants » (1).

Origin of the Ozarkian flora. — The Ozarkian uplift, dating, like the Appalachian region, from the close of the Permian, was likewise invaded, by Upper Cretaceous times, by the same arctotertiary species that moved into the eastern part of the continent. Doubtless this flora has « continuously occupied the Ozark uplift, since it still harbors many old species, although not so many as the Appalachians uplift of the same latitude, from which it was isolated during the Tertiary by the oceanic waters of the Mississippi Embayment. This isolation and the proximity of the Ozarkian region to prairie and Sonoran floras on the west have led to considerable differentiation between the Ozarkian and Appalachians forest centers » (2). Species common to both the Ozarks and the Southern Appalachians include *Quercus alba, Q. macrocarpa, Q. palustris, Q. borealis, Juglans nigra, Hicoria ovata, Acer saccharum, Celtis occidentalis, Diospyros virginiana, Populus deltoides, Platanus occidentalis* and many others (3).

(1) GUPPY, *Fossil Botany in the Western World: An Appreciation. Am. Journ. Sci.*, ser. 4. 49: 372-374. 1920.

(2) GLEASON, *l. c.*, 57.

(3) HARSHBERGER, *Phytogeographic Survey of North America*, 510-516. 1911.

Tertiary segregations. — Fossil evidence indicates that the arctotertiary flora had little or no latitudinal differentiation at least as far north as 70°. The presence in northern latitudes of *Ficus, Artocarpus, Bromelia, Sabal, Anona* and other genera now restricted to warm climates has been taken to denote a mild climate in those regions (1). The fossil evidence also indicates, according to Gleason, that both gymnosperms and angiosperms were included in the arctotertiary flora. The next « great floristic development affecting our region was the general segregation of these two groups into a northern flora, with gymnosperms predominating, and a southern one, in which angiosperms were dominant. This probably began only with the approach of the first glacial period and may not have been completed until the ice age was well under way. The process... involved also the permanent disappearance from both floras of a number of species belonging to genera whose modern representatives are tropical » (2).

The uplift of the Cordillerans, leading to the development of semi-arid conditions over the Great Plains, resulted in the differentiation of a third floristic type, the western grasslands (3).

The period of pleistocene glaciation. — In late Tertiary times a gradual lowering of temperatures throughout the northern hemisphere progressed steadily until the climate was essentially arctic over more than half of the North American continent. Enormous glaciers and ice sheets then formed and spread southwards, filling river and lake basins, covering the mountains and burying the lowlands beneath a vast sea of ice. There is abundant evidence that the ice advanced and retreated more than once, and at least four glacial periods have received names, the Nebraskan, Kansan, Illinoian and Wisconsin stages, with corresponding interglacial stages between.

Little evidence is available concerning the migrations of flo-

(1) Knowlton, *A Catalogue of the Mesozoic and Cenozoic Plants of North America. U. S. Geol. Surv. Bull.*, 686. 1919.

(2) Gleason, *l. c.*, 58.

(3) Gleason, *l. c.*, 57, 58.

ras during and between the various stages of glaciation but a vast literature deals with the cumulative effects of the period. It has been long customary to state that the extraordinary changes of climate indicated by the spread of the glaciation led to southward migrations of the floras of the Arctic and temperate zones, and that the colonies of northern species inhabiting the southern Appalachians are relicts of this southward movement. More recently some botanists have cast a shadow of doubt upon this classic conception. Fernald says: « The effect upon vegetation of ice-sheets hundreds of miles away was probably not so great as was formerly supposed. Witness the occurrence today... at the ice-free margin of otherwise ice-capped Greenland of such plants of sea-level in the eastern United States as *Woodsia ilvensis, Cystopteris fragilis, Equisetum sylvaticum, E. hiemale, Deschampsia flexuosa, Carex brunnescens, Streptopus amplexifolius, Corallorrhiza trifida, Stellaria borealis, Ranunculus Cymbalaria, R. reptans, Coptis groenlandica, Potentilla palustris, Viola Selkirkii, Epilobium angustifolium, Cornus canadensis, Pyrola secunda, Andromeda glaucophylla, Vaccinium Oxycoccos, Menyanthes trifoliata, Utricularia intermedia* and *Linnaea borealis* var. *americana* » (1).

The fallacy in this argument, of course, consists in the selection, for the list, of species having a wide range of requeriments and in the failure to state that the *normal climax forest type* of the eastern United States does not approach the Greenland glaciers by hundreds of miles. There seems to me no reason to doubt that a climate cool enough to have produced glaciers within 25 miles of the northern tip of West Virginia could not but have exerted a profound influence upon the vegetation of the mid-Appalachians region and that West Virginia, southern Ohio and southern Pennsylvania must have presented the aspect of an Arctic tundra (2), while many Canadian species were forced

(1) FERNALD, *l. c.*, 51, footnote (1931).

(2) SEARS, *(Glacial and Post-glacial Vegetation, Bot. Rev.* 1 : 37-51. 1915) says that the absence of a record of tundra at the bottom of present bog profiles «does not preclude the possibility of a long tundra stage. The basins suitable to peat formation may have been occupied by dead ice

hundreds of miles farther south. As noted above, it is possible that the segregation of the old arctotertiary flora into the northern coniferous forests and the southern deciduous forests was finally completed during the period of Pleistocene glaciation. Whether it was during the cooling of the climate that portended the approach of the glaciers or not until the glacial age itself that the segregation occurred, the very fact is evidence of the significant influence exerted by the cold. Since it is apparent that temperature is one of the principal factors limiting the distribution of the Canadian forests along the crests of the southern Appalachians, it must be inferred that they came there originally through same cause; since the climate was formerly much cooler, the altitudinal lower limits of the coniferous forests must have more nearly approached sea-level and the total area covered must have been correspondingly greater. The present Canadian element of the southern Appalachians undoubtedly migrated there as soon as the cooling climate of the pre-glacial age, which brought about the segregation of the coniferous forests, made conditions congenial for it so far south.

The retreat of the ice. — Upon the decay of the ice that presently marked the amelioration of the climate, the northern boundary of the tundra persisted until destroyed by the warmer temperatures or by the succession of the evergreen forests. In this migration numerous relict colonies were left behind, especially in extreme habitats, as on exposed crests or in bogs. Many of these have since disappeared but many still remain. These bogs, known locally in the Appalachian region as mountain « glades », are inhabited by such northern species as *Aspidium simulatum, Larix laricina, Carex trisperma, Pogonia ophioglossoides, Calopogon pulchellum, Alnus incana, Coptis trifolia, Drosera rotundifolia, Geum rivale, Vaccinium Oxycoccos, V. macro-*

until the forest returned northward to surround them. Tundra may possibly have been followed by steppe conditions so dry as to preclude peat formation ». Antevs *(The Quaternary Ice Age in North America- Brooklyn Bot. Gard. Rec.,* 21*:* 186-202. 1932) also believes there was a region of tundra, although possibly a rather narrow one.

carpon and *Menyanthes trifoliata,* as well as numerous species of *Sphagnum, Politrichum* and *Cladonia* (1).

Adams has described in detail the migrations of the deciduous and coniferous forests which accompanied the northward retreat of the ice (2). An evolution of species evidently characterized the migration of the northern flora into the southern Appalachians, resulting in the development of a group restricted to the southern highlands but having their nearest relatives in the Canadian Province. Among these may be mentioned *Abies Fraseri,* paired with *A. balsamea* of the north ; *Tsuga caroliniana,* paired with *T. canadensis :* and *Rhododendron catawbiense,* paired with *R. maximum.*

Post-Wisconsin xerothermic period. — There is abundant evidence that a climate somewhat warmer and drier than that of the present existed in the post-Wisconsin of eastersn North America. According to Gleason, such a « xerothermic period, occurring in comparatively recent times, and without any subsequent geological episodes to modify greatly the trend of plant migrations, would certainly have left an impress on the distribution of vegetation which would still be visible. Among the effects which might be expected is a great extensión of the prairie flora toward the east, taking advantage of the favorable climate. This should now be evidenced by relic prairie colonies and by isolated stations of western species at the east and by a deficiency of hydrophytic and mesophytic boreal relics at the west. Both of these results are actually demonstrable at the present time » (3). « The eastern migratión of the prairie proceeded as a wedgeshaped extension between the coniferous vegetation at the north ant the deciduous forests at the south and reached limits considerably beyond the eastern margin of modern continuous prai-

(1) Core, *Some Aspects of the Phytogeography of West Virginia. Torreya,* 32 : 65-71. 1932.

(2) Adams, *Postglacial origin and migrations of the life of the northeastern United States. Journ. of Geog.,* 1 : 303-310, 352-357. 1902.

(3) Gleason, *l. c.,* 67.

ries. Numerous relic colonies formerly occurred, before they were destroyed by agriculture, in eastern Indiana northwestern, Ohio and southern Michigan » (1). Transeau agrees with this account, stating that « A late postglacial prehistoric dry period with more wide spread drought conditions and more prolonged droughts than at present is definitely indicated by certain bog pollen studies, by soil profiles, by the succession in bog profiles, by the absense, or rare occurrence, of many tree, shrub, and herbaceous species from the region of the Peninsula, and by the present distribution of prairie colonies, and prairie species. The indication of a Xeric Period by bog pollen studies has recently been questioned. If pollen studies of the upper layers of peat within the Peninsular region fail to show a period of this kind either the methods of pollen analysis or the assumptions upon which they are based need further investigation » (2). Sears, reviewing studies on the stratigraphic distribution of fossil pollen in peat deposits of eastern North America, concludes that here is an « independent line of evidence strengthening the inferences drawn by Gleason on floristic grounds » (3).

While Gleason regards it as reasonably certain that extensive prairies were not developed east of Cleveland, yet the discontinuous distribution in the Appalachians of such western species as *Vernonia fasciculata, Opuntia compressa, Astragalus distortus, Silphium perfoliatum, Pentstemon canescens*, and *Asclepias verticillata* indicates that some elements of the prairie flora entered the highlands and persisted there. In addition to these, the eastward advance of the prairie was evidently accompanied by some specific evolution among species, accounting for the origin of such species as *Phymosia remota, Woodsia scopulina, Senecio antennariifolius, Pachistima Cambyi, Eriogonum Allenii*, and *Trifolium virginicum*, although Wherry suggests that their « ancestors presumably crossed... northern North America... and

(1) Gleason, *l. c.*, 71.

(2) Transeau, *The Prairie Peninsula, Ecology* 16 : 423-437. 1935. See also his *Forest Centers of eastern America. Amer. Nat.* 39 : 875-889, 1905.

(3) Sears, *Postglacial Climate in Eastern North America. Ecology* 13 : 1-6. 1932.

came down the Alleghenies during pre-Glacial times, but subsequent climatic changes destroyed all traces of them, leaving behind » these endemic species (1).

Recent migrations from the southern migrations. — Presently a change in the climate ocurred, with a slight lowering of the temperature and a considerable increase in the total amount of rainfall. Gleason notes that « the increase fell chiefly during the winter months ant changed the climate from one of summer rains, such as is now characteristic of the prairies farther west, to one of fairly equable rainfall. This change first made itself felt in the east and gradually progressed toward the west » (2). The effect of this climatic change was a disturbance of the old relationship existing between forest and prairie, leading to an advance of the desiduous forests northward and westward from their glacial center of preservation in the southern Appalachians. The westward migration was participated in chiefly by species of *Quercus,* and *Hicoria,* of the drier uplands, and by species of *Quercus, Ulmus, Fraxinus, Juglans, Acer, Celtis, Populus, Gleditsia, Gymnocladus, Aesculus,* and *Platanus,* of the lowlands. These two types of forest advanced together upon the retreating prairie, until their outposts are now to be seen in Missouri, Kansas and Nebraska. The northward migration, continuing the advance started at the close of the ice age, gave rise to the species which constitute the present Alleghenian element in the flora of New York and New England, more or less mixed with boreal elements as they migrated into a retreating coniferous forest. Moving slowly northward behind the decaying glaciers, some of the species turned finally to the west and northwest, entering Michigan, Wisconsin and Minnesota. Gleason compares the combined effects of the two migrations to a vast U, with its base in the southern Appalachians, one arm reaching west to the Ozarks, the other north and west to Minnesota. Through continued northward movements of the sou-

(1) WHERRY, *Plants of the Appalachian shale-barrens. Journ. Wash. Acad. Sci.* 20 : 43-52. 1930.

(2) GLEASON, *l. c.,* 73.

thern migrants along river valleys, the U tended gradually to be closed in (1).

The forest migration was also accompanied by specific evolution and various species have been described from the Middle Western forests, at least a few of which have been derived from parent species of the Appalachians. Thus *Agalinis paupercula* of the Middle West is regarded as derived from *A. purpurea* of the Appalachians, and *Aureolaria Pedicularia* has given rise to the variety *ambigens.*

Changes in the prairie flora took place at the same time. Distinctly western species either withdrew entirely from the eastern extension or, as mentioned above, left relicts behind in especially favorable xerophytic habitats. Many of these, subjected to persistent succession by the forests, have doubtless been entirely obliterated or reduced in size. As the xerothermic period drew to its close, numerous southeastern herbaceous species migrated into the prairie arm and, being better able to exist with the increasing rainfall, finally became dominant over the western species. Gleason notes that the four most important grasses of the Illinois prairies, *Andropogon furcatus, A. scoparius Sorghastrum nutans,* and *Spartina Michauxiana,* are all of eastern origin. « Here we have the origin of the flora of the eastern arm of the Prairie Province, early recognized by Pound and Clements as distinct from that of the western plains and designated by them the prairie-grass formation. Just as the original western plains were segregated from the arctotertiary forests by climatic differentiation, so the xerothermic period produce an analogous vegetation thousands of years later from the same stock. In the later case, however, the process was one of selective migration, rather than of extermination and evolution, and most of the southeastern species now characteristic of the prairie-grass formation still live also in the forested region of the southeastern states » (2).

Transeau, however, does not agree with this interpretation. He declares that « the tall prairie grasses dit not 'come out of

(1) Gleason, *l. c.,* 73-75.

(2) Gleason, *l. c.,* 77.

the deciduous forest' and they probably did not cross the Alleghany Mountains, but reached the eastern seaboard by way of the New York State lowlands and the ancient coastal plain. From there they have followed up many of the eastern slopes of the Alleghenies » (1).

SUMMARY

To summarize, then, the following floristic groups and plant migrations seem to have participated in the evolution of the modern flora of the Southern Appalachians:

1. The old Paleozoic flora, composed mainly of Pteridophytes and Pteridosperms, was, through the Appalachian Revolution, modified by extermination and evolution of forms into the early Mesozoic vegetation.

2. The peneplained Appalachian region was invaded not later than Lower Cretaceous times by the newly-evolved and rapidly spreading Angiosperms, then pantropical in their distribution.

3. The uplift at the close of the Mesozoic caused these tropical forms to migrate into the newly emerged Coastal Plain, leaving, however, numerous relict colonies in the Appalachians.

4. The newly elevated highlands were occupied by the arctotertiary forests, then circumboreal in extent but now limited to a few widely separated geographical regions.

5. Cooling climates of the Late Cenozoic caused a segregation of the originally homogeneous arctotertiary flora into a northern coniferous forest and a southern deciduous forest.

6. The Pleistocene glaciation caused the migration into the southern highlands of many northern forms.

7. The retreat of the ice permitted the coniferous forests to migrate northwards, reoccupying their formed area, but leaving an extensive remnant behind in the higher and cooler regions of the southern Appalachians.

It is recognized that the foregoing statement is quite imperfect. However, an attempt is made to present, for the first time,

(1) TRANSEAU, *l. c.*, 426 (1935).

a chronological account of the various vegetational migrations that have resulted in the present characteristic flora of the southern Appalachian mountain region. The piecemeal work of many botanists will be required to fill in the gaps and provide evidence to modify the hypotheses here discussed.

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