

The Insects of Virginia: No. 1

PART I

Introduction to the Series of Bulletins
on the Insects of Virginia, with
a Literature Review

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PART II

The Biotic Regions of Virginia

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I—Introduction to the Series of Bulletins on the Insects of Virginia, with a Literature Review

Michael Kosztarab

Objective

The insects of Virginia are poorly known, although the first North American insect (the tiger swallowtail butterfly) was described from "Virginia" (Forbes, 1928, as quoted from Moufet, 1634), and systematic collections of insects from the state started with the establishment of the Virginia Agricultural Experiment Station, as early as 1888 (Alwood, 1890). Smyth (1895, 1899) collected insects intensively and studied their biology for over 30 years, concentrating on Montgomery County Lepidoptera. After Dr. Smyth retired in 1925, very few of the new V.P.I. staff members or other workers did systematic and distributional studies on the Virginia insects. For example, the only published comprehensive systematic work on a group of insects in Virginia is the study by Clark and Clark (1951) on the butterflies of Virginia. There is a real gap in this type of study in Virginia, compared with the amount of work done in other states. To make up for this deficiency, the author intends with this paper to initiate a series of publications recording the insect fauna of Virginia: a systematic treatment which includes records on biology and ecology of the different Virginia insect groups. It is sincerely hoped that many professional and amateur insect enthusiasts will contribute to this series of papers. Nine scientists to date have offered to prepare 11 publications for this series.

Economic Importance

A series of publications dealing with the insects of Virginia and including general information of their distribution, life history, ecology, economic importance, and supplemented (where possible) by identification keys, should be valuable to many people whose work is directly or indirectly affected by insects. It is in the interest of farmers, orchard owners, nurserymen, gardeners, and the householders of the towns and spreading suburbs of Virginia to know the best method for controlling insect infestations and the best time for insecticide application. Other information, e.g. the host preference, overwintering sites, time of adult appearance and egg hatching, duration of the different life stages, parasites and predators of pest species, and number of yearly generations under the different climatic conditions in Virginia, should also be useful in timing the control measures.

The correct identification of the pest is the starting point of any control program. Therefore, besides the compilation of the insect faunistic data for Virginia, this work should be expanded in the future to include detailed taxonomic treatment for the insect orders and families. This will be achieved by preparing adequate descriptions and illustrations for each species, and by providing keys for their identification. Examples of insect damage from the state are being preserved at V.P.I. for aiding as reference materials in future identification work and descriptions (Kosztarab, 1966).

How Many Species In Virginia?

It was estimated by Borror and DeLong (1964) that there are 84,557 insect species known from North America north of Mexico. Brimley (1938, 1942) and Wray (1950) reported 11,094 different insect species from the bordering state of North Carolina, but Wray assumed that this number would be at least doubled if intensive collecting was done over the entire state. Leonard (1928) listed 15,450 species occurring in New York state. Because of the diversity of the life zones in Virginia (Hoffman, 1969), it is estimated that over 20,000 species of insects occur in this state. The economic insect survey file at V.P.I. includes more than 10,000 individual reports on over 1,500 insect pest species of agricultural and medical importance. Conservative estimates show that there are over 2,100 beneficial insect species in Virginia, belonging to 11 orders. These include the parasites and predators of pest insects and a large number of pollinating bee species.

Thousands of individual collections were made in Virginia since 1888, from which about 100,000 specimens are stored in the V.P.I. insect collection (Covell and Kosztarab, 1966). A large proportion of the Virginia insects collected before 1925 was donated by Professor E. A. Smyth, Jr., to the U. S. National Museum.

Who Can Contribute and How?

The authors of this series may be any of the following: members of the V.P.I. faculty, students or former students who want to publish research work completed at V.P.I., associated workers in co-authorship with V.P.I. faculty members, individuals willing to deposit significant Virginia insect material in the V.P.I. collection, persons identifying large sections of the V.P.I. insect collection, or workers contributing individually or through their institutions toward the cost of printing their publications.

It is planned to publish each contribution separately; however, for economic reasons, publications on related groups or subjects, totaling 16 or fewer printed pages, may be printed together in the same issue. All manuscripts for this series should be submitted to the Head of the Department of Entomology, V.P.I., who will arrange for review and editing of each manuscript for uniformity before submitting it to the Administration of the V.P.I. Research Division for approval. The Editor of the Research Division Bulletins will proceed with the final editing procedures of each manuscript before printing. Each issue will be published in a uniform style and size so that several may be bound together in book form. Contributors are urged to consult the Style Manual for Biological Journals (1964) before preparing manuscripts for publication for this series.

Since a large portion of the insects collected in Virginia is stored in the U.S. National Museum, it is expected that researchers working up records on any insect group will check the specimens from Virginia at the U.S.N.M. during the preparation of their articles. The Virginia Polytechnic Institute collections, library, insect survey files, and other facilities will be available for workers who want to contribute papers.

Projected Goals

It is hoped that this beginning on the Virginia insects will lay the foundation of an organized natural history survey, especially of a "Virginia State Natural History Survey" in the near future. It should lead to a better realization of the value of such work by our legislators, state officials, and others who may read the various bulletins.

The pollution of our rivers and of the air in the metropolitan areas is becoming an alarming problem. Information is still not available on how the pollution changes the structure of our present plant and animal communities in Virginia. This series and similar projects in other disciplines may one day make such information available. The Illinois State Natural History Survey has a staff of over 100 professional employees presently working on these types of problems (Mills, *et al.*, 1958). The "Virginia State Natural History Survey" could work in coordination with the yet-to-be established "Virginia Museum of Science and History" suggested by MacCord (1967).

Review of Selected Works

There were several persons who, as general collectors of insects in Virginia, contributed toward the knowledge of our state fauna, and whose names should not be left out of this review. Several of these scientists were, or are, employees of the U.S. National Museum or the U.S.

Department of Agriculture, who have lived or are still living in northern Virginia. Two of these workers were Harry A. Allard and his son Howard, who, while living in Arlington, took many collecting trips in Virginia. Among the 254 papers written by H. A. Allard (Gurney, 1964), there are several dealing with Virginia Orthoptera and cicadas although his major interest was in plant physiology. Nathan Banks lived in Fairfax County and collected a wide range of insects in the state between 1904 and 1912. Herbert S. Barber, as a U.S. National Museum specialist of Coleoptera, made extensive collections, especially of beetles (Chrysomelidae, Lampyridae) in Virginia during the 1930's and 1940's. J. C. Bridwell and Donald W. Clancy from the U.S.D.A., while stationed at Charlottesville, collected many insects, especially mealybugs, in that area. Bridwell's main interest was in weevils. Their material was incorporated in the U.S. National Museum Collection. Oliver S. Flint (1956-66) and Ashley B. Gurney (1963), workers at U.S.N.M., are among the most enthusiastic present-day general collectors in Virginia. Henry G. Hubbard and Eugene A. Schwarz specialized in Coleoptera of the state around the turn of the century. Henry Ulke, another coleopterist and noted Virginia collector, was interested in the smaller beetles, Pselaphidae, Scydmaenidae, and Silphidae. His collection was given to the Carnegie Museum. George B. Vogt, of the U.S.N.M., made collections of Buprestidae, Cerambycidae and Chrysomelidae in the state. Many insect specimens from forest and ornamental plants, especially from nurseries in Virginia, were collected by Messrs. F. R. Freund, W. H. Matheny, and C. R. Willey of the Virginia Department of Agriculture and Commerce, and by Mr. C. L. Morris of the Virginia Division of Forestry. From this material were built collections of insects for their respective offices, while many samples were sent to the U.S. National Museum for identification and verification.

Other general insect collectors associated with V.P.I., either in the past or at present, are: W. B. Alwood, J. M. Amos, J. L. Bishop, M. L. Bobb, L. R. Cagel, D. H. Cochran, C. V. Covell, Jr., C. B. Dominick, J. McD. Grayson, L. A. Hetrick, C. H. Hill, R. L. Hoffman (now at Radford College), W. S. Hough, O. W. Isakson (1967), M. Kosztarab, H. M. Kulman, D. E. Messersmith, R. R. Mills, A. P. Morris, S. E. Neff, R. L. Pienkowski, J. L. Phillips, E. M. Raffensperger, J. O. Rowell, W. J. Schoene, J. C. Smith, E. A. Smyth, W. A. Tarpley, E. C. Turner, Jr., G. W. Underhill, D. F. Vest, and A. M. Woodside.

Young (1945) prepared a list of the activities and publications of the Virginia Agricultural Experiment Station between 1889-1944. His list contains useful records for persons interested in the papers published and

work done by biologists and entomologists employed by the Experiment Station.

It is not the objective of this review to refer to all publications giving information on insects of Virginia. There are many records on Virginia insects in monographs covering some of the North American insect families and genera. Cited here are only those relatively few publications that are more or less specific studies on Virginia insects, and of taxonomic nature.

The compilers of this series would like to help future workers studying Virginia insects, and to give proper credit to authors, by providing a preliminary list of references for each insect order and family in the issues to follow. For this, authors who have included records on Virginia insects in their papers are asked to supply the compilers with reprints, and with information regarding the whereabouts of the Virginia specimens they have studied.

Work on Specific Groups

New species of PROTURA were described by Ewing (1921) from Virginia. DIPLURANS (Japygidae) were collected by Richard L. Hoffman and included in a study by Smith and Bolton (1964). Springtails as agricultural pests in the state were reported by Smith (1917). Maynard (1951), in his monograph on the COLLEMBOLA of New York State, included descriptions and distributional records on several species present in Virginia. MICROCORYPHIA collected by R. L. Hoffman were sent to Dr. P. Wygodzinsky of the American Museum of Natural History, who will publish on these later.

Banks (1904c) reported on 4 genera of EPHEMEROPTERA. About 6,600 specimens have been collected in central Virginia by Pugh (1956), who recognized 36 species. Reid R. Gerhardt, as a graduate student, enlarged the insect collection of Virginia Polytechnic Institute with many adults. Traver's (1932-1933) work on the mayflies of North Carolina should be a useful reference to any person studying Ephemeroptera in Virginia.

Among the early workers on Virginia ODONATA were Calvert (1890), Williamson (1903), and Banks (1908a). Each added new distributional records to the Virginia faunal list. Odonata of Virginia have been collected and studied more recently by R. L. Hoffman, D. Innes, D. E. Messersmith, J. K. Novack, M. D. Ries, and G. M. Simmons. Gloyd (1951) determined Odonata in the V.P.I. collection through 1948, and included several new species records for Virginia. Byers (1951) published some notes on the Odonata fauna of Mountain Lake,

while Donnelly (1961), presented many records from Northern Virginia. Ries and Cruden (1966) gave the known distribution of *Anax longipes* in the state. At present, Mrs. Donald T. Ries is preparing a manuscript on the Odonata of the York-James Peninsula. She informed this author about the availability of about 50 titles, as references to the Odonata fauna of Virginia. Odonata is one of the orders which probably will be worked up taxonomically for this series soon.

ORTHOPTERA have been more extensively collected in Virginia than any other group of insects. Most of the material and the organization of the V.P.I. insect collection is due to R. L. Hoffman, R. R. Mills and W. A. Tarpley. Other collectors and also publishers on Virginia Orthoptera were: H. A. Allard, A. N. Caudell, H. Fox, A. B. Gurney, M. Hebard, and J. A. G. Rehn. Allard (1914, 1916, 1930, 1939) added some new state records on crickets, and described in detail several of the sound-producing Orthoptera. Caudell (1928, 1929) recorded the Chinese mantid as far south as Virginia, and described a new variety of Tettigoniidae from Cape Henry. Caudell and Allard (1930's) prepared a monograph on the Orthoptera of the District of Columbia, Maryland, and Virginia. Unfortunately this manuscript was never completed and published, but it is available at the U.S. National Museum for persons interested in bringing it up to date for publication. Fox (1917, 1938) gave distributional and ecological notes on over 100 species and subspecies of Virginia Orthoptera. Gurney (1941) presented detailed taxonomic and bionomic notes, with distribution in Virginia and other states, on the grasshopper, *Melanoplus impudicus* Scudder. In a previous study Rehn and Hebard (1916) included 93 Orthoptera and one DERMAPTERA species from Virginia. Some Tettigoniidae were reported from Virginia by Hebard (1938, 1945). In 1945, Hebard listed 86 species from the Appalachian mountains in the vicinity of Hot Springs, Bath County, Virginia.

Two new species of termites, ISOPTERA, were described, one from Falls Church by Banks (1907a); the other from Cape Henry by Snyder (1924, 1925).

PLECOPTERA distributional records were given by Banks (1904c), and descriptions are available on two species of *Allocaënia* (Ross, 1964; Ross & Yamamoto, 1967).

Banks (1904c) reported several species of PSOCOPTERA from the state. Ewing (1930) gave distributional records, morphology and taxonomy of one MALLOPHAGA species in Virginia, while Emerson (1964a, 1964b) listed distributional records from many host animals present in the state.

The THYSANOPTERA fauna of Virginia is very poorly known. Three new species were described from material collected in the state by Crawford (1943), and Hood (1916, 1952).

HEMIPTERA lists and new state records were compiled by Banks (1907b, 1912), Girault (1915b), Rehn & Hebard (1916), Knight (1918), McAtee (1919b, 1923), and Hoffman (1953). New species were described: Reduviidae, by Banks (1910); Corixidae, by Abbott (1916); Miridae, by Knight (1926); and Nabidae, by Harris (1940). Bobb (1950) concentrated on the aquatic and semi-aquatic hemipterans while preparing a detailed Ph.D. study at the University of Virginia. In his dissertation 90 species were treated. His specimens are in the collections of the U.S. National Museum, University of Kansas, and at V.P.I. It is the author's sincere hope that this work will be brought up to date and published in the near future. Bobb's publications (1951a, 1951b, 1953) include life history studies and distributional records on three aquatic species. Nonaquatic Hemiptera have been worked up taxonomically by R. L. Hoffman, and his manuscript on this interesting and economically important group is currently under preparation.

HOMOPTERA groups, probably due to their economic importance in agriculture, have been studied intensively in Virginia. Cicadas of Virginia have been listed by Davis (1922), McAtee (1927) and Allard (1938). Davis (1922) also described a new species from the state. Stearns (1927) published a faunal list of the leafhoppers of Virginia, which was later supplemented by Wene and Dominick (1941). Wheeler (1942) collected 30 species of *Empoasca* in light traps. Ball (1928) reported on the spittlebug, *Aphrophora saratogensis*. McAtee (1919a) prepared a key to the *Eupteryx* species, including records on one species from Virginia. Baker (1916) gave biological data on the species of the genus *Eriosoma* found in Virginia. Smulyan (1920) investigated the morphology of some economically important species of aphids, and prepared descriptions and keys for three species of *Aphis*.

There are several publications dealing with the scale insect species of economic importance in Virginia, but among the early workers only Hough (1922, 1925) conducted morphological investigations to clarify species differences. Morrison (1939) described a new species of *Matsucoccus* from Virginia. Kosztarab has been studying the Virginia scale insect fauna since 1959. Results of this study will be published through this series in the near future. However, some records on Virginia armored scale insects were included in one of his publications (Kosztarab, 1964). Russell C. Brachman is investigating the mealybug fauna while Mike L. Williams the soft scales of the state at present.

NEUROPTERA seems to be one of the most neglected insect orders in Virginia. Banks collected and reported on a few species (1904c), and on a rare neuropteran, *Dilar americana*, near Falls Church (1907c). Flint (1964a, 1965b) gave distributional records and morphology for some *Sialis* and one *Neohermes* species. Three *Chrysopa* species present in Virginia were described with distributional records by Bram and Bickley (1963).

Early studies on Virginia COLEOPTERA were conducted by Horn (1868), Banks (1912), Girault (1904, 1913a, 1913b, 1915b), McAtee (1916), Snyder and Shannon (1919), and Knull (1920, 1927). Hoffman (1937) reported *Pseudolucanus placidus* from Virginia. Robinson (1941) partly based his new species description of *Trox tytus* on Virginia material. King (1942) described the taxonomic distinction between *Cylene robiniae* and *C. caryae*. While working at V.P.I. for a Master of Science degree, King (1947) studied the species variation in the hind wings of *Silpha* and *Saperda*. Barr (1960, 1962, 1965) described new Carabidae species and one new genus from southwest Virginia material. Richard L. Hoffman collected many Coleoptera specimens, especially Cerambycidae and Scarabaeidae from Virginia, and is preparing a manuscript on the Cerambycidae of Virginia.

Pierce (1918) included in his comparative morphology work several host records on STREPSIPTERA present in Virginia.

Banks (1904c) reported on two genera of MECOPTERA. Specimens collected by R. L. Hoffman in Virginia were sent for study to Mecoptera specialist G. W. Byers. Parfin (1955) and Tombes (1956) gave information on the occurrence of two species in the state.

TRICHOPTERA larvae and adults more recently have been collected in southwest Virginia by Charles V. Covell, Jr., Richard L. Hoffman, Stuart E. Neff and Judy A. Wilburn. Most of their materials have been included in the V.P.I. collection. Almost all the adult specimens were identified or verified by O. S. Flint. Banks (1904a, 1904c) listed several species, including new ones, from the state. Betten (1934) included some Virginia records in his study on the caddisflies of New York State. Ross (1938, 1939, 1962) gave distribution for some and described two new species, while Flint (1958, 1965a), reported three new species from Virginia. Flint (1956, 1960, 1962, 1964b, 1966) presented distributional and biological data, also morphological descriptions for several species from Virginia. Flint and Wiggins (1961) reported three additional species from the state.

The LEPIDOPTERA fauna of Virginia was systematically studied by Ellison A. Smyth from 1891 to 1925. He was especially interested

in the Sphingidae, but added several new records to the Virginia fauna list on other groups of Lepidoptera. Smyth (1902a) reported that the V.P.I. Lepidoptera collection included about 3,300 species. The diverse interest and quality of his work proved him to be one of the outstanding biologists of his times. He prepared morphological descriptions of Lepidoptera larval stages (Smyth, 1900b, 1912), and conducted rearing experiments to clarify the species. He also described their seasonal forms (Smyth, 1902b, 1908), and studied their biology where this was possible (Smyth, 1900a). Other workers who studied Lepidoptera in Virginia were: Braun (1908, 1920); Dyar (1910); Girault (1908, 1913a, 1913b, 1913c, 1913d, 1915b); Wood (1916); Wood and Gottschalk (1942a, 1942b, 1942c); Skinner (1920); Jones (1926); Clark and Clark (1939, 1951). There were many other collectors of Lepidoptera who specialized in Virginia butterflies, but because they were listed in a detailed bibliography by Clark and Clark (1951), were not included in this review.

The only comprehensive study available at the present on a group of Virginia insects is "The Butterflies of Virginia", prepared by Austin H. Clark and Leila F. Clark (1951). Intensive collections of Virginia Lepidoptera were made by Charles V. Covell, Jr. in 76 counties, especially from 1960 to 1965, while studying at V.P.I. He also revised and enlarged the V.P.I. Lepidoptera collection, published on the occurrence of *Satyrium kingi* in Virginia (Covell, 1962), revised and brought up-to-date the faunal list of the Virginia butterflies and skippers (Covell, 1967). His Ph.D. dissertation (Covell, 1965) includes several records on the species of *Scopula* (Geometridae) in Virginia.

DIPTERA are among the orders studied more intensively in Virginia, especially those families of medical and veterinary importance.

The first faunal list of the mosquitoes (Culicidae) of Virginia was compiled by Dyar (1922). Mosquito surveys have been conducted in the Williamsburg area by Dorsey (1944). An annotated list of the mosquitoes of Virginia was published by Dorer, Bickley, and Nicholson (1944), with some further information on their distribution, added to this list by Bickley (1957) with two new species records for Virginia. Gladney worked on some phases of ecology of 23 species of mosquitoes in Southwest Virginia. Gladney and Turner (1969) completed a manuscript for publication in this series on the mosquitoes of Virginia, with new records for the state.

Investigations on the *Culicoides* (Ceratopogonidae) of Virginia (survey, bionomics, transmission of infectious synovitis) were the subject of two doctoral studies (Messersmith, 1961, 1964, 1965, 1966; and Hair, 1966) and a M.S. thesis (Werheim, 1962) at Virginia Polytechnic In-

stitute. Wirth (1951) listed over 30 species from Virginia, of which 8 were new. The larval habitats of 21 *Culicoides* species were described by Hair, Turner, and Messersmith (1966).

Underhill (1940) reported the distribution of two simuliid species feeding on turkeys.

Other workers who contributed to the knowledge of the Diptera fauna of Virginia are listed in the following paragraph:

Johannssen (1929) described *Sciara lurayi* as a new species from the caverns of Luray, while Fisher (1943) listed species of Mycetophilidae from Virginia. A new species of Itonididae was described by Foote (1953) as a pest of holly in 3 eastern states, including Virginia. Banks (1904b) redescribed and gave the life history of the "yellow fly", a tabanid, from the Dismal Swamp. Thompson (1967) recorded some Tabanidae from the state in his recent work. Cresson (1920) studied Virginia specimens of *Pogosoma* (Asilidae). New species of Dolichopodidae were described from the state by Van Duzee (1914a, 1914b, 1915). A new *Phyllomyza* species (Milichiidae) was described by Steyskal (1942), while Cresson (1924) selected the type of *Rhyso-phora robusta* (Ephydriidae) from Virginia material. Levitan (1952) listed 28 species of Drosophilidae from southwest Virginia. A new species, *Fannia americana* (Anthomyiidae), was described from the state by Malloch (1927). Tachinid new species were described by Townsend (1916) and Reinhard (1958), while Rowe (1932) recorded *Polidea areos* from Virginia. Banks (1907d, 1912) captured 121 species of Diptera in the state.

Parasitic dipterans were investigated by Townsend (1916) and by Bobb (1942, 1963), while a case of human myiasis due to green bottle fly larvae was reported by Pratt (1956).

Fortunately, two of the present V.P.I. staff members (Stuart E. Neff and E. Craig Turner, Jr.) are interested in the Diptera of Virginia. The V.P.I. Diptera collection is under revisionary work and organization by G. Tanner. J. Bruce Wallace has completed a Ph.D. study on the ecology and description of immature stages of the genus *Cordilura* under the direction of Neff, who himself is working on the ecology and description of immature stages of Scatophagidae. Roth and Neff (1964) observed the larvae of five Diptera species in the profundal bottom fauna of Mountain Lake, while Neff and Berg (1966) reported six species of *Sepedon* (Sciomyzidae) from Virginia.

A quick check of the publication by Ewing and Fox (1943) on the fleas of North America shows how little is known on the SIPHONAPTERA fauna of Virginia. Jan G. Humphreys, a Ph.D. candidate in the Department of Entomology at V.P.I. is preparing a publication on

the Siphonaptera of Virginia, which may be printed in this series on the Insects of Virginia.

Distributional records on miscellaneous HYMENOPTERA from Virginia were given in a series of publications by Girault (1904, 1913a, 1913d, 1915a, 1915b, 1916). Two new species of sawflies of the genus *Neodiprion* were described by Ross (1955), while Morris, Schroeder and Bobb (1963) gave a detailed account on the biology of the pine sawfly. Woodwasp distributional records from the state were presented by Rohwer (1918). Morrison (1917) and Muesebeck (1936) described three new species of braconid wasps from Virginia. Trigonaliidae and Roproniidae wasps were reported by Banks (1908b). Fouts (1924) in his revision on the North American Platygasterinae included descriptions and distributional records on 11 species from Virginia, with 15 additional ones from the District of Columbia. He (Fouts, 1948) also reported 10 species, including two new ones, of *Trimorus* (Scelionidae) from the state. Krombein (1951, 1952, 1962) who is living in Arlington, Virginia, listed with biological notes several species of wasps (Dryinidae, Tiphidae, Mutillidae, Vespidae, Pompilidae and Sphecidae) from northern Virginia. Two Ampulicidae were recorded from the state by Bradley (1934).

The sphecid wasps have been among the more intensively studied Hymenoptera in the state. Plate (1934) reported on one species, while Will (1935) described the epidemics of the giant sand wasp (*Sphecius speciosus*) at Narrows, Virginia. Prey records, including distributional records, on several species in the state were given by Krombein in a series of articles (1948b, 1956, 1958a, 1963). Krombein (1958b, 1959, 1961) also studied the dispersal of introduced species of sphecid wasps in Virginia.

Bees were recorded in the state by Swenk (1907), Lovell (1909), Cockerell (1908, 1915), Ellis (1915), and Jackson (1920). The biology of miscellaneous beneficial parasitic wasps was studied and their distribution recorded by Gahan (1933), Krombein (1948a), and Bobb (1962, 1963, 1965).

LIST OF SELECTED LITERATURE
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The INSECTS of VIRGINIA: No. 1

Part II: The Biotic Regions of Virginia

*Richard L. Hoffman**

Introduction

From the standpoint of biogeography, the Commonwealth of Virginia enjoys an especially favorable position. In an east-west direction, the state embraces no less than five of the major physiographic provinces of eastern United States, with a resultant diversity of topography and habitat types. Through the combination of latitudinal location (36.30 to 39.30° N.) and a considerable range of vertical relief (sea level to 5,720 feet), a variety of biotic associations determined primarily by climatic factors is found within the political boundaries of Virginia. To a greater extent than in adjoining states, the surface drainage is shared among basically old and geographically important river systems. Yet, despite the long and venerable tradition of education and culture in Virginia, relatively little attention has been paid to the biota of the state — we still know only very imperfectly what kinds of plants and animals occur here, to say nothing of the patterns and dynamics of their distribution.

So far only a few groups of organisms have been surveyed as regards their occurrence in Virginia, namely the birds, mammals, and various small groups of vascular plants. For the state there exist a recent manual on the ferns and allied forms (Massey, 1944); a fairly detailed account of the butterflies (Clark and Clark, 1951); a checklist of the avifauna (Murray, 1952); and a popularized handbook of the mammals (Handley and Patton, 1947). Aside from these, one must turn to technical literature—monographs and other systematically oriented papers—for in-

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formation on the occurrence of animal and plant life in our state. What is presently known about the major patterns of distribution is inherited from the original work of C. Hart Merriam and his collaborators in the development of the "Life Zones" in North America; the boundaries drawn through Virginia by Merriam in his map of 1910 have not been altered since that time, nor have they even been refined in detail by local studies with the notable exception of small modifications resulting from ornithological studies. Moreover, although the Merriam life zones established some general patterns of distribution and provided a great impetus for the study of North American biogeography, they were defined largely on the basis of temperature as the dominant environmental influence, and in recent years the concept of "life zones" has come to be doubted as an ideal means for the expression of distributional phenomena.

As originally conceived and defined by Merriam and his co-workers near the end of the last century, life zones were major continent-wide belts characterized by thermal parameters; they extended generally in an east-west direction but turned southward down the major mountain chains and northward along the seacoasts. Because of their great geographic extent, the biota of these areas naturally varied greatly from one place to another—the climatically defined "Lower Austral" of California having virtually no common denominators with the same zone in Georgia insofar as representative animals and plants were concerned.

The vast majority of organisms of eastern North America can be readily distinguished as being basically either *boreal* or *austral*, either as regards their individual ranges or in reference to the distribution of the larger groups to which they may belong (Professor J. Chester Bradley [1956] suggests the alternate terms *thermophygic* and *thermophilus* in an important recent discussion of insect distribution). In this sense, Merriam's emphasis upon temperature is obviously well-founded, but it is nonetheless little more than the application to North America of the same principles that distinguish arctic, temperate, and tropical biotas on a global scale. In more recent years, attempts have been made to distinguish more localized and biotically homogeneous regions in North America, characterized especially by large numbers of both animals and plants sharing similar ecological requirements and geographic distributions. Such regions have been defined under the names "biome" and "biotic province" and are discussed in such readily obtainable references as Shelford's *Ecology of North America* (1963) and Dice's *Natural Communities* (1952). In a general way, both of the categories mentioned are based to a large extent upon the evaluation of numerous environmental factors of which climate and physiography—in the broadest

sense of both concepts—are predominant. To a considerable extent, such regions often correspond closely with physiographic provinces, since local climate is strongly influenced by local topography.

Generally speaking, biomes appear to be especially useful to students of ecology, whereas biotic provinces are of greatest interest to students of biogeography. Although the entire country of Mexico has recently been zoned into such provinces, the principles of Dice's approach seem to have been applied so far to only one eastern state, in an excellent study of the biotic provinces of Oklahoma by W. F. Blair and T. H. Hubbell (1938).

Several states however have been divided into natural regions on the basis of one group of organisms or another: birds, mammals, butterflies, reptiles, and some plants (notably forest types, see especially Braun, 1950). It is obvious enough that although such studies are valuable and interesting in themselves, a synthetic concept of biogeography in a given area must be a distillation of evidence from as many groups as possible compiled against a framework of climatophysiography.

Although Dice's various major provinces no doubt accurately and adequately reflect spatial distribution of characteristic animal and plant associations, they appear somewhat too inclusive for eastern United States (most of which is contained in the single Carolinian Province) and may desirably be rendered into smaller and more localized subgroupings. Possibly a modified usage of "life zones" will provide the necessary local refinement, although a satisfactory definition and delineation of biotic districts in Virginia will require the accumulation of far more detailed information than is now available. For the purposes of this provisional statement regarding conditions that may influence the occurrence and distribution of insects in this state, one can only resort to a subjective account of the more obvious factors and apparent regions. It is earnestly hoped that this subject can be given the careful investigation that it so richly deserves before the increase of the human population and artificial conditions alters or destroys our original natural environment forever.

Environmental Factors

We may envisage several categories of environmental influences that tend to affect the distribution of organisms at a local level. To a large extent these factors are mutually interacting; for example, the soil composition of a given region may be a function of both vegetation cover and rock type, and the relationship between elevation and temperature is well known. It seems appropriate to consider first such lithospheric

categories as geological and physiographic regions, and various climatic variables. In this respect, the textual material may be regarded as little more than commentary upon the various maps which actually present the important information in precise and condensed form.

OVERALL GEOLOGICAL FEATURES

Briefly stated, the surface rocks now exposed in Virginia represent a nearly complete section from Precambrian to the present time, with deposits of Permian and Jurassic age omitted, and with only minimal traces of Triassic beds remaining. West of the Blue Ridge, there are extensive formations of Paleozoic sedimentary rocks extending upward to about the middle Pennsylvanian, and scattered intrusions of volcanic origin, perhaps of Cretaceous age. East of the Piedmont, the so-called Coastal Plain is composed of poorly consolidated clastic sediments derived from the Appalachian region, and dating in age from upper Cretaceous to Pleistocene. The intervening regions, Piedmont and Blue Ridge, are largely crystalline volcanic and metamorphic rocks, often highly mineralized, and extremely variable in chemical composition. Much of the Piedmont has a characteristic appearance; the rocks upon weathering produce reddish lateritic clay which is often micaceous and tends to choke small streams with a glittering silt. The Blue Ridge is formed of considerably more resistant rocks: granites, schists, greenstone, and slates are common.

Geological History

The geological history of Virginia is common to that of the entire central Appalachian region. The area now included in the western third of the state was an active geosyncline during most if not all of the Paleozoic, during which time about four miles of sediments were accumulated from a source area (the so-called "Appalachia") presumably located on the present site of the Coastal Plain and the Continental Shelf. Up to and including part of the Mississippian, the deposition was entirely marine, but during the late Paleozoic, gradual emergence of the entire region permitted the formation of fresh water lacustrine and terrestrial formations, including carbonaceous shales and coal. Fossils of terrestrial organisms are frequent in Pennsylvania beds.

During the Permian the entire basin of deposition was subjected to lateral compression and general uplift, resulting in extensive folding and faulting along a northeast-southwest axis. This activity was strongest in the eastern part of the geosyncline, where the original width was reduced by more than half; in the western region (the area now

occupied by West Virginia), folding was negligible and the Paleozoic beds remained basically horizontal. The structural deformation of this time largely set the stage for the eventual development of the present topography by erosional cycles millions of years later in the Tertiary.

Contemporaneously, the eastern source areas continued to be lowered both by continued erosion and by subsidence of its eastern part beneath the Atlantic. Erosion of the newly elevated western region was in progress, and by Triassic time an extensive level plain (the so-called Fall Zone Peneplain) is thought to have developed, with its western margin located somewhere east of the present Virginia-West Virginia boundary. During this time, the region now included in the Piedmont of Virginia, Pennsylvania, and New Jersey developed basins of deposition accumulating chiefly terrestrial sediments, some of the latter being red sandstones with the footprints of small three-toed dinosaurs.

During the Jurassic the entire area was above sea level, and erosion continued; in the early Cretaceous, sediment from the folded Appalachians was deposited along the shore line, corresponding roughly with the present boundary between Piedmont and Coastal Plain. Later in the Cretaceous there was a general uplift that rejuvenated the existing drainage systems and commenced a new cycle of erosion that continued for some millions of years to the Miocene time of late middle Tertiary age. This erosional process resulted in the formation of the so-called Schooley Peneplain, thought by Fenneman (1938) to have been an undulant, poorly drained landscape with isolated knobs and ridges standing perhaps a thousand feet above the mean level. It is considered that many of the highest existing peaks and ridges of the folded Appalachians represent degraded remnants of the Schooley peneplain surface.

An uplift of the region, perhaps during the late Miocene, initiated a new erosional period extending into the Pliocene, during which time the Harrisburg Peneplain was developed. This physiographic level is presently represented by the Shenandoah Valley and the Piedmont, as well as along larger rivers within the folded Appalachians. Further uplift since the Pliocene has caused a new erosional cycle which is still cutting into the Harrisburg level and producing a number of small localized erosion surfaces.

Throughout most of the Tertiary, the Coastal Plain has been subject to gradual emergence, and its innermost surfaces were involved in the afore-mentioned erosional activities. At the present time, the Coastal Plain consists of a number of wave-cut terraces running parallel to the Fall Belt; the history of these terraces is involved with the sequence of glaciated periods during the Pleistocene when the shorelines receded

drastically sea-ward, and deep gorges were cut by the major rivers across the coastal plain beds. At the present, the Coastal Plain appears to be in a period of submergence; its outer extent (including Chesapeake Bay and major estuaries) under many fathoms of water.

Physiographic Provinces

The land surface of any area may be classified into discrete regions on the basis of local homogeneity of topographic features. These, as might be expected, result from the interaction of erosional forces and subsurface lithologic units, and to a certain extent agree closely with the major geological provinces. However, the structural orientation and/or deformation of the rock types is as significant (or more so) in the origin of physiographic regions as their lithological composition, chiefly because of the resultant effect upon the behavior of both surface and ground water. The two major provinces, Ridge and Valley and Appalachian Plateaus, are developed from essentially similar upper Paleozoic sedimentary rocks, but the different degree of folding, thrusting, faulting, and so on, has influenced the totally different surficial form of these provinces.

The outstanding general reference upon this subject as it concerns our area is Fenneman's *Physiography of Eastern United States* (1938) which should be consulted for characterizations of the provinces and subprovinces and landform features endemic to each. Simplified maps are available in numerous textbooks of physiography and general geology. The following remarks pertain chiefly to the significance of the various regions as they occur in Virginia and actually or potentially influence distributional patterns. Five provinces in two primary categories (Fig. 1) may be outlined as follows:

- | | |
|------------------------------|----------------------------|
| 1. Coastal Plain | |
| 2. Piedmont Plateau | } Appalachian
Highlands |
| 3. Blue Ridge | |
| 4. Ridge and Valley Province | |
| 5. Appalachian Plateaus | |

The Coastal Plain is an essentially flat-lying region of sands and poorly-consolidated beds of clays, marls, and gravels. It corresponds very closely to the part of Virginia known as "Tidewater" since most of the larger streams that cross the coastal plain are essentially at base level and are subject to tidal movements. Geologically the region consists of sediments ranging in age from Cretaceous to Upper Tertiary laid down unconformably upon a basement of crystalline rocks extending eastward from the Piedmont. During the Quaternary glacial periods,

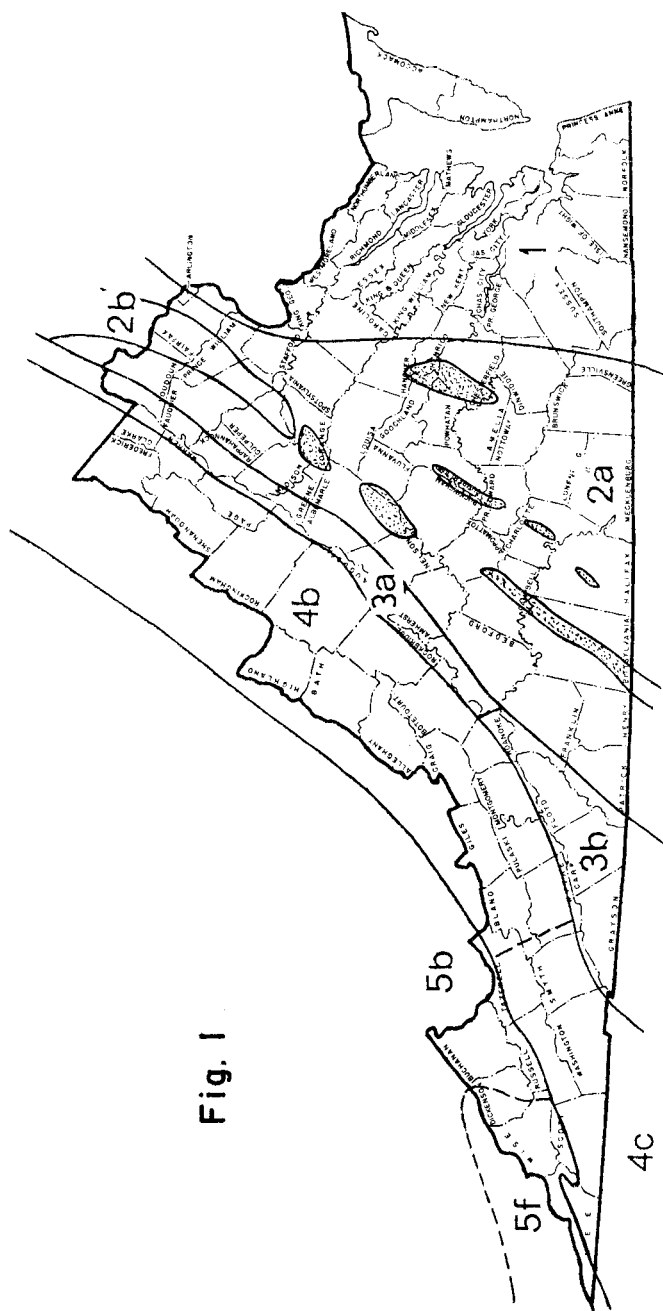


Fig. 1

FIGURE 1.—Physiographic Provinces of Virginia, adapted from Fenneman, 1938, and with the same index numbers. 1, Coastal Plain. 2a, Piedmont Upland; 2b, Piedmont Lowland. 3a, Blue Ridge, Northern Section; 3b, Blue Ridge, Southern Section (separated at the Roanoke River). 4a, Ridge & Valley, Middle Section; 4b, Ridge & Valley, Southern Section (arbitrary boundary between these sections runs southeast from the vicinity of Tazewell approximately on the New-England drainage divide). 5a, Unglaciaded Alleghany Plateau; 5b, Cumberland Mountains. Triassic Lowlands in the Piedmont are stippled.

an appreciably lower sea level caused a greater seaward extension of the Coastal Plain than is now evident, although this fluctuation is commemorated by deep submerged river valleys that cut across the bottom of the Chesapeake Bay and some of the larger estuaries. From west to east, beginning at the base of the so-called Fall Belt that extends from Great Falls to Fredericksburg to Richmond and southwestward, a number of progressively lower wave-cut terrace levels are distinguishable and have been given names derived from areas of classical exposure. The larger rivers—James, York, Rappahannock, and Potomac — are bordered along much of their extent by prominent steep cliffs cut in the calcareous Yorktown beds (Miocene in age), but many other rivers that are less deeply entrenched, such as the Blackwater, flow slowly through broad and often swampy floodplain basins that duplicate habitats more characteristic of the southeastern states. Physiographically the Coastal Plain has been divided into the Atlantic and Gulf regions. In Virginia it is not possible to readily distinguish subdivisions aside from the previously-mentioned terrace levels.

In the usage of Nevin M. Fenneman (1938), the Appalachian Highlands region is divided into six major provinces, four of which extend through a part of Virginia in a diagonal northeast-southwest direction. Aside from being components of the great mountain system of eastern North America, these provinces have little in common either lithologically or structurally and each has developed a very characteristic topography.

The Piedmont region extends from southeastern Pennsylvania to central-western Georgia, as a rolling peneplain established upon a base of crystalline metamorphic rocks. Entering Virginia from the north it is a relatively narrow strip between Great Falls and Harper's Ferry; in going southward the Piedmont widens strongly and along the southern boundary of the state occupies all of the region between Emporia and Stuart. Basically well-drained, the Piedmont nonetheless contains several lowlands in a central strip extending southward (the well-known Triassic Lowlands) in which lotic environments are developed. Running down the western third of the Province are a variety of hills and ridges essentially parallel to the Blue Ridge and averaging about 20 miles east of it. These outliers include Bull Run Mountains east of Warrenton, Carter's and Southwestern Mountains in Albemarle County, Smith Mountain northwest of Chatham. Between this chain of ridges and the Blue Ridge itself, the Piedmont assumes a distinctly more hilly and diverse relief and is sometimes referred to as the "Inner Piedmont" in contrast to the more monotonous "Outer Piedmont" that rolls eastward to the Fall Belt. But this latter subregion itself shows sporadic higher

relief; the somewhat surprising Willis Mountain in Buckingham County may be considered a monadnock.

The naturalist crossing Virginia from the east must be inspired with admiration upon his first sight of the majestic Blue Ridge. Rising a thousand feet from the rolling Piedmont, this grand and well-named range of sharp peaks and broad rolling ridge crests divides the state into two radically different parts. From a relatively low and narrow mountain, cleft by the Potomac at Harper's Ferry, the Blue Ridge gradually gains in stature in going southward until south of Roanoke it becomes an elevated plateau nearly 3000 feet above the sea, upon which in turn stand the great fir-capped peaks of the Iron Mountains: White Top and Mount Rogers.

The Blue Ridge is composed primarily of metamorphosed igneous rocks (granites, granodiorite, slates, and green stone) although Lower Cambrian formations lie upturned all along its western slopes both in Tennessee and Virginia. It is possible to distinguish two quite different regions in Virginia, referred to by Fenneman (1938) as the Northern and Southern Sections, separated approximately at the Roanoke River. Between the Roanoke and Potomac water gaps, the Blue Ridge consists of a jumbled range of broad-topped ridges, some 3000 to 3500 feet in elevation, with frequent peaks extending nearly or quite to 4000 feet. This Northern Section, which extends on into eastern Pennsylvania, is here about five miles in average width, often becoming much narrower in the vicinity of major wind and water gaps. To the west lies the broad flat Shenandoah Valley, to the east is the even lower Piedmont Plateau; the Blue Ridge is here clearly isolated, its exile still being enforced and increased by the progressive baseleveling of the Shenandoah, a process that commenced during the late Cretaceous, according to the studies of Watson and Cline (1913).

South of the Roanoke gap the Blue Ridge begins to assume the increasing height and breadth that culminates in western North Carolina in the great ranges of the Blacks, the Balsams, and the Great Smokies where dozens of peaks exceed 6000 feet in elevation. Driving south on U.S. Interstate Highway 81 as it passes Salem, Virginia, one gets an excellent view of the beginning of the Southern Section of the Blue Ridge, where this region terminates at Poor Mountain in Roanoke County, a prominence standing 3000 feet above the river that skirts its northern base. Southward along the western edge of Franklin and Patrick counties the Blue Ridge forms a high escarpment behind which lies the rather high, intermontane plateau drained by the upper New River and its two major tributaries, Little River and Big Reed Island Creek. This region,

embraced chiefly in Floyd, Carroll, and Grayson counties, is bordered on the west by a series of essentially continuous ridges beginning with Poor Mountain and ending at the Tennessee-Virginia state line on Iron Mountain. Locally this range is broken into short segments by water gaps: Pilot, Macks, and Poplar Camp are the successive unit names, although in actuality, all are synonymous with Iron Mountain. The relief of the Blue Ridge intermont plateau in Floyd County is one of deeply dissected valleys and ravines, although a few notable elongated ridges stand above the plateau level: Alum Ridge, Indian Ridge, Willis Ridge, and Buffalo Mountain. In the vicinity of the last-named eminence (one of the scenic highlights of the region) many square miles lie above 3000 feet. Both Little River and Big Reed Island Creek have carved magnificent deep gorges across the Iron Mountain chain. The biota of both areas must be studied immediately before they are destroyed forever by needless damming of these beautiful wild streams. The western third of Grayson County contains the tallest and most scenic mountains in Virginia, Mount Rogers and Whitetop, which together comprise the aptly-named Balsam Mountains. These two adjacent domes, separated by a pass 4000 feet above sea level, are clad with extensive forests of red spruce and Fraser fir analogous to those of the northern evergreen biome.

West of the Blue Ridge extend the sedimentary formations of Paleozoic age that are divided on the basis of structural factors into two provinces. In a broad belt ranging from New Jersey to Alabama occur the complexly folded and faulted beds of the Ridge and Valley Province, in which the original extent of the formations was reduced to less than half by lateral compression. The name of this physiographic unit derives from the topography of narrow, elongated, parallel ridges and intercalated valleys that developed upon this base following its peneplanation during the Cretaceous. The drainage today represents very strikingly the "trellis" pattern.

Within the Ridge and Valley Province it is possible to recognize two quite different topographic regions, which may be referred to as the Great Valley and the Alleghanies respectively. The first of these is a broad, gently undulant plain lying immediately west of the Blue Ridge, which it follows from Pennsylvania to Alabama, developed by the base-leveling action of various major streams upon chiefly limestone and shales of Cambrian and Ordovician age. In Virginia, the Great Valley is divided into several segments corresponding closely to local drainage systems; thus we have from north to south the Shenandoah, Roanoke, New, and Holston Valleys in succession. The first two mentioned drain eastward

into the Atlantic and range in average local elevation between 800 and about 1200 feet above sea level. The last two contain the headwaters of west-flowing streams and are in fact really high plateaux of 1000 up to 2500 feet in height. Because of this drastic difference in valley floor elevation, the Great Valley as it crosses southwestern Virginia is bordered on each side by relatively less distinct ridges, although these may actually be as high here as farther north. The Valley may be as much as 30 miles in width in northern Virginia, and yet narrows down to less than a mile in the vicinity of Buchanan where it is largely closed off by ridges projecting in from the west. At such a place, the Valley obviously is scarcely the same zoogeographic barrier as elsewhere, and the same thing is true farther south, in the vicinity of Wytheville and Marion, where local peaks and ridges constitute a sort of higher-elevation "land-bridge" from the Iron Mountains across to the Alleghanies. The Great Valley connects with the Piedmont at two narrow water gaps, those of the Potomac and James Rivers, and one broad low one, where the Roanoke crosses the Blue Ridge. This last passageway constitutes a major entry for lowland species making their way upstream.

The Valley of the Holston River, represented by three major headwaters, is again relatively broad and flat. From an eminence such as Mount Rogers one can discern the outline of Clinch Mountain nearly 30 miles across the valley to the west.

Immediately along the western edge of the Great Valley the topography changes abruptly and dramatically for the entire length of western Virginia. Here begins a belt of alternating high narrow ridges and broader valleys ranging in width from about 35 miles in the latitude of Winchester to about half that distance in southwestern Virginia. This region owes its characteristic relief almost entirely to the occurrence of a single geological formation, the Clinch (Tuscarora) sandstone of Silurian age. Although not especially thick, this bed of white marine sandstone is unusually resistant and uniform throughout the extent of the Alleghanies, and forms a protective cap supporting the tops of the highest ridges in the region. It is admirably shown in such outlying features as House Mountain near Lexington, and in the winter months may be seen like the ramparts of a castle at many places in western Virginia.

The ridges and mountains may be classified structurally into two chief types, synclinal and anticlinal, of which the latter is perhaps the more frequent. Anticlinal ridges are formed by the removal of the domed or arched part of a large fold, leaving behind the two sloping sides which usually face each other across a valley of older formations

comprising the interior of the original arch or fold. Usually the Clinch Sandstone is exposed along the upper edge and outer slopes of these ridges, subtended lower on the inner slopes by extensive outcrops of Ordovician shales. In several instances, the breached anticline may have been originally an elongated or lens-shaped dome, and the resultant erosion of its softer interior beds produces a rather high, narrow, "canoe-shaped" anticlinal valley, examples of which are Burkes Garden, Tazewell County; White Rock Valley, Alleghany County; and Bolar Valley in Bath and Highland Counties. Usually one end of the valley is produced into an exceptionally elevated part of the rim of mountain top. At Burkes Garden the high point is Beartown Mountain (4705 feet) on the southwest end of the bowl, in the case of Bolar Valley, it is Sounding Knob (4390 feet) at the northeast end that comprises the highest place. In all three of the localities mentioned, the valley floor is nearly or quite 3000 feet above sea level, and such regions tend to remain relatively cool, even in midsummer. They usually contain extensive cave systems, sinks, and springs.

Synclinal mountains are formed by the preservation of resistant sandstone beds along the central axes of larger synclines, thus both slopes of such mountains may be composed of shale deposits and the tops may be relatively broader and flatter than in the case of the rather sharp-crested anticlinal ridges.

Probably the most extensive synclinal systems in Virginia are to be found in the western part of Augusta and Rockingham counties: Great North Mountain attains a height of 4458 feet at Elliott's Knob, and Reddish Knob on the Virginia-West Virginia state line is nearly as high (4397 feet), but such dimensions are somewhat exceptional. In southwestern Virginia, the impressive *vis-a-vis* prominences, Butt Mountain and Angel's Rest in Giles County, are part of a previously continuous synclinal mountain now breached by the New River at Pearisburg.

As remarked, the drainage pattern throughout the region is dominantly of the trellis type, with numerous and often impressive water gaps breaking the parallel ridges. Because of the relative depth and narrowness, these gaps often remain cool and damp throughout the year and afford local havens for the survival of various thermophygic species. Unfortunately, the same physical characters make water gaps attractive to dam-builders, and the naturalists must make haste to study these regions before they have all been inundated or otherwise despoiled.

The southwesternmost counties of Virginia (Lee, Dickinson, Wise, Scott, Russell, Buchanan, and Tazewell) lie partly or entirely within the Appalachian Plateaus Province, the surface features of which are de-

veloped on Upper Paleozoic sedimentary rocks that are virtually horizontal, and only rarely interrupted by faulting. As a result, the drainage pattern is dendritic, and has developed a great ramifying system of deep, narrow valleys draining to the west by way of the Big Sandy and Cumberland rivers. At many places the uppermost resistant sandstone beds may stand out like great battlements, winding their way for miles along the contour of a particular elevation. Coal beds are abundant and have been exploited for decades by tunnel and strip mining, the latter process often resulting in vast, unsightly terraces following the coal seams along the mountainsides. In this region, the province does not attain much height, and appears as a low plateau with rolling hills and valleys to an observer looking west from the summit of Clinch Mountain. As might be expected, the difference in relief and elevation results in rather striking differences in the biota of the Appalachian Plateau. From its easternmost limits (as at Sandy Ridge, forming the boundary between Russell and Dickenson-Buchanan counties), there is a gradual westward downslope virtually to the Kentucky state line, which follows Pine Mountain to its culmination at the Russell Fork River at Breaks. Northeast of this river there is no geographical demarcation between Virginia and Kentucky. In Lee County, the province is represented for the most part only by the eastern escarpment of Cumberland Mountain, although in the region of St. Charles and Pennington Gap, the state line curves westward to encompass some of the Black Mountain range, the latter being well represented in Wise County.

CLIMATIC FACTORS

It is difficult to present detailed information about the distribution of temperature and precipitation in Virginia except in the most general terms. Despite the relatively good coverage of the state by recording stations, the fluctuations of climate, especially in mountainous regions, is often so localized as to escape detection or to be impossible to show on a map. Climatic information, both tabular and graphic, is available for Virginia in "Climate and Man: 1941 Yearbook of Agriculture" and more extensive and recent data of the same type in "A Handbook of Agronomy" (Bulletin 97, Cooperative Extension Service, Virginia Polytechnic Institute, 1966), from which the following notes have been abstracted.

Average Precipitation

Average annual precipitation in the state ranges from about 35 to 51 inches in a somewhat irregular pattern of high and low areas (see Figure 2). In general we can recognize three areas of greater annual

Fig. 2

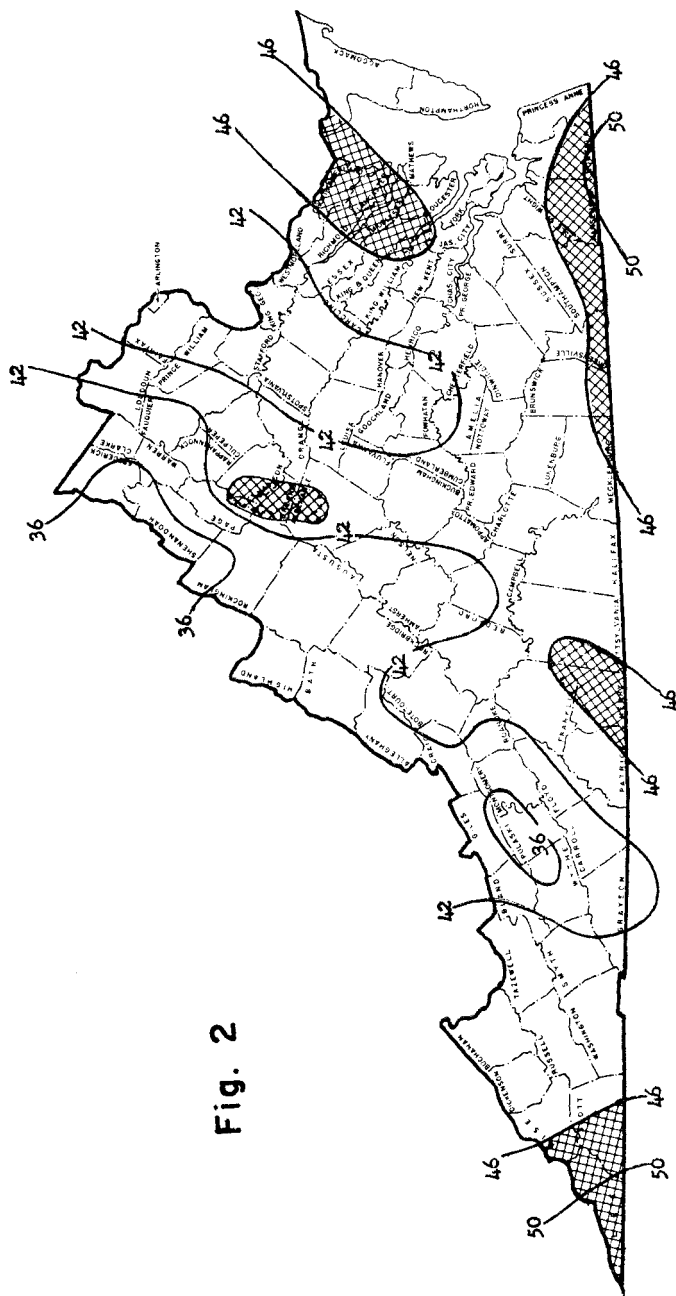


FIGURE 2.—Average annual precipitation in Virginia. For clarity, only arbitrarily selected isophenes are mapped. Areas receiving over 46 inches of precipitation are shaded.

precipitation: in the central Blue Ridge from the Peaks of Otter north to Hawksbill Mountain; in the Dismal Swamp region, and in the extreme western half of Lee County. There are two areas of low precipitation: one in the western part of Rockingham, Shenandoah, and Frederick counties, and a much smaller one centered in Pulaski County. Perhaps these two areas fall in a "rain shadow" of high mountains lying just to the west of them.

Snowfall records indicate that the southeastern Coastal Plain receives the lowest amount for the state (less than 10 inches per annum); it therefore receives a greater relative amount of rainfall than other parts of the state. The central Blue Ridge and the Burkes Garden region record the maximum snowfall, according to the maps, but almost certainly the Mount Rogers region also must fall into this category.

Growing Season

To a considerable extent, the thermal characteristics of a given region are reflected by the number of frost-free days per annum, or by the length of the effective growing season. For the great majority of Virginia's counties the growing season lasts from 150 to 200 days. In two local regions (the higher mountains in Tazewell and Smyth counties, and in parts of Bath and Highland counties) the figure drops considerably below 150 (only 136 at Burkes Garden, 3000 feet). Three areas enjoy a growing season longer than 200 days: the Holston Valley near Bristol; a part of the Inner Piedmont in Albemarle, Nelson, Campbell, and Appomattox counties; and a large part of the outer Coastal Plain, where a state maximum of 254 days is recorded at the Norfolk Airport (see Figure 3).

It must be emphasized that statewide maps of climatological data inevitably must be oversimplified, and fail to reflect local vagaries which may be quite pronounced within the space of one or two miles. Even in mountainous regions where such variation is most pronounced, most weather stations are located in the lower valleys and we cannot rely on official records to show local patterns.

The effect of elevation upon temperature is well-known, and I need cite only one example that is already familiar to many biologists: the contrast between Blacksburg (in the Great Valley at 2100 feet) and Mountain Lake (only 10 miles to the northwest but in the Ridge and Valley Province at 3800 feet). Within the limits of my personal experience, the difference of 1700 feet vertically creates a thermal difference of about 20° F., perhaps even greater during the night. In the winter, snow appears on the higher ridges (above 3500 feet) several

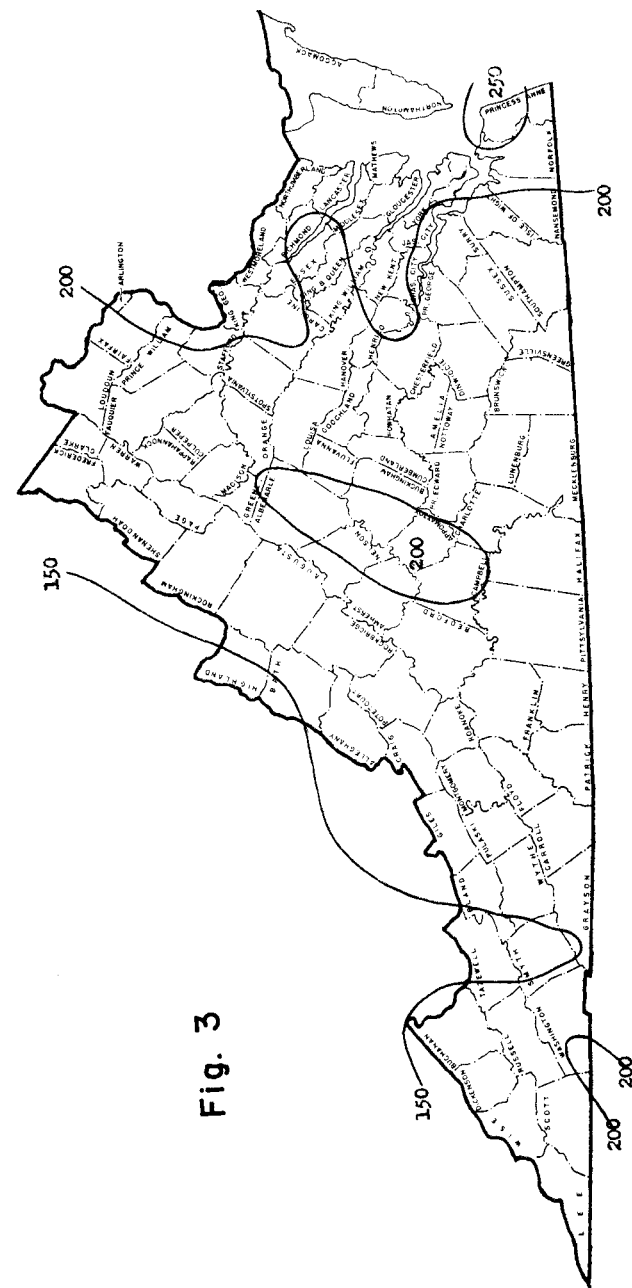


Fig. 3

FIGURE 3.—Distribution of the length of growing season in Virginia. Only three isophenes are mapped in order to indicate the major pattern and avoid an overcrowded map. As emphasized in the text, the shorter growing season interval is undoubtedly more extensive in the mountains than suggested by the "less than 150 days" isophene, and the area so characterized doubtless in fact extends southward into North Carolina instead of ending, as shown here, in Grayson County.

weeks before falling first in the valleys, and may persist an equally longer time in the spring. It is not unusual, as a corollary, for various flowers to be found in bloom at 4000 feet for 6 to 8 weeks after their season is over at 2000 feet or lower. Obviously, however, the accurate delineation of local weather patterns would require data from thousands of strategically-placed stations within a relatively small area.

FOREST TYPES

The classic reference source on the forest cover of our region remains the exceptionally useful *Deciduous Forests of Eastern North America* (Braun, 1950), which provides additionally a wealth of information on physiography and forest ecology in general. Braun recognized nine major deciduous forest regions, of which four occur in Virginia. Their approximate distribution is shown by Figure 4.

1. Mixed mesophytic region
 - a. Cumberland Mountains
 - b. Alleghany Mountains
 - c. Cumberland and Alleghany Plateaus
2. Oak-chestnut region (Braun's 4th region)
 - a. Southern Appalachians (on map as 4a)
 - b. Northern Blue Ridge (4b)
 - c. Ridge and Valley (4c)
 - d. Piedmont Section (4d)
3. Oak-pine region (Braun's 5th region)
 - a. Atlantic Slope section (on map as 5a).
4. Southeastern evergreen region
 - a. Mississippi Alluvial plain (6a)

The majority of Braun's book is devoted to a detailed consideration of the characteristics and distribution of the various regions and sections. It is therefore possible to present here only a very brief outline of the situation in Virginia with the expectation that the interested student will have or find access to Braun's manual.

The definition of regions and smaller divisions is somewhat subjective and arbitrary. Braun remarks that "Even though a region is named for the climax association normally developing within it, it should not be assumed that the region is coextensive with the area where that climax can develop." As defined by her, a climax association is said to possess a unity throughout its geographic extent resulting from:

1. some uniformity in particularly the dominant floristic components,
2. essential uniformity in physiognomy (general appearance), and
3. common historical and/or genetic origin.

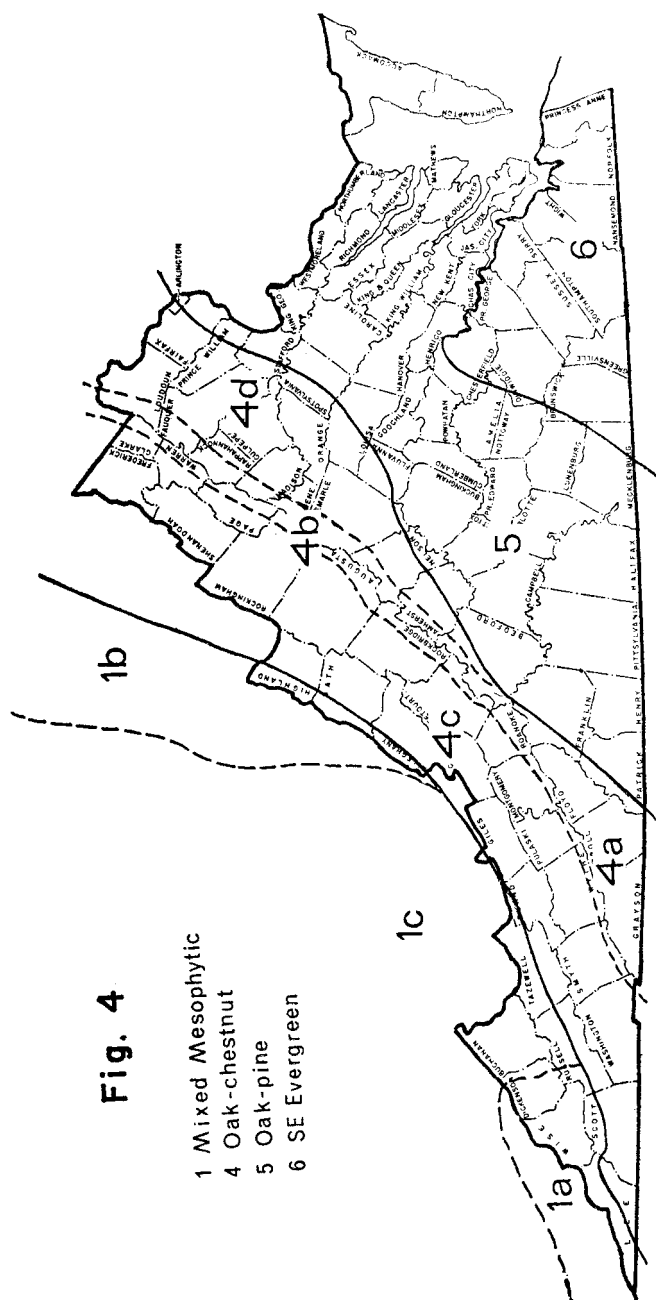


Fig. 4

- 1 Mixed Mesophytic
- 4 Oak-chestnut
- 5 Oak-pine
- 6 SE Evergreen

FIGURE 4.—The distribution of forest regions in Virginia, after Braun, 1950, and with the same index numbers. 1a, Cumberland Mountains; 1b, Alleghany Mountains; 1c, Cumberland & Alleghany Plateaus. 4a, Southern Appalachian Section; 4b, Northern Blue Ridge Section; 4c, Ridge & Valley Section; 4d, Piedmont Section, of the Oak-Chestnut Forest Region. 5, Oak-Pine Region, Atlantic Slope Section. 6, Southeastern Evergreen Forest Region. The general distribution of many of these sections invites comparison with physiographic regions, Figure 1.

However, there exists considerable variation within any region or section as regards the composition of the flora or proportional representation of the dominant species. Such variation can be geographical, altitudinal, local, or successional. In general, the various regions are defined primarily on the basis of their areas of most characteristic development, but this does not preclude the occurrence of localized pockets of a given region outside its mapped range. For instance, the Mixed Mesophytic Region per se occurs only along the very westernmost periphery of Virginia, yet it is possible to note the occurrence of fairly characteristic mixed mesophytic associations at suitable places in the Ridge and Valley and Blue Ridge Physiographic provinces (where they are referred to as "cove forests").

Although the distribution of the various forest regions is largely determined by climatic factors, it is interesting to compare Figures 1 (physiographic provinces) and 4 (forest types) to note an obvious relationship. Thus, the Mixed Mesophytic corresponds closely to the Appalachian Plateaus Province; the Oak-Chestnut to the mountains and Northern Piedmont; and the Southeastern Evergreen to the Coastal Plain. Even a person who has little botanical knowledge can appreciate the obvious and characteristic facies produced by the combination of a particular forest association and a certain physiographic unit.

It must be recalled that on the basis of other criteria, quite different mapping of forest types will result. The recently published map of Kuchler (1964) bears no resemblance to that of Braun, owing to the fact that its various forest regions are defined in different terms. Kuchler shows most of Virginia to be occupied by oak-hickory-pine forest; the Blue Ridge and southern half of the Ridge and Valley by "Appalachian oak forest", and a few scattered areas by northern hardwoods, mixed mesophytic, and southern floodplain forest. As one who has lived and traveled in the region for decades with some awareness of vegetational cover, I feel partiality to Braun's arrangement.

The regions recognized by Braun may be very briefly summarized as follows:

Mixed Mesophytic Forest

The mixed mesophytic forest is characterized by the sharing of dominance among several species of trees, notably beech, tulip poplar, basswood, sugar maple, sweet buckeye, chestnut, red and white oak, and hemlock. This association develops only on moist but well-drained soils. Braun states: "It occupies a central position in the deciduous forest as a whole, and from it or its ancestral progenitor, the mixed

Tertiary forest, all other climaxes of the deciduous forest have developed." The importance of this region in the study of particularly humus-inhabiting organisms must therefore be emphasized as it represents an environmental type of considerable antiquity and stability. In Virginia the best development of this forest is to be seen in the far southwestern counties of Wise, Dickenson, and Buchanan, although decades of promiscuous logging have considerably altered the original aspect of the association in most places. To be sure, small local pockets of this association are to be found in deep, cool watercourses along the Blue Ridge and in many watergaps of the Alleghanies. A feature not emphasized by Braun is the frequency of magnolias of several species, notably *Magnolia tripetala*.

Oak-Chestnut Forest

Braun defines the oak-chestnut forest region by "... the former dominance of oak-chestnut forest on most of its slopes, and by the dominance of white-oak forest, particularly on the broad expanses of the Great Valley." As shown in Figure 4, the region and its several local sections occupy most of mountainous Virginia, and in fact extend also to the east across the northern Piedmont. Compare this eastern boundary with that of the Alleghanian Biotic region (Figure 7). It must be recalled that within the region as mapped, there exists a complex mosaic of oak-chestnut (now largely oak-hickory) forest with pine forests in drier environments and mixed mesophytic in the damper. Often all three forest types may be seen in contiguous places along a given mountain range.

At higher elevations (chiefly above 4500 feet in the Iron Mountains of Virginia) the oak-chestnut forest is replaced by a more boreal type of association in which sugar maple, yellow birch, beech, and buckeye are the dominant trees. This "northern hardwood" forest is conspicuous on the eastern slope of Mount Rogers, for instance. It is in turn succeeded above by the spruce-fir stands with scarcely any intergradation. Along the streams the northern hardwood facies merges into cove forest with no intercalation of oak-chestnut.

Oak-Pine Forest

The oak-pine forest is correctly considered by Braun as a sort of transitional region between the Appalachian forest and the evergreen region of the Southeast. The climax association is one of oak and hickory, but the abundance of pines in secondary forests and their general occurrence, even in the climax, justifies the recognition of a major region-

al type. It is best developed in Virginia in the southern Piedmont ("Southside Virginia").

Southeastern Evergreen Forest

In the usage of Braun, the Southeastern evergreen forest region extends from the James River south and west as far as eastern Texas, and is distinguished by the preponderance of evergreens, particularly longleaf pine. It contains however, abundant broadleaf forest representation.

Braun arbitrarily draws the northern limit of this region at the James, partly because of a major change in soil type there, and because the characteristic longleaf pine does not extend further north. She emphasizes, however, that numerous other species characteristic of the region do occur sporadically as far northward as New Jersey.

Kuchler's map of "Potential Natural Vegetation" (1964) does not include a southern evergreen category; however his "Southern Floodplain Forest" characterized by oaks, blackgum, and cypress, likewise terminates in Virginia south of the James.

Although the Coastal Plain is a relatively young surface as far as its availability as an environment is concerned, nonetheless the Southeastern Evergreen Region contains a number of ancient types of plants which are either endemic or else represented sporadically in the Appalachians or the interior of the continent. The Coastal Plain populations in these forms must be considered as migrant relicts which have survived fragmentation of their original distribution and which have moved into areas which have become available since that event. M. L. Fernald devoted many years to the flora of southeastern Virginia, but much field work remains to be done and the speed at which the region is being urbanized or otherwise modified imparts a sense of urgency to such studies.

Biotic Regions

With some background of local geology and physiography, and a general idea about the distribution of climatic factors, we may now turn to the consideration of animal and plant distributions within Virginia and must face at the outset the existence of several difficulties.

First, any attempt at zonation or districting must largely exclude aquatic and semiaquatic species whose ranges normally follow stream systems that may cross the boundaries of regions defined on the basis of terrestrial forms. This restriction is unfortunate, since the fauna of the Clinch, Powell, and Holston rivers has a distinctly "Mississippian" flavor, as, to a lesser extent, does that of the New-Kanawha system.

About the only aquatic species that lend themselves well to inclusion in zonation studies are those with clear-cut temperature and/or oxygen threshold requirements and which thereby are either restricted to high mountain streams or sharply excluded from them.

A second and more trenchant difficulty in the zonation of a given political area is the handicap of treating only local situations without much reference to the continent-wide relationships. This is especially true if one attempts a synthesis along the lines dictated by new or different criteria, with the result that there may be no comparable information available for other regions.

Thirdly, in a state such as Virginia, where biological reconnaissance has lagged so drastically, the compiler of biogeographic data is often at a loss for information on most or all groups of organisms.

For these, as well as unstated reasons, the first attempt at recognition of biotic regions in Virginia is predestined to be inadequate and unsatisfactory. The following ideas are advanced with considerable temerity, more in the sense of suggestions to stimulate future work than as confident delineation of natural areas.

Primary stimuli for the study of biotic zonation in North America came from the pioneering work of C. H. Merriam and co-workers in the old U.S. Biological Survey, which was based to a large extent upon the influence of climatic conditions upon plant and animal distribution. Some of the recent objections to Merriam's "Life Zone" principles have been mentioned above (page 24); a few others may be noted.

As regards eastern North America, the Life Zone classification consisted of the following hierarchy:

<i>Region</i>	<i>Life Zone</i>	<i>Faunal Division</i>
BOREAL	Arctic	
	Hudsonian	
	Canadian	
AUSTRAL	Transition	Alleghanian*
	Upper Austral	Carolinian*
	Lower Austral	Austroriparian*
TROPICAL	Tropical	

The three starred faunal divisions were represented in western North America by equivalent units of the three life zones involved, with a basically similar climatic correspondence but appreciably different biotic assemblages. The three boreal zones were not distinguished regarding

eastern and western faunas. The following map (Figure 5) represents the apportionment of Virginia into life zones following the criteria of Merriam's system, on the basis of the 4th Provisional Zone Map of 1910.

It must be recalled that the life zones were worked out originally on the basis of the distribution chiefly of higher vertebrates and seed plants. It may be obvious that a zonation made using the ranges of invertebrates and cryptogamic plants might well be somewhat different in detail! We know, for instance, that the climatic conditions needed to produce a "Canadian Zone" effect may exist at much lower elevations and in smaller areas for small arthropods than for trees, birds, and mammals.

My personal reaction to the foregoing classification is that the Transition Life Zone ("Alleghanian" in Virginia) might better be moved into the Boreal Region, as its characteristic life forms seem dominantly to be clearly thermophytic and basically northern in their distribution or in their lines of taxonomic affinity.

The possibility of distinguishing a "Transition" zone of any type seems to me somewhat questionable. If we admit to the generalization that there are only two basic biotas in North America, following the reasoning of Professor J. C. Bradley (1956, p. 257), it appears obvious that any area of broad overlap between them contains an admixture of thermophytic and thermophilus forms and has little if anything characteristic to itself. For instance, to the best of my knowledge, all of the species of Virginia animals whose inland distribution matches the limits of the Carolinian Division occur also in the Austroriparian. A large number of "Alleghanian" species also occur commonly in the Canadian, and most northern forms normally associated with spruce-fir biomes occur well down in the presumed Alleghanian.

It is easy enough to compile a list of species, both animal and plant, whose northernmost (or southernmost) limits coincide closely with the life zone boundaries. But with a little effort, one can make similar lists of species whose known ranges collectively define totally different kinds of patterns. Like the mathematicians who are sometimes accused of being able to prove anything by numerical manipulation, the student of distribution can set up biotic districts or regions in great variety by judicious selection of his indicator species. One basic assumption in both the Life Zone concept and the Biotic Province alternative of Dice is that we must visualize and formally delineate geographic regions that are mutually exclusive and thereby do not overlap except at their peripheries. Yet, may we not reasonably ask the question, is not this premise

a great oversimplification of the distributional facts, especially in regions of considerable topographic variety and vertical relief? Might one take the point of view that in certain areas, even of the same general elevation, major distributional patterns may conform clearly to geographic outlines that overlap very broadly, and thus give in effect a sort of three-dimensional set of districts or provinces? It seems reasonable to assume that various sets of organisms disperse and maintain themselves in response to entirely different combinations of environmental factors, and I hope to make a case in the following pages for this approach to the zonation or districting of Virginia.

As a final reaction to the Life Zone principle, one can look upon it as a sort of Procrustean Bed into which species must be arbitrarily fitted, sometimes in defiance of observed phylogenetic facts. To illustrate this point, we can consider in Virginia the vicinity of Mount Rogers, which lies on the north side of the blunt triangle of Southern Blue Ridge that extends into Virginia from a much greater base in North Carolina and Tennessee. Mount Rogers and nearby White Top still contain extensive spruce and fir forests (which apparently were much greater in earlier times) and many of the various concomittant species characteristic of the Canadian Zone, to which, along with the Blacks, the Balsams, and the Smokies, the region has traditionally been referred. There is no gainsaying that a number of strictly boreal organisms extend southward from Canada into the Southern Blue Ridge and of course occur at Mount Rogers, the lygaeid bug *Blissus leucopterus hirtus* being a good example. Yet these same mountains contain a considerable variety of endemic species and genera having no demonstrable relationship with Canadian species or higher taxa; their affinity for high, cool, evergreen forests (or at least adjacent sugar maple-beech forests) may be a local adaptation from some essentially tropical ancestor at a time when the Southern Appalachians served as a refugium during climatic changes. Numerous animals of the high southern Blue Ridge barely extend into Virginia; we may mention the longhorned beetle *Michythisoma paradoxum* LeC., numerous terrestrial gastropods, and plethodontid salamanders such as *Plethodon welleri* and *Desmognathus wrighti*. None of these species are related to true boreal or holarctic groups and it would be a misnomer to tag any of them as "Canadian Zone" indicators even though they may be virtually confined to this zone as currently defined by, for instance, ornithologists. Braun (1950:479-80) discusses the same situation in vascular plants, and raises the question "If the disjunction of the Southern Appalachian spruce-fir forest was an event of the Pleistocene . . . how did it acquire so large a number of species not

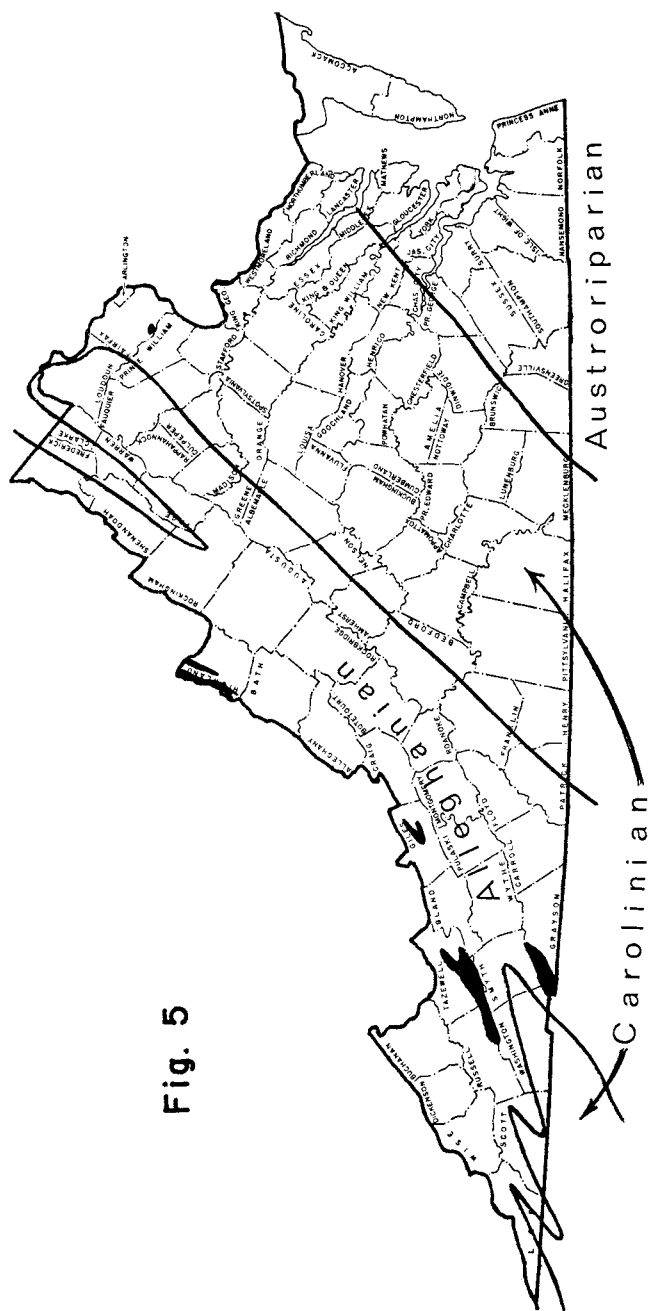


Fig. 5

FIGURE 5.—Distribution of Life Zones in Virginia, slightly modified from Merriam, 1910. The Canadian Zone is shown by the isolated black shading, perhaps exaggerated in the Tazewell County region.

common to the northern spruce-fir?" She concludes that "... the northern forest extended into the Alleghanies of West Virginia but no farther south . . .".

The number of organisms that cross from West Virginia to North Carolina by way of the still rather high divide between the New and Tennessee Rivers is quite large, and a distinct pattern can be distinguished at a level below the spruce-fir zone; yet this pattern is much less extensive than the traditional "Alleghanian" life zone upon which it is superimposed.

In the present state of our ignorance about the distribution of Virginia plants and animals, I think it would be a mistake to attempt a masterly synthesis of the various patterns that can be defined. Instead I wish merely to set forth these regions in the form of preliminary maps, with some indication of characteristic species as a basis for future studies. The names proposed are tentative and perhaps can be replaced at some future time if it be later established that this system has enough merit to warrant its continuation. My personal experience with the topography and ecology of regions outside of Virginia is relatively quite limited beyond the extent of the Southern Blue Ridge.

In the following pages are given rather brief accounts of the parts of Virginia that appear to comprise natural regions characterized by the general concordance of plant and animal distributions en masse. Obviously only some of the most conspicuous "index species" can be mentioned; these tend to be drawn from the ranks of the fairly well-known vertebrates. Too little is known about the occurrence in Virginia of most invertebrate groups, while plants tend to become difficult because of the large number of species to be considered. It is admitted at the outset that a considerable amount of the delimitation of regions is purely subjective and intuitive in nature, and based upon the subconscious evaluation of some 25 years of field experience in Virginia. Of course this is not scientific, and no doubt will elicit criticism. It is offered at the present primarily in the hope of stimulating further interest in the biogeography of this state.

Some obvious areas of controversy are (1) the adoption of broadly overlapping biotic regions instead of the mutually exclusive, side-by-side zones and districts of previous systems, (2) the failure to admit a special region for the spruce-fir "Canadian" zone of Merriam's classification.

I can only say on point (1), as I did in a previous paragraph, that I can see no reason why, in a mountainous area, that two or more major distributional patterns cannot overlap on a map, as in actuality there may be distinct stratification either through different local environments

or vertical relief throughout the areas of overlap. Such distributional patterns obviously are tangible and the result of numerous species of organisms adapting themselves to a given geographic surface wherever they find the appropriate ecological situations. Regarding point (2), although I agree fully that the spruce-fir-biome is an ecological reality in the sense of being an environmental continuum, I still feel that it is geographically confusing and incorrect to associate the high evergreen forests of the southern Blue Ridge with those of Canada chiefly on the basis of the two dominant trees, several species of birds, and one or two mammals. Certainly other biotic elements of the southern spruce-fir biome are quite endemic in their own right, and in many cases have no true boreal affinities whatever.

I have adopted the term "Region" partly because it is not so likely to be confused with the term Province as used in both biogeography and physiography, and partly because, being noncommittal, it is endowed with some flexibility in the future refinement of this arrangement. I believe that all of these "regions" would fall within the limits of Dice's "Carolinian Biotic Province". Perhaps future work will show the desirability of reclassifying some of my regions as "districts" or as "subdistricts", instead of regarding them all as essentially equivalent, which is doubtless a naivete on my part.

As regards proper names, some have been taken directly from the older work of Merriam where correspondence seemed evident. Instead of "Austroriparian" I prefer a geographic name, and suggest in its place "Floridian" since the index species of that region are probably most abundant and widespread in Florida. The new name "Shenandoan" is proposed for the Blue Ridge between the Potomac and Roanoke Rivers in recognition of its high degree of endemism; perhaps the more conservative would prefer regarding this a subregion of the Alleghanian.

We can assign the various regions to two main groups on the basis of climatic dominance and/or directions of affinity of the index species or groups:

Austral:

Littoral

Floridian

Carolinian

Boreal:

Alleghanian

Teaysian

Shenandoan

Cumberlandian

LITTORAL REGION

Along the coastline and the margins of the major rivers and estuaries of the Atlantic Coast occurs a biotic zone of rather sharply-defined facies. (Figure 6). Including chiefly tidal areas, this region may also

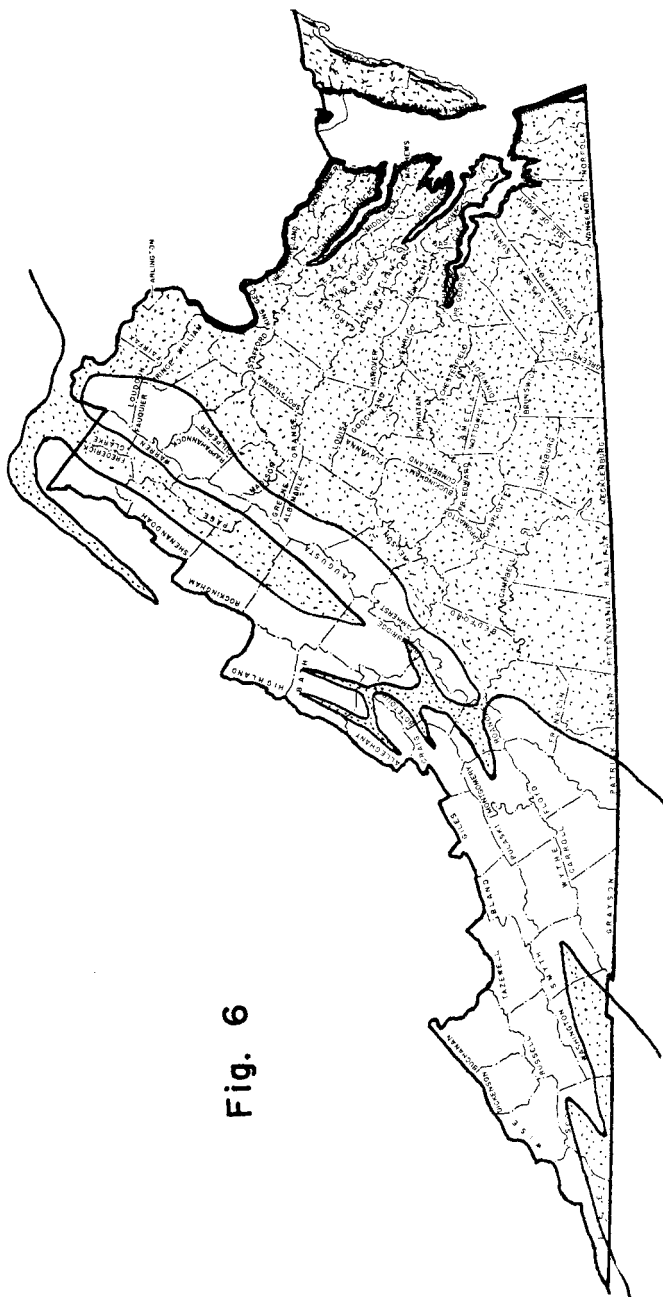


Fig. 6

FIGURE 6.—Approximate extent of the Littoral (solid black) and Carolinian Biotic Regions in Virginia. The latter overlaps broadly upon the Floridian (Figure 7) in eastern Virginia, and with the Alleghanian in the northern and central western part of the state, although intermingling of the faunas is usually not very pronounced.

embrace lagoons and brackish-to-fresh water environments, as well as some low dunes and beach areas. In Virginia, one thinks at once of the Back Bay area, the lower Rappahannock, and much of the Eastern Shore, in this frame of reference.

The plant life is dominated by species of the genera *Spartina* and *Scirpus*, and there is a variety of floating and emergent forms such as *Typha* and *Sagittaria*. Along the sandy beaches and dunes may be dense copses of *Myrica* and scrub oak. A characteristic reptile is the diamond-backed terrapin, and two closely related treefrogs, *Hyla cinerea* and *H. squirella*, likewise appear to be essentially restricted to the Littoral. Index species of insects are perhaps best represented in the Orthoptera (Fox, 1917, for an extended account), of which may be mentioned *Orphulella olivacea*, *Clinocephalus elegans*, *Trimerotropis maritima*, and at least five species of *Neoconocephalus*.

FLORIDIAN REGION

Partly coincidental with the "Austro-riparian" zone of Merriam, the Floridian region in my usage extends a little farther inland along the larger streams (Figure 7). I see no reason that it should not extend northeastward to the Potomac or indeed into southern New Jersey.

The region is less well-defined than others, and is worthy of much further study; for one thing there is considerable indication of relictual distribution patterns. The water moccasin, for instance, fairly swarms in the Norfolk area and again in swamps along the lower Appomattox River, but there are no known intervening colonies. The water snake *Natrix rigida* is so far known only from New Kent County in Virginia, its next northernmost locality is in South Carolina. The range of the treefrog *Hyla femoralis* jumps from the Dismal Swamp to southern Maryland. The cricketfrog *Acris gryllus* teems in every ditch and marsh south of the York River, yet appears to be absent from identical situations between the York and Potomac estuaries.

Aside from the sporadic occurrence of basically austral forms, there is a considerable admixture of organisms having northern lines of affinity. The presence of cold springs in the lower Coastal Plain presumably affects the local biota considerably. At such a spring near Live-ly (Lancaster County), only a few feet above sea level, I once discovered the red salamander *Pseudotriton ruber* and the small aquatic hemipteron *Microvelia fontinalis*, both of which seem to be more at home in upland streams and springs. In a small collection of Trichoptera which I made in May, 1962, on Lake Drummond in the Dismal Swamp, Dr. H. H. Ross identified chiefly species that he would consider char-

acteristic of the Adirondacks (pers. comm.). An additional caddisfly of this type was recorded by Gurney (1963) who gives additional remarks of interest on the distribution of insects in the Dismal Swamp region. It might eventually be shown that the Swamp in fact represents a relict of a northern swamp biome which has been subsequently invaded by austral organisms migrating northward after the last glacial withdrawal.

The lack of pronounced geographic features (aside from terrace levels and large estuaries) renders subdivision of the Floridian Region somewhat difficult. Many of its most typical species coincide fairly well with the Coastal Plain Province, but some others extend inland in various degrees, making it hard to delimit the Floridian from another region located chiefly on the Piedmont and in the larger valleys of the mountains.

Such a large number of animals and plants are confined to the outermost part of the Coastal Plain of southeastern United States, reaching their northernmost limits near Cape Henry, that one might justify the recognition of a separate region to include the two lowest terrace levels. The name "Sabalian" might be revived to denominate such a region.

CAROLINIAN REGION

In general distribution and biotic content, the Carolinian region (Figure 6) corresponds to Merriam's Carolinian Life Zone but is displaced somewhat farther inland and overlaps broadly with the Alleghanian Region. The common species are those which are abundant in the Piedmont, with many extending also into the Great Valley along the larger rivers; few if any occur in the part drained by New River and the upper Tennessee system.

Most of the Carolinian index species occur also in the Floridian, but may be less abundant or form a less conspicuous part of the biota there.

There are two interesting variations upon the general distributional pattern: one in which species may occur widely in the Piedmont and in the Roanoke-Shenandoah valleys (often well up the James River too), but not into southwestern Virginia. These include the treefrog *Acris crepitans*, the racerunner lizard *Cnemidophorus sexlineatus*, the snake *Lampropeltis calligaster rhombomaculata*, the salamander *Eurycea guttolineata*, and the turtle *Pseudemys floridana concinna*, to mention some well-known vertebrates.

In the second pattern, the various species usually do not extend quite so far inland, often failing to reach the Inner Piedmont, but conversely do follow the valley of the Tennessee River northward into the south-

western counties of Virginia, where they may occur in distinctly montane environments. Here we may mention the microhylid frog *Gastrophryne carolinensis*, the mud salamander *Pseudotriton montanus*, sweetgum (*Liquidambar styraciflua*), and the common holly *Ilex opaca*. Some snakes show the same pattern: the southern greensnake *Opheodrys aestivus* and the kingsnake *Lampropeltis getulus*.

It seems possible that these two patterns may have originated independently from quite different originals, in that the first may represent fairly recent northeastern migrations, and the second may be the result of previously widespread distributions dating back to the Cretaceous peneplanation, having been disrupted by the development of the Appalachian region through Tertiary erosion and uplifting.

If these basic differences eventually can be confirmed, it would seem desirable to provide a designation for the second type appropriate to its presumptive origin. Botanical literature contains numerous references—summarized in a fairly recent review by L. G. Carr (1940)—to the occurrence in the Appalachian region of plants otherwise characteristic of the Coastal Plain. The “residual” interpretation suggested to account for the plant species would, it seems probable, be equally valid in the case of animals having similar distributions. Most of these forms appear to be biologically conservative in the sense of not being abundant and active colonizers, perhaps another indication of their antiquity and their relictual status.

Unfortunately, little is known about the distribution of insect species that conform to either of the foregoing variations on the Carolinian pattern, although perhaps the occurrence of an undescribed species of *Saica* (a genus of subtropical reduviids) in the New River valley may fit here.

ALLEGHANIAN REGION

To a considerable extent, the Alleghanian region (Figure 7) matches closely the Alleghanian Life Zone of the Merriam System, and extends from Canada southward into central Alabama along the main axis of the Appalachians but also embracing part of the Inner Piedmont as well. In Virginia, the eastern limit would extend basically from the vicinity of Great Falls to Gordonsville, Lynchburg, and Martinsville. Innumerable species conform to this limitation, and most of them tend to be scarce or missing from the Shenandoah Valley. North of the Potomac, the Alleghanian swings toward the coast to include most of Pennsylvania and the northern third of New Jersey.

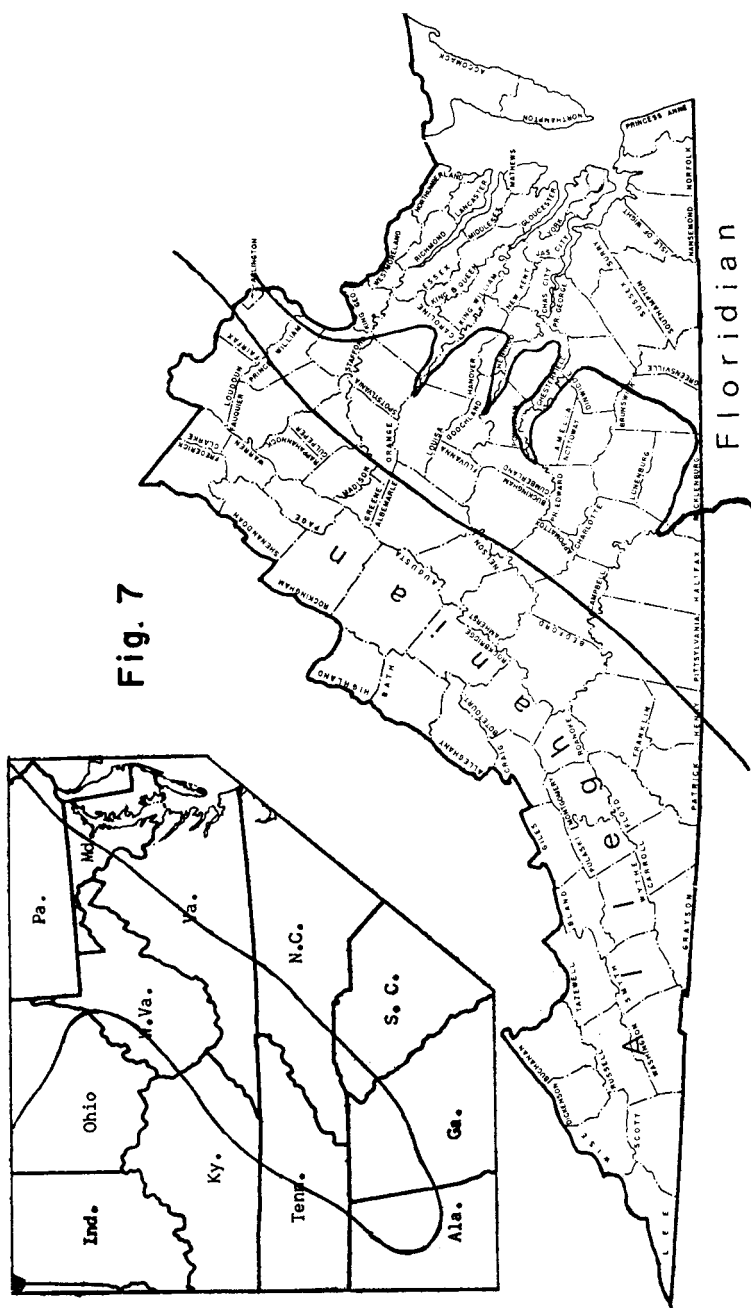


Fig. 7

FIGURE 7.—Approximate extent of the Floridian and Alleghanian Biotic Regions in Virginia. The latter region is somewhat more inclusive than the Life Zone of the same in the usage of Merriam and his followers.

Some characteristic amphibians are the salamanders *Ambystoma jeffersonianum*, *Gyrinophilus porphyriticus*, and *Eurycea longicauda*, and the woodfrog *Rana sylvatica*. The grasshoppers *Encoptolophus sordidus*, and *Camnula pellucida*, and the katydid *Scudderia pistillata* are good index species, also among the true bugs the reduviid *Oncerothachelus acuminatus*, the stilt-legged bug *Neides muticus*, two lygaeids *Blissus hirtus* and *Zeridoneus costalis*, numerous mirids, and the pentatomid *Meadorus lateralis*. All of these are species that are basically thermophytic and are mostly widespread and common in New England and southern Canada. The list could be extended greatly.

In the Ridge and Valley Province of central western Virginia, many of the typical Alleghanian species rather tend to be confined to the higher elevations (above 1500 feet and replaced along the larger valleys by vicariating lowland forms, or not at all.

SHENANDOAN REGION

The Shenandoan region (Figure 8) is the only one known to be contained entirely within the state: it corresponds closely to the Northern Section of the Blue Ridge Physiographic Province between the Potomac and Roanoke Rivers. The age and completeness of its geographic isolation must be considerable (probably since middle Tertiary), for here we find the greatest extent of endemism insofar as animals are concerned. Interestingly enough, the major lines of affinity are to the north and west instead of southward along the Blue Ridge, with only a few exceptions.

The following organisms may be cited as representative:

Abies intermedia Fulling (Pinaceae) (=? *phanerolepis* Fernald). Whether this taxon is a valid endemic species in the Hawksbill region, or only an isolated population of *A. balsamea* apparently remains to be settled. In any event, the occurrence of balsam fir in the northern Blue Ridge establishes a boreal tree type in the Shenandoan Region.

Clematis verticillaris DeCandolle (Ranunculaceae). This northern plant extends more or less continuously south along the Alleghanies to northeastern West Virginia; it is represented, however, by a weakly defined variety *cacuminis* Fern. at the Peaks of Otter and probably elsewhere at higher places along the Blue Ridge.

Stygobromus spinosus Hubricht & Mackin (Gammaridae). This small, blind amphipod is so far known only from four localities in the Blue Ridge north of Rockfish Gap.

Scytonotus virginicus (Loomis). A small species of the diplopod family Polydesmidae which is common and generally distributed throughout

the region as far south as the Peaks of Otter. Its nearest relative occurs in the Teaysian Region from Mount Rogers south to the French Broad River.

Semionellus placidus (Wood) (Xystodesmidae). Although not endemic to the region, this small milliped is common there and unknown elsewhere in Virginia. The remainder of its known range extends from western Maryland north and west to Minnesota.

Nannaria morrisoni Hoffman (Xystodesmidae). Another endemic, small milliped, occurring between the Potomac and James Rivers, replaced in the Peaks of Otter area by a related but so-far undescribed congener.

Fontigens orolibas Hubricht (Amnicolidae). This minute spring snail is said to be abundant along the Blue Ridge south as far as Rockfish Gap, a few miles beyond which its range terminates abruptly despite no apparent change in environment. Its closest relatives occur in limestone springs of the Ridge & Valley Physiographic Province.

Plethodon richmondi hubrichti Thurow (Plethodontidae). Endemic to the higher elevations of Apple Orchard Mountain, just north of the Peaks of Otter. The nominate subspecies occurs in the central Appalachians and the southern part of its range coincides closely with the Teaysian Region.

Plethodon richmondi shenandoa Highton and Worthington (Plethodontidae). Endemic to the Hawksbill Mountain area, this salamander has been only recently distinguished and named.

Desmognathus monticola jeffersoni Hoffman (Plethodontidae). The range of this subspecies coincides closely with that of the Region: the Blue Ridge between the Roanoke and Potomac Rivers. The range of the nominate subspecies is from central Pennsylvania south to Georgia along the Alleghanies and southern Blue Ridge.

TEAYSIAN REGION

Named in reference to the presumptive drainage system of the ancient Teays River, the Teaysian region (Figure 8) in the broad sense includes most of the Southern Blue Ridge south to the latitude of Asheville, a majority of West Virginia, the narrow isthmus of southwestern Virginia, and southwestern Pennsylvania. So encompassed is the region of greatest overall elevation in the central Appalachians and virtually all of the southern stands of spruce and balsam fir (the mountains south and west of the French Broad River probably warrant separation into a distinct Region).

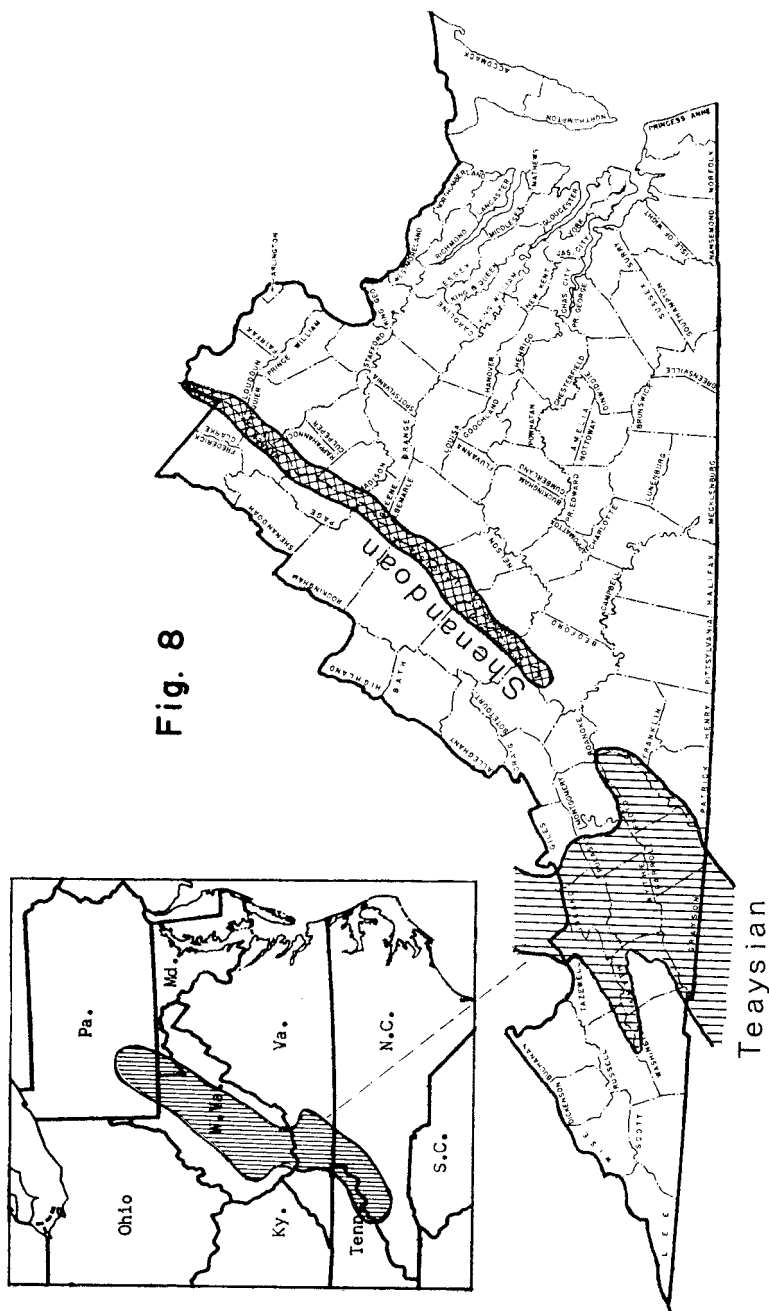


Fig. 8

FIGURE 8.—Approximate extent of the Shenandoan (crosshatched) and Teaysian Biotic Regions in Virginia. The inset map indicates in a general way the overall occurrence of the Teaysian, although perhaps extending a little too far northward. As thus drawn, the boundary embraces a majority of the high and cooler terrain of the two Virginias. There is probably justification for excluding the Great Smokies and Balsams as a separate region set off by the French Broad River, which appears to reflect a major faunal change.

The region is defined however on the basis of innumerable distributions in many groups of both plants and animals. Many amphibians in particular may be mentioned, for instance the salamanders *Desmognathus ochropheus*, *Desmognathus monticola monticola*, and *D. quadramaculatus* (see maps in Bishop, 1943), as well as *Plethodon richmondi* and *P. wehrlei* (maps in Highton, 1962).

Various other salamanders occur in the southern part of the region but do not cross over to the Ridge and Valley in Virginia: *Leurognathus marmorata*, *Desmognathus wrighti*, *Plethodon welleri*, *P. yonahlossee*. *P. jordani* crosses over and is abundant in the Clinch Mountain area but does not extend into West Virginia (Hoffman 1967). A similar range is shown by the milliped *Cambala hubrichti*, which extends from Georgia north to Patrick County, Virginia; it is known also from one station on Big Walker Mountain (map in Hoffman, 1958). Other millipeds that occur in the central part of the Teaysian and are virtually endemic to Virginia are *Apheloria kleinpeteri*, *Dixioria pela*, and *Brachoria ethotela*. The milliped *Brachoria separanda* (northeastern West Virginia) is represented by three close relatives in the upper New River drainage, *B. calcaria* in Pulaski and Montgomery counties, *B. versicolor* in Wythe and Bland counties, *B. hamata* at Burkes Garden. All four are probably geographic races of a Teaysian species extending to the north of the Virginia offset.

It will be noted that in West Virginia, the Teaysian is bordered on the east by the Greenbrier and Potomac River valleys, on the west by the edge of the Appalachian Plateaus Province. In Virginia, the eastern edge is formed primarily by the Atlantic-Gulf drainage divide. The western edge is somewhat diffuse, but is approximated by the hills and ridges around Marion. Farther southwest the biota is distinctly Carolinian again. The Teaysian Region is somewhat overlapped in West Virginia by the following region which is, however, distinctly more thermic climatically and characterized by lower elevations generally.

CUMBERLANDIAN REGION

The name of the Cumberlandian Region (Figure 9) is suggested because of the influence of the somewhat centrally-located Cumberland Plateau. In general this region coincides closely with the Appalachian Plateaus Physiographic Province and is most clearly defined in the dissected parts of West Virginia and Kentucky where the horizontal beds are exposed for miles along the contours of the valleys; there is a relatively high rainfall and the Mixed Mesophytic Forest occurs in its most typical form. Curiously, in the southern part of its extent, this region

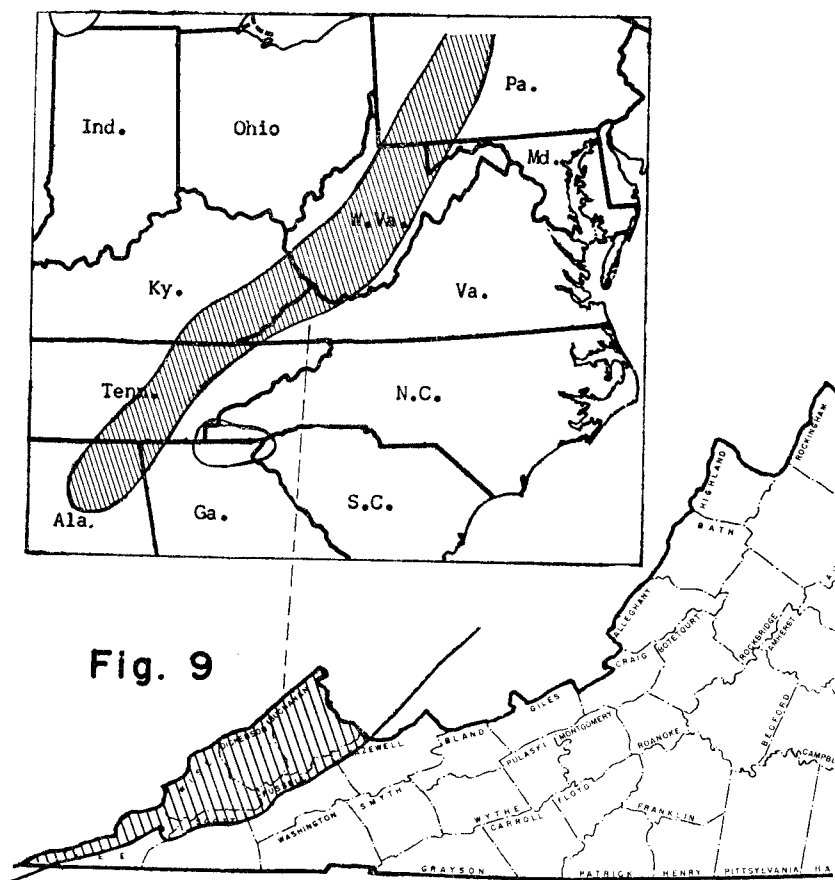


Fig. 9

FIGURE 9.—Approximate extent of the Cumberlandian Biotic Region in Virginia and (inset map) over its entire extent. The situation in Alabama and Georgia is not satisfactorily known at the present.

must be carried eastward into the southernmost end of the Blue Ridge as shown by the range of its two most characteristic animal species: the spider genus *Hypochilus* (Hoffman, 1963) and the salamander *Aneides aeneus* (the map in Bishop, 1943, is incorrect; see instead that by Gordon, 1967). The mountain chorus frog, *Pseudacris brachyphona*, ranges from western Pennsylvania to Alabama; at the southern end of this range it likewise swings east into the western tip of North Carolina, but in Virginia it is commonly found only west of the folded Alleghenies (there are a few scattered records for Tazewell and the western edges of Wythe and Pulaski counties). North of the New River it is strictly confined to the Appalachian Plateaus.

A majority of the known species of the milliped genus *Brachoria* are endemic to the Cumberlandian Region, five in the Virginian part alone (data from Keeton, 1959, 1965). The distribution of the milliped *Euryurus leachii* subsp. nov. (Hoffman, in MS) coincides almost exactly with the Region as here defined. A herbaceous plant that appears to have a similar range is the alumroot *Heuchera parviflora*.

In entering the Cumberlandian Region from the east, as along the New River or crossing Sandy Ridge into Dickenson County, I have never failed to be impressed by the different topography and certainly by the greater variety and abundance of the woody plants among which the species of *Magnolia* are conspicuous. One "senses" the occurrence of a quite distinctive biota even before the index species are first encountered. The Cumberlandian fauna at least appears to be distinctly less "boreal" in its orientation, and less involved in the higher elevations in the places where they overlap, than the Teaysian. A considerable number of species widespread in the interior of eastern United States find their easternmost limits along the edge of the Cumberlandian region, including some that are also widespread in the Gulf Coastal Plain.

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