MISCELLANEOUS PUBLICATIONS MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 50

A CONTRIBUTION TO THE KNOWL-EDGE OF VARIATION IN OPHEO-DRYS VERNALIS (HARLAN), WITH THE DESCRIPTION OF A NEW SUBSPECIES

ву ARNOLD B. GROBMAN

ANN ARBOR
UNIVERSITY OF MICHIGAN PRESS
March 26, 1941

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FREDERICK M. GAIGE
Director of the Museum of Zoology

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INTRODUCTION

It is agreed by most biologists¹ that the problems of speciation are akin to the problems of raciation. Raciation is a dynamic process, probably having its entire origin in population variation. Population and individual variation can best be analyzed by a biometrical study of large samples.

The northern green snake, Opheodrys vernalis (Harlan), provides admirable material for such a study. The species is common enough, over many parts of its range at least, to have been widely collected. Considerable numbers have reached museum collections; the University of Michigan Museum of Zoology alone has well in excess of 150 specimens with accurate locality data. The range is considerable and hence embraces a diversity of habitat conditions. As a species it is remarkably distinct and cannot conceivably be confused with any other American species.

There are two well-differentiated races represented in the accumulated material,² and it was necessary to define these races and to determine their ranges before the frequency variations of the several scale characters could be described and interpreted. An analysis of the accumulated data on correlations, linear measurements, ratios, and life history may be presented at a later time.

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

Over eight hundred specimens of the northern green snake have been examined from the following collections. Thanks are due the authorities at these institutions for the loan of specimens and for numerous other courtesies:

American Museum of Natural History (A.M.N.H.)
Academy of Natural Sciences, Philadelphia (A.N.S.P.)
Baylor University Museum (B.U.M.)
Carnegie Museum (C.M.)
Canadian National Museum (C.N.M.)
Cincinnati Society of Natural History (C.S.N.H.)
Cornell University Museum (C.U.)
Department of Zoology, University of Illinois (D.Z.U.I.)
Field Museum of Natural History (F.M.N.H.)
Collection of Frank N. Blanchard, University of Michigan (F.N.B.)

- ¹ Goldschmidt (1940) does not agree with this and suggests that species formation (macroevolution) is an entirely different process from raciation (microevolution).
 - ² Dr. Frank N. Blanchard had suggested this possibility to me some years ago.

Iowa State College (I.S.C.)
Kansas State Agricultural College (K.S.A.C.)
Museum of Birds and Mammals, University of Kansas (K.U.)
Collection of Laurence M. Klauber (L.M.K.)
Museum of Comparative Zoology, Harvard University (M.C.Z.)
University of Minnesota (M.U.)
Museum of the University of South Dakota (M.U.S.D.)
Museum of Vertebrate Zoology, University of California (M.V.Z.)
Ohio State Museum (O.S.U.)
Royal Ontario Museum of Zoology (R.O.M.Z.)
Toledo Zoological Society (T.Z.S.)
University of Michigan Museum of Zoology (U.M.M.Z.)
United States National Museum (U.S.N.M.)

After the scale counts were recorded they were punched on International Business Machine cards which were then put through the various interpreting and sorting machines. I am indebted to Alan D. Meacham, of the University of Michigan Sorting and Tabulating Station, for instruction in the operation of the machines and permission to use them.

Of especial value in the variational study was the large series of specimens taken by Stuart Criddle during the fall of 1934 from a hibernating situation in southern Manitoba. The majority of these have been deposited in the Canadian National Museum.

Several interested persons have materially lightened the work by supplying scale counts and by other assistance. Dr. Frieda C. Blanchard has kindly permitted me to use the data that had been accumulated by the late Dr. Frank N. Blanchard. For this, and for many other kindnesses of greater magnitude, I am deeply grateful. It gives me pleasure to acknowledge the generosity of M. Graham Netting for the scale counts of the West Virginia vernalis in the Carnegie Museum; of Roger Conant for those of Ohio specimens; and of Harold Trapido for those of the Cornell University specimens. For assistance in making counts on specimens in the University of Michigan Museum of Zoology, and for other varied and numerous aids, I am indebted to my fellow students, Dr. Joseph Bailey, James Oliver, Hulda Gross, Grace Orton, William H. Stickel, T. P. Haines, and Hugh Clark. Constructive criticism of the manuscript during several stages of its preparation was furnished by Drs. Howard K. Gloyd and Charles Walker, and by Anita E. Daugherty. Assistance in the preparation of the color descriptions was given by Dr. Pierce Brodkorb; certain nomenclatorial matters profited by the advice of Drs. Leonhard Stejneger and Carl L. Hubbs; information on biometrical methodology from L. M. Klauber and Dr. Donald R. Charles has been very helpful; a detailed map of the original vegetation of Minnesota was kindly made available by Dr. Raphael Zon.

I am most grateful to Dr. Norman E. Hartweg, under whose guidance

the major part of this work has been done, to Dr. Sherman C. Bishop, under whom it has been completed, and to Mrs. Helen T. Gaige for innumerable reasons.

HISTORICAL SUMMARY

The history of *O. vernalis*, starting with its discovery, proceeds through a descriptive stage to detailed observations on habits and relationships, which is probably a fairly representative picture of the development of our knowledge of many of the commoner reptilian species. The first published description was that of Richard Harlan (1827), although DeKay's manuscript notes that he showed to Harlan, in anticipation of the latter's publication, already carried the name *vernalis* for this species.

Aside from a few casual notes on the life history and range, for many years little was published other than characterizations of the species and methods of distinguishing it from *O. aestivus*. Holbrook (1842: 79) and DeKay (1842: 40) wrote excellent pioneer definitions which were, in turn, followed by more detailed descriptions that, during the last quarter of the nineteenth century, were mostly copied or compiled from those of the earlier workers.

The beginning of accurate natural history observations and the concept of a "natural range" for the species may be identified with O. P. Hay (1892: 493). In his paper it is stated that vernalis is "rare or not found in the Southern States," that because of its color it must depend on concealment for safety, and that it is a grass dweller. Hay also gives the locality, conditions, and date for an observation upon the hatching of a batch of eggs in nature. In the ensuing period many locality reports were published, and these were accepted uncritically by almost every subsequent worker. State and museum lists were common. Ditmars (1896: 10) and Surface (1906: 130) discussed feeding habits as observed by dissections of stomachs, and Blanchard (1933: 493) from direct observation on the feeding of young captive specimens. Ecological, experimental, psychological, and geographical notes appeared. Coloration was discussed from several aspects (Weed, 1922: 87; and Gloyd, 1928: 122). Woodbury (1931: 71) listed hitherto unpublished scale counts for specimens from a restricted area (Utah) and noted that these differ from those of eastern vernalis. An outstanding contribution was Blanchard's paper (1933) on the eggs and young. Authentic notes on the hibernation of the species first appeared in 1937 (Criddle, 1937: 142).

Boulenger's allocation of *vernalis*, together with many Old World forms, to *Contia* (1894: 258) was primarily for ease in handling and not an indication of true relationships. In 1935 Pope (p. 281) pointed out the close relationship of the species to Chinese forms, assigning them to the same

genus, and in this view he has been followed by Schmidt and Necker (1936) and by subsequent writers.

TAXONOMY

Three American species of the genus Opheodrys Fitzinger have been recognized recently (Schmidt and Necker, 1936: 64). They may be distinguished by the following key:

Dorsal scales smooth, in fifteen rows ______B B. Upper labials normally 6; sum of ventrals plus caudals greater than 240; dorsal color light brown O. mayae (Gaige) Upper labials normally 7; sum of ventrals plus caudals less than 240; dorsal color O. vernalis (Harlan)

Opheodrys vernalis (HARLAN)

Coluber vernalis Harlan, 1827: 361 (reference is made to DeKay's manuscript notes, indicating that the name is DeKay's; the description given is probably of a specimen in the Academy of Natural Sciences of Philadelphia, for Harlan said: "A specimen in the Cab. of A. N. S. (Not before described)."; it is therefore reasonably clear from the publication that DeKay is the author of the name and Harlan has published the first description, which was probably his own. In conformance with Article 21 of the International Rules of Zoological Nomenclature Harlan is recognized as the author of the name, for he published the name and a description for the first time, and it is not clear that any other person is responsible for this description; "Inhabits Pennsylvania and New Jersey"). Holbrook, 1842: 79. DeKay, 1842: 40.

Chlorosoma vernalis Baird and Girard, 1853: 108. Baird, 1859: 15, Pl. 32, Fig. 81. Herpetodryas vernalis Hallowell, 1856: 243.

Cyclophis vernalis Günther, 1858: 119. Yarrow, 1874: 539. Cope, 1875: 38. Garman, S., 1883: 39, 146. Duméril and Bocourt, 1908: 815.

Liopeltis vernalis Cope, 1860: 560; 1900: 178, 781-83, 785, 1216. Brown, 1908: 122. Contia vernalis Boulenger, 1894: 258. Werner, 1929: 145.

Eurypholis vernalis Pope, 1935: 281 (vernalis is believed to be congeneric with several Chinese forms that he assigned to Eurypholis). Gaige, 1936: 300.

Opheodrys vernalis Schmidt and Necker, 1936: 63 (all the former generic allocations of vernalis are discussed, and it is shown that Opheodrys and Entechinus alone are tenable; the writers accept Stejneger's suggestion to refer vernalis to Opheodrys, as the Chinese forms, having weakly keeled scales, are believed to be intermediate between aestivus and vernalis).

Within Opheodrys vernalis (Harlan) there may be recognized at present two well-defined races which may be identified by the following key:

Males with less than 131 ventrals, females with less than 140 ventrals.

O. v. vernalis (Harlan)

Males with 131 or more ventrals, females with 140 or more ventrals.

O. v. blanchardi, n. subsp.

Opheodrus vernalis vernalis (Harlan)

HOLOTYPE.—Lost. Formerly in the collection of the Academy of Natural Sciences of Philadelphia. From eastern Pennsylvania or New Jersey.

DIAGNOSIS.—A smooth-scaled *Opheodrys* usually with less than 140 ventrals in the females and 131 in the males.

Opheodrys vernalis blanchardi,3 new subspecies

HOLOTYPE.—U.M.M.Z. No. 62439, adult male, collected by Helen T. Gaige at Spanish Peaks, 8,000 feet, Colorado, on July 25, 1925.

Paratypes.—U.M.M.Z. No. 62440, male, type locality; U.M.M.Z. No. 59181, male, Mt. Timpanogos, Utah; U.S.N.M. No. 9095, male, Merino Valley, New Mexico; M.V.Z. No. 24848, male, Chaves Creek, 10 miles northeast of Tierra Amarilla, New Mexico; L.M.K. No. 1534, male, Santa Fe Canyon, Santa Fe, New Mexico; L.M.K. No. 24685, male, Vernal, Utah; U.T.A.H. No. 35, male, Aspen Grove, Utah; U.S.N.M. No. 40199, female, Vallecito, Colorado; U.S.N.M. No. 22377, female, Mesilla Valley, New Mexico; U.S.N.M. No. 25438, female, Ruidosa at Forks, New Mexico; U.S.N.M. No. 8425, female, Abiquiu, New Mexico; F.M.N.H. No. 29389, female, San Miguel County, New Mexico; M.C.Z. No. 5277, female, Santa Fe, New Mexico; Utah No. 99–863, female, Vernal, Utah; L.M.K. No. 24684, female, Beaver Creek, Utah; and U.S.N.M. No. 1476, female, road to Bridger's Pass, Wyoming.

DIAGNOSIS.—A smooth-scaled *Opheodrys* closely related to *O. v. vernalis* from which it differs most conspicuously in having a greater number of ventrals.

Description of holotype.—Ventrals, 138; caudals, 84; dorsal scale rows, 15,4 first and second rows having the largest scales; supralabials, 7, the sixth largest, the third and fourth contacting the eyes; 1 preocular and 2 postoculars; the loreal and nasal fused; small single anterior temporal; 6 irregularly shaped scales across the occiput between the last upper labials; posterior chin shields in contact with each other for the anterior half of their lengths; median gulars, 4; minute tubercles present on mental, anterior lower labials, and anterior chin shields; head plates normal, as described by Cope (1900: 782); anal plate divided; region about position of loreal, second supralabial, and preocular depressed as in *Coluber*.

Total length, 434 mm.; tail length, 152 mm., or 0.35 of the total length. Dorsal color (in alcohol) blue (nearest Medici blue of Ridgway, 1912); ventral half of rostral, lower three-fourths of the first five supralabials and under surface of the head yellowish ivory; ventrals yellowish ivory anteriorly, becoming lighter toward the vent; anterior subcaudals ivory, diffused with blue posteriorly.

Description of two of the paratypes.—U.M.M.Z. No. 62440, male, has

³ Dedicated to Dr. Frank N. Blanchard, in recognition of his remarkable achievements in herpetology.

⁴ The scales are deformed on the right ventrolateral surface opposite the fifteenth ventral.

131 ventrals, 69 caudals (tail incomplete), a separate loreal and nasal on each side, a normal temporal formula of 1+2, and 8 irregularly shaped scales across the occiput between the last 2 supralabials. The total length is slightly over 345 mm. The coloration is similar to that of the holotype.

U.M.M.Z. No. 59181, male, differs from the holotype in possessing 137 ventrals, 2 anterior oculars on each side, a separate loreal on each side which is elongated anterioposteriorly, a normal temporal formula of 1+2, 9 irregularly shaped scales across the occiput between the last 2 supralabials, and posterior chin shields which are in contact with each other for a lesser distance than their anterior halves. The total length is 452 mm.; the tail length is 155 mm., or 0.34 of the total length. The coloration is similar to that of the holotype except that the color is slightly denser in the head region and slightly more diffuse on the posterior half of the ventral surface of the tail.

RANGE

The range of *Opheodrys vernalis* is, as far as this study has shown, definitely correlated with certain aspects of the physiography, vegetation, and glacial history of the land over which it ranges (see Map 1). The range of the species may be defined tersely as the mountainous and glaciated areas east of Nevada and south of latitude 52° N. into Mexico.

In the Appalachian Highlands the most southern record for O. v. vernalis is Madison County, North Carolina (M.C.Z. No. 2287). East and south of the Highlands v. vernalis does not enter into the Atlantic coastal plain nor the Piedmont Province. The single exception available is a specimen (A.N.S.P. No. 5673) from Trenton, New Jersey. It ranges at least as far north as Tabusintac, New Brunswick (C.M. No. 1977), which is considerably below the southern edge of the subarctic forest. West of the highlands the southern limit of distribution seems to coincide with the southernmost extension of the Pleistocene glaciation. Conant wrote (1938: 47): "The Ohio records for the smooth green snake are all in the glaciated part of the state."

In the west the subspecies intergrade along the prairie-forest vegetation boundary. The restriction of $v.\ vernalis$ to the area of the original eastern forest and of $v.\ blanchardi$ to the more western prairie and plains area is marked, although, as the variation is now understood, not complete. Specimens from Anoka County, Minnesota (M.U. Nos. 164–67, 172–73) must be assigned to $v.\ blanchardi$ on the basis of the number of ventrals despite the fact that this county is to the east of the boundary. The vegetation of Anoka County, however, is almost completely wet prairie and oak openings, so it is probable that intergradation is not as widespread as geographic interpretation would have it seem. There is an interdigitation of prairie and forest cover each with islands and peninsulas of the other and the two

subspecies seem to be distributed accordingly. Representative collections of populations from along this boundary must be obtained before more definite statements on the area of intergradation may be made. Until such are available it seems best to regard these forms as of subspecific rank, for at least one series from one locality (Forest Lake, Washington County, Minnesota) contains some individuals referable to $v.\ vernalis$ (M.U. Nos. 169–70) and some to $v.\ blanchardi$ (M.U. Nos. 179, 181) on the basis of scutellation.

The distribution of v. blanchardi, as a western grassland form invading the east, in and slightly beyond the prairie peninsula, is a further bit of herpetological evidence for the postglacial eastward extension of the steppe in North America as set forth by Schmidt (1938: 396). This distribution also supports the conclusions of Ruthven (1908a: 391) that "many of the forms from the eastern forest region are here [prairie] replaced by others whose principal range is to the westward of the prairie."

The southern limit of the Pleistocene glaciation and of the range of v. blanchardi appears to coincide, at least as far west as the Great Plains in Nebraska. Westward the subspecies is found in the high plains of Nebraska north of the Platte River. The form ranges at least as far north as southern Manitoba (C.N.M. No. 1996). It continues westward into the Rocky Mountains system, as far north as the middle Rocky Mountains of Wyoming (U.M.M.Z. No. 85104), and west (Payson Canyon, Utah County, Utah; Tanner, 1940: 142) and south (Mesilla Valley, Dona Ana County, New Mexico; U.S.N.M. No. 22377) into the Basin and Range Province.

The southern limiting factors of both forms in the mountains are harder to determine; probably temperature plays an important part.

The species has been listed as a member of the upland (Fowler, 1906: 164), Alleghanian (Roddy, 1928: 38), and Boreal (Dunn, 1931: 117) faunas. That it is an upland northern species extending south of the glaciated areas only at the higher altitudes is certainly true. The range of Opheodrys aestivus in the south probably complements the range of the northern green snake to a greater degree than has hitherto been realized. M. Graham Netting has told me that in West Virginia aestivus is found in the valleys and vernalis in the mountains; that although they occupy the same general geographic area they are ecologically isolated. The former might be considered an ecological equivalent (Hesse, Allee, and Schmidt, 1937: 79) of the latter.

Several locality records, both in literature and in museum catalogues, are obviously in error. These records should be deleted from the known range of the species and for this reason are listed below.

Arkansas, Arkadelphia.—Hurter and Strecker (1909: 25) accepted this record (the specimen was reported to have been deposited in the Field

Museum) from a list given them by Meek of Chicago. Schwardt (1938: 8) and Dellinger and Black (1938: 20) followed Hurter and Strecker by accepting Meek's Arkansas record. However, Clifford Pope of the Field Museum wrote (in a letter, August 16, 1940) that there is a specimen of Opheodrys aestivus (F.M.N.H. No. 405) from Arkadelphia that had been identified and catalogued as vernalis. Since this is undoubtedly the Meek specimen there is yet no evidence to indicate that the species occurs in Arkansas.

District of Columbia.—Hay (1902: 136) wrote that "there are several records for the capture of this . . . snake within" this region but neither records nor actual specimens have been located during the present study.

Florida, Escambia County.—Carr (1940: 80) recorded a specimen from this locality which has been lost. Concerning this record Goin wrote (in a letter, February 26, 1940): "I strongly suspect that it was an escaped specimen. When animals are used for pets as these are and one is turned up so far from other records I certainly do not feel that such a record should be considered a true part of the creature's range until verified by intervening records."

Florida, Florida Keys.—A specimen of O. vernalis (U.S.N.M. No. 10003) bears this locality data and concerning it Doris M. Cochran of the United States National Museum has written (in a letter, May 15, 1939): "This entry originally applied to an Engystoma carolinense, now lost. Dr. Stejneger says that it is surely the wrong number for the snake."

Florida, Manatee.—A specimen in the Cornell University collection (C.U. No. 2686) is listed as having been collected at this locality by W. Newcomb, who collected in the south during the 1840's. It hardly seems likely that, in a state as well explored herpetologically as is Florida, O. vernalis has remained unobserved for almost a century. Until additional specimens from Florida and specimens from Alabama and Georgia (for which there are no records) are found the existence of populations of O. v. vernalis in Florida must be doubted.

Kansas.—Branson (1904: 409) gave several *vernalis* county records for southern and western Kansas that were probably based upon specimens of *aestivus*. It is likely that he had the two species confused, for he wrote (p. 373) that he had not seen a specimen of *aestivus* from Kansas, yet he recorded *vernalis* from localities where other collectors had found *aestivus* but not *vernalis*.

Mexico.—Yarrow (1883: 99) listed specimens in the U.S.N.M. reserve series, two of them (U.S.N.M. No. 434) from Mexico. It does not seem advisable to record O. v. blanchardi from Mexico until more definite information can be gathered than is offered by these two specimens.

Mississippi.—Baird and Girard (1853: 109) gave the scale counts for one

specimen from "? Mississippi." This record should not be accepted without further confirmation.

North Carolina, Fort Macon.—Coues and Yarrow (1878: 27) listed this species as very common near Fort Macon. Specimens have not been deposited in any museum, and this locality report remains unverified; doubt as to its validity is suggested by the lack of any reliable coastal plain records for *vernalis*. Since the occurrence of *aestivus* is not noted in this report the two green snakes might have been confused, as *aestivus* inhabits the coastal plain of North Carolina.

Oklahoma.—In the University of Kansas collection there is a smooth green snake bearing no other data than "southern Oklahoma." In regard to this specimen C. D. Bunker, of the Museum of Birds and Mammals at the University of Kansas, has written (in a letter, March 13, 1939): "That is all the data that we have on that specimen in our catalogues. I have inquired of several members of the faculty here and they can give me no more information." This museum record led Smith and Leonard (1934: 194) to include O. vernalis in their list of Oklahoma reptiles. Ortenburger (1927: 208; 1930: 220) has indicated his doubt of the existence of this species in Oklahoma. Since any locality in southern Oklahoma would be more than 250 miles from the nearest reliable record for the species and since the single record from this region has not been vouched for, it seems best to delete vernalis from the Oklahoma faunal list.

South Carolina.—A specimen in the Philadelphia Academy's collection (A.N.S.P. No. 5674) bears the datum "South Carolina." Although the range of O. v. vernalis may be found to include the extreme northwestern mountainous section of that state, the above specimen should not be considered as evidence.

Tennessee, Franklin County.—Two specimens (U.S.N.M. Nos. 55945-46) are listed as collected at this locality by Julius Hurter. Franklin County is in the Appalachian Plateau, and farther north in this same physiographic province in West Virginia v. vernalis is rather common. Both of these specimens, however, have the rather high number of ventrals characteristic of v. blanchardi. Since Hurter lived in St. Louis, Missouri (where v. blanchardi occurs), not far from Franklin County, Missouri, the accuracy of this locality record is questionable.

Texas, Owassa.—U.S.N.M. No. 1401 and Owassee (U.S.N.M. No. 1489). In a letter dated May 15, 1939, Dr. Doris M. Cochran wrote: "Dr. Stejneger has never located this place."

Texas, Clifton.—C.M. No. 442 is listed as collected by Atkinson and Link on May 29, 1907, at Clifton, Bosque County. Since "at least half a dozen of Atkinson's Texas records have been questioned by various students" (M. Graham Netting, in a letter, March 4, 1939), since the nearest

other record is the equally illogical one from southern Oklahoma, and, finally, since its scutellation indicates that it is a member of the eastern race, it seems justifiable to delete this as a valid *vernalis* record.

Texas, Deming's Bridge.—Garman (1892: 11) described two specimens collected by F. W. Walmsley at Deming's Bridge in Matagorda County. One of these now bears No. 19887 in the Museum of Comparative Zoology. The locality record seems authentic, yet if a population of v. blanchardi does truly exist there, or anywhere else along the Gulf coast, other specimens probably would have been found during the fifty years that have elapsed since these specimens were collected.

Texas, Washburn.—Bailey (1905: 46) reported a specimen collected by Gaut in July, 1904, at Washburn. The specimen upon which this record has been based has not been located. The accepted records that are represented by reliable museum specimens and that are south of the junction of the Ohio and Mississippi rivers are from the mountains, which is not true of any of the Texas locality records.

Texas, Waxahachee.—A specimen in the University of Michigan Museum of Zoology (No. 84096) bears the following: 10 miles south of Waxahachee, Texas, collected by Charles Burt, in April, 1931. This locality is likewise remote from the normal range of the species, and until additional specimens are collected from this region the existence of populations of v. blanchardi at this locality is doubted.

In order to define more accurately the ranges of the forms under consideration the following county list gives the accepted record from those states which are considered marginal. Museum specimens are given preference over literature records, and only one record is listed for each county.

Accepted records for O. v. vernalis:

Maryland	Bradford (C.M. 6166)
Allegany (A.N.S.P. 5676)	Cambria (Surface, 1906: 164)
Garrett (C.M. 13908)	Centre (C.M. 6682)
New Jersey	Clinton (C.M. 8845)
Bergen (C.M. 5577)	Crawford (C.M. 11464)
Mercer (A.N.S.P. 5673)	Cumberland (U.S.N.M. 1502)
Morris (A.M.N.H. 28661)	Elk (C.M. 13496)
Sussex (A.M.N.H. 6849)	Erie (U.M.M.Z. 74737)
North Carolina	Fayette (C.M. 9504)
Madison (M.C.Z. 2287)	Franklin (C.M. 9673)
Pennsylvania	Fulton (Surface, 1906: 164)
Adams (Surface, 1906: 164)	Huntingdon (C.M. 7577)
Allegheny (C.M. 1978)	Indiana (C.M. 8727)
Beaver (C.M. 771)	Jefferson (C.M. 6642)
Bedford (C.M. 11371)	Juniata (Surface, 1906: 164)
Berks (Surface, 1906: 164)	Luzerne (Surface, 1906: 164)
Blair (C.M. 12703)	Lycoming (C.U. 2387)

Mercer (C.M. 6070)	West Virginia
Monroe (Surface, 1906: 164)	Fayette (M.C.Z. 2285)
Perry (Surface, 1906: 164)	Grant (C.M. 9614)
Pike (U.S.N.M. 48838)	Hardy (C.M. 13947)
Somerset (C.M. 7507)	Marion (C.M. 9457)
Sullivan (M.C.Z. 5300)	Mineral (C.M. 11623)
Union (Surface, 1906: 164)	Ohio (C.M. 5321)
Washington (C.M. 6139)	Pocahontas (C.M. 9949)
Wayne (A.M.N.H. 3802)	Preston (C.U. 1675)
Westmoreland (C.M. 9569)	Randolph (C.M. 9586)
Wyoming (A.N.S.P. 14969)	Tucker (C.M. 6965)
Accepted records for O. v. blanchar	rdi:
Colorado	Cuming (Taylor, 1891: 331)
Archuleta (U.S.N.M. 55947)	Garfield (A.N.S.P. 5683)
Boulder (Ellis and Henderson, 1913: 100)	· · · · · · · · · · · · · · · · · · ·
Costilla (U.M.M.Z. 62439)	Colfax (U.S.N.M. 9095)
El Paso (U.S.N.M. 55948)	Dona Ana (U.S.N.M. 22377)
La Plata (U.S.N.M. 40199)	Lincoln (U.S.N.M. 25438)
Las Animas (K.S.A.C. 2947)	Rio Arriba (M.V.Z. 24848)
Indiana	San Miguel (F.M.N.H. 29389)
Lake (F.M.N.H. 2110)	Santa Fe (L.M.K. 1534)
La Porte (M.U. 176)	North Dakota
Kansas	Benson (U.M.M.Z. 54461)
Franklin (U.M.M.Z. 67021)	Morton (U.S.N.M. 53079)
Geary (A.N.S.P. 5666)	Ramsey (U.M.M.Z. 54460)
Riley (M.C.Z. 5424)	Ward (U.M.M.Z. 74344)
Missouri	Utah
Jackson (Hurter, 1911: 189)	Uintah (U.T.A.H. 99–863)
Johnson (Hurter, 1911: 189)	Utah (U.M.M.Z. 59181)
Randolph (Hurter, 1911: 189)	Wasatch (L.M.K. 24684)
St. Charles (U.S.N.M. 55943)	Wyoming
Nebraska	Natrona (U.M.M.Z. 85104)
Buffalo (A.N.S.P. 5672)	Uinta (U.S.N.M. 1476)
Accepted records from the states	,
Illinois	Butler (U.S.N.M. 10662)
Adams (F.M.N.H. 2048)	Crawford (T.Z.S. 2281)
Cook (F.M.N.H. 3526)	Erie (U.M.M.Z. 39115)
Henry (D.Z.U.I. 336)	Fayette (T.Z.S. 2044)
Lake (F.M.N.H. 719)	Franklin (U.S.N.M. 1472)
Madison (Hurter, 1911: 189)	Geauga (Conant, 1938: 47)
Marion (U.S.N.M. 2204)	Hamilton (Conant, 1938: 47)
McLean (U.M.M.Z. 32335)	Hardin (T.Z.S. 1683)
Monroe (Hurter, 1911: 189)	Lorain (Conant, 1938: 47)
Vermillion (C.U. 1972)	Summit (O.S.M. 85.1)
Manitoba	Trumbull (T.Z.S. 444)
Glenwood (C.N.M. 1996)	South Dakota
Lansdowne (C.N.M. 1808)	
Norfolk (A.M.N.H. 9569)	Clay (M.U.S.D.) Custer (U.M.M.Z. 76499)
Ohio	Lawrence (U.S.N.M. 63268)
Ashland (T.Z.S. 2011)	Roberts (M.U.S.D.)
(and o was	

HABITAT

A comprehensive discussion of the habitat preferences of this species cannot be entered into until competent herpetologists have made exhaustive collections and observations in all available habitats in different parts of the range at different times of the day and year. A description of the situations in which the green snakes have been found may be largely a description of the habitats worked most thoroughly by collectors, just as a locality spot map may merely indicate the distribution of collectors. Nevertheless, from a review of the literature and from limited personal experience, the following statements may be offered.

Opheodrys v. vernalis is found in many grassy situations: meadows (Holbrook, 1842: 79), marshes (DeKay, 1842: 42), sphagnum bogs (Wright, 1919: 10), open woods, clearings (Gaige, 1915: 5), and sand ridges (Thompson and Thompson, 1913: 217). In southern New York I found specimens to be common in a large, grassy, poplar-bordered field which remained boggy for several days after a heavy rain. There were no boards or rocks in the field; all the specimens collected were in the grass. Only once was a green snake found under cover, along a roadside where there were a number of Thamnophis s. sirtalis, and it was in the pre-shedding condition characterized by milk-colored eyes. Other workers (Allen, 1899: 68; and Thompson and Thompson, 1913: 217), obviously collecting in dissimilar habitats, record vernalis from under boards and stones. Several Michigan reports (Blanchard's notes and U.M.M.Z. field labels) list sandy areas about mixed aspen country.

The habitat may vary in different parts of the range, though definite information on this is lacking. O. v. blanchardi in Iowa often climbs into bushes (Guthrie, 1926: 175). Woodbury wrote (1931: 72): "Its habitat in Utah is unknown... does not appear to be found in the low valley or desert areas."

It seems that two of the essential requirements for *Opheodrys vernalis* are a high altitude or latitude, and a relatively moist grassy situation.

VARIATION

COLORATION

Living examples of O. v. blanchardi have not been available, and a detailed color description of that form cannot be given here. It seems possible, however, that there may be a color difference between the two subspecies. Gloyd (1928: 122) suggested this when, in describing a specimen from Kansas, he wrote: "... the color of this specimen in life was different from that of others seen by the writer in the eastern portion of its range." Woodbury (1931: 71) in his description of the general features of the smooth green snake in Utah wrote: "A dark green snake." Hurter

(1903: 83) described Missouri specimens similarly. In order to facilitate future comparisons an account of the coloration of two specimens of v. vernalis from Douglas Lake, and one from Grand Traverse County, Michigan, are given here. The color terms are those of Ridgway (1912).

Female from Douglas Lake.—Dorsally spinach green darkening to elm green on tail; laterally lumiere green; ventrally throat white with yellowish wash over ventrals; caudals pale yellow-green; upper labials picric yellow; flecks of cerulean blue and light cerulean blue throughout the lower rows of dorsal scales.

Male from Douglas Lake.—Dorsally cerro green darkening to hellebore green on tail; laterally dull green-yellow; ventrally throat white with yellowish wash over ventrals; caudals lumiere green; supralabials martius yellow; many of the lateral scales with pale cerulean blue margins.

Female from Grand Traverse County.—Dorsally Lincoln green, dark ivy green on tail; laterally apple green, forming a definite stripe occupying the first one and a half scale rows; ventrally white on throat with greenish wash over ventrals and Kildare green on the caudals; supralabials martius yellow.

It has been suggested that the green in certain snakes is caused by the blending of blue and yellow pigments (Weed, 1922: 87; Necker, 1939: 27; and Cott, 1940: 9). Necker mentioned six specimens of *vernalis* which were yellowish buff and one which was blue and suggested that the blue has been aberrantly lost in the former and the yellow in the latter.

The green of normal specimens, after they have been in preservative for a time, fades to a shade between light blue and blue-black, due to the loss of yellow pigment, and the preservative assumes a yellowish tinge. Although the coloration of the alcohol may be associated to some degree with the disintegration of some of the internal tissues, this yellowish tint may be partly the result of the loss of similarly colored pigment from the specimens. In this connection H. W. Parker (in Cott, 1940: 9) suggested that the green color of certain snakes is produced by a combination of structural blue, which is unaffected by alcohol, and an alcohol-soluble pigment.

One specimen (U.M.M.Z. No. 47342) collected by Helen T. Gaige in Schoolcraft County, Michigan, was, in life, a buff-colored snake; that is, the blue was absent. As a preserved specimen, with both the blue and the yellow lacking, this snake is not colorless but gray. It seems, then, that the color of vernalis is dependent upon the combination of yellow, blue, and gray. The union of yellow and blue determines the hue, and the amount of gray fixes the value of the color. A normal green snake has the three colors; a buff individual has gray and yellow; and a blue one has gray and blue. When the yellow has disappeared after preservation, the buff snake becomes gray; the normal green snake becomes blue, the degree of darkness depending upon the amount of gray present.

The pattern of the light supralabials as contrasted with the darker uniform color of the head and dorsum in *Opheodrys vernalis* is duplicated in the brownish *Opheodrys mayae* (Gaige) and approximated in the green *Opheodrys major* Günther (here the green almost obliterates the lighter color on the supralabials).

CORRELATED SCUTELLATION

RACIAL

Ventrals.—As was indicated in the diagnosis of *Opheodrys vernalis blanchardi* there is a distinct difference between the two races in the number of ventrals. A graphic presentation of the ventral scutellation in both sexes of the two recognized races is presented in Figure 1. The scale counts of snakes from the region of intergradation (Ohio, Indiana, Illinois, Wisconsin, Minnesota, and Manitoba) and of three South Dakota and Wyoming specimens (discussed below) are not included in these histograms. The separation is satisfactory for nomenclatorial purposes, for over 97 per cent of the females and over 98 per cent of the males may be correctly associated with the proper geographic range. This correlation could undoubtedly be improved if done on an ecological basis.

Two males from the Black Hills in South Dakota (U.M.M.Z. No. 76498) and U.S.N.M. No. 63268) and a female from Natrona County, Wyoming (U.M.M.Z. No. 85104), have the lower number of ventrals characteristic of the eastern forest race. Since the racial variation in ventral scutellation seems to be ecologically correlated, this might be expected, for the Black Hills and the locality from which the Wyoming specimen was taken (as told to me by the collector) are heavily forested. If the present range is a discontinuous distribution reduced from an historically accumulative range that embraced both areas (i.e., the Black Hills and the eastern forested region) these snakes should be allocated to v. vernalis. number of ventrals is the result of parallel development in a similar set of ecological conditions, vernalis, as used here, must be regarded as diphyletic, with these individuals considered as morphologically similar to, but phylogenetically different from, the eastern subspecies. These specimens, then, may be considered to represent either a population derived by parallel development or a relict population of v. vernalis.

Individuals from the region of intergradation between *vernalis* and *blanchardi* have the ventral range of both forms. Although a series of forty-eight specimens from Cook County, Illinois, include a large number of the counts of both forms, the entire range and variation within it do not appear to be any greater than in any like series from a locality where typical specimens of one form may occur. The Manitoba hibernating sample probably represents a true breeding population, which should be the unit of study in variational work.

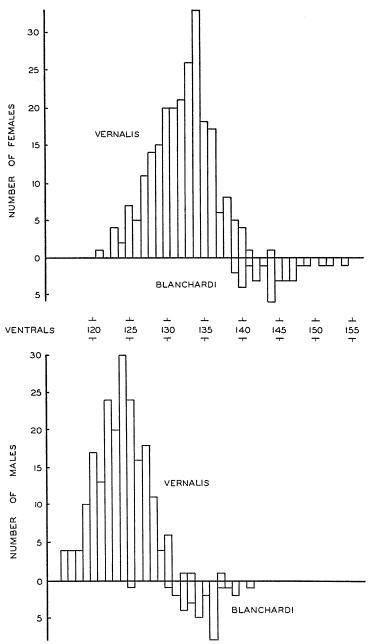


Fig. 1. The number of ventrals in specimens, excluding individuals from the area of intergradation, of both sexes of the two recognized races.

In Opheodrys vernalis, a subspecies is composed of many intra-5 and interbreeding populations—continuity of characters is largely dependent upon the free interbreeding of intrabreeding populations. When the opportunity for this interbreeding is lessened the chances for characters to become differentiated through isolation are enhanced. In an area of intergradation between two subspecies, the populations are not so freely interbreeding as they are elsewhere, but they must be as freely intrabreeding or they could not survive. A true intrabreeding population from the area of intergradation, such as the Manitoba series probably represents, should be, on the average, no more nor less variable in its meristic characters than a like population from an area of typical forms. Further, it should be no more and probably less variable than either of the subspecies it connects, for it is a single population. The latter is true of the Manitoba series, for the variation in the number of ventrals is less than that for either subspecies. This may be expressed numerically by the coefficient of variation which appears in Table I. The lesser value of the coefficient for the Manitoba specimens as compared with either the v. vernalis or v. blanchardi coefficient is highly significant (the probability level equals 4 standard errors) in the females, but, although lower, is not as significant by mathematical tests as that in the males.

The region of intergradation, then, is more than an area of intermixture of subspecies. It is as definitely delineated as is the range of either subspecies, and its populations are, on the average, as static as the populations of the subspecies it connects. Moreover, a population from this area of intergradation has the same relative constancy, in any character under consideration, as does a population from an area of typical specimens.

The term population is used here in a restricted sense. It is meant to refer to a group of animals in which there is free protoplasmic exchange. A series of individuals collected from a restricted locality during the summer months when the snakes are active and foraging for food and nesting sites is not necessarily a true population. In the northern latitudes, at least, the hibernating aggregation is probably a breeding colony and this is assumed to represent the population.

This concept of intergradation in O. vernalis may be condensed as follows. A population is an assemblage of consistently similar individuals which interbreed freely. A subspecies is an assemblage of populations which resemble each other more than they do populations within other subspecies, and which interbreed comparatively freely. Where the range of one subspecies meets the range of another subspecies the characters of the populations are intermediate, yet they are just as constant in all of their characters as are the populations within the range of either subspecies.

⁵ This is probably the same as Dobzhansky's (1937: 146) microgeographic race.

Ventrals and Caudals in the Manitoba Series, Opheodrys v. vernalis and O. v. blanchardi TABLE I

	ries	Females	$140.3 \pm .25$ $136 - 45$ $.014 \pm .001$ 60	$74.9 \pm .37$ $70 - 80$ $.036 \pm .003$ 54
	Manitoba Series	Males	$129.4 \pm .41$ $123 - 34$ $.020 \pm .002$	$87.6 \pm .60$ $79 - 96$ $.041 \pm .005$
	chardi	Females	$144.5 \pm .66$ $139 - 54$ $.026 \pm .003$ 31	$75.0 \pm .68$ $68 - 82$ $.048 \pm .006$
	O. v. blanchardi	Males	$134.4 \pm .54$ $125 - 41$ $.022 \pm .003$ 31	88.3 ± 1.00 78 - 95 .060 ± .008
	ernalis	Females	$132.1 \pm .25$ $121 - 44$ $.030 \pm .001$ 268	$73.2 \pm .35$ $60 - 89$ $.070 \pm .003$
	O. v. vernalis	Males	$123.7 \pm .24$ $116 - 37$ $.027 \pm .001$ 203	$84.8 \pm .35 \\ 74 - 95 \\ .055 \pm .003 \\ 181$
		Characters	Ventrals Average Extremes Coef. variation No. of specimens	Caudals Average Extremes Coef. variation No. of specimens

Caudals.—The western race has slightly more caudals than the typical form if the averages of male and female $v.\ vernalis$ and $v.\ blanchardi$ caudals, given in Table I, are representative. The differences between these means, within each sex, approach an acceptable limit of significance, as t is 1.9 for the females and 3.6 for the males. As will be shown, however, there is enough geographic variation in caudals to cause this apparent genetic difference. If southern $v.\ vernalis$ are compared with northern $v.\ blanchardi$ it is found that the averages are reversed. Therefore, if a racial difference in the number of caudals does exist, it is very slight and is insignificant in comparison with the sexual and geographic variations.

Loreals.—In 1445 specimens about half (.517) have a squarish loreal, a quarter (.272) have the loreal elongated anteroposteriorly, many (.127) have the loreal fused with the nasal. In the remainder the loreal is very small (.048), very large (.030), or divided (.002). The only significant variation from these percentages in any area appears to be a higher proportion of specimens with an elongated loreal in v. blanchardi.

SEXUAL

Ventrals.—There is a sexual dimorphism in the number of ventrals. In the sample of the hibernating specimens from Manitoba there is an absolute separation by two scutes (see Table I). The dimorphism between the sexes in the Manitoba series is eleven ventrals. In v. vernalis the sexual difference is about eight and a half, and in v. blanchardi about ten. cannot be construed to mean that there is a difference between v. blanchardi and v. vernalis in the amount of sexual dimorphism, for the coefficients of variation for the males and females of both races are very similar (see Table Since the differences between these coefficients are probably not significant it appears that the greater absolute sexual dimorphism in v. blanchardi is merely an expression of the greater number of ventrals in this subspecies. This is also suggested by the recently introduced coefficient of divergence (Klauber, 1940b: 208), which, when used here, is .066 for v. vernalis and .072 for v. blanchardi—figures whose difference is probably due solely to errors of random sampling.

Caudals.—The sexual dimorphism in caudals is marked, being almost complete in the Manitoba hibernating sample (see Table I). A pictorial presentation of the number of caudals in both sexes of each race is given in Figure 2. It is apparent from an inspection of these histograms that there is a similar sexual dimorphism in both subspecies. The coefficient of divergence between the sexes is .147 for v. vernalis and .163 for v. blanchardi. The difference between these two coefficients is probably a reflection of random sampling errors.

A comparison of the coefficients of divergence that have been deter-

mined for the ventrals and caudals of other snakes is given in Table II. Besides the figures for O. vernalis this descriptive statistic has been worked out by Klauber (1940b: 208) for two other forms From these few data

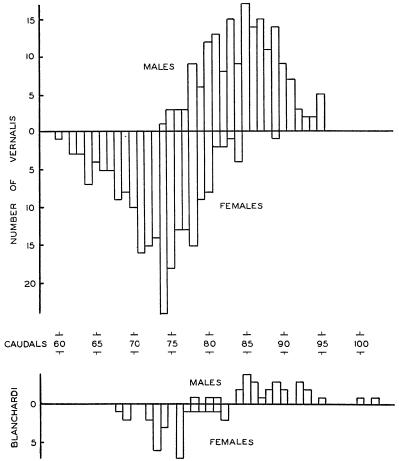


Fig. 2. The number of caudals in specimens, excluding individuals from the area of intergradation, of both sexes of the two recognized races.

TABLE II
COEFFICIENTS OF DIVERGENCE

Form	Number of Specimens	Ventrals	Caudals
Lampropeltis getulus californiae O. v. vernalis O. v. blanchardi Phyllorhynchus decurtatus perkinsi	271	.009	.073
	391	.066	.147
	56	.072	.163
	225	.073	.256

several tentative conclusions may be derived which are in accord with those of Klauber for the two forms in Table II on which he has worked.

- 1. Sexual dimorphism manifests itself to a greater degree in the caudals than in the ventrals.
- 2. Forms with the same sexual dimorphism in the ventrals do not necessarily have a similar sexual dimorphism in the caudals. (O. vernalis and P. d. perkinsi have approximately the same coefficient of divergence for the ventrals, but in the latter the caudal dimorphism is 3.5 times greater than the ventral, whereas in the former the caudal dimorphism is hardly twice that of the ventral.)
- 3. The ratio of caudal to ventral sexual dimorphism varies greatly among different forms and may be useful as an indication of relationship. (This ratio for L. g. californiae is 8 to 1 and for P. d. perkinsi 3.5 to 1. For both races of O. vernalis, however, the ratio is practically the same, 2.2 to 1.)

Preoculars.—The preoculars were most commonly single (1036 times), often double (406 times), and rarely triple (3 times). The variation does not appear to be significantly correlated with race or geographic distribution.

A certain amount of correlation of the number of preoculars with sex is present. In Table III appears a summary of 1414 specimens. The three occurrences of 3 postoculars and a small sample of twenty-eight cases, in southern *vernalis*, are not included.

TABLE III

NUMBER OF SPECIMENS OF Opheodrys vernalis, ARRANGED BY SEX AND GEOGRAPHIC GROUP, THAT HAVE A SINGLE PREOCULAR

Sample		iber of cimens	mens w	n of Speci- rith One cular	Difference Between the Male and Female	Contri- bution to χ^2	t	P
	Males	Females	Males	Females	Proportions	ν χ		
A*	86	120	.92 ± .029	.82 ± .034	.10	4.3	2.1	.036
В	89	118	$.80 \pm .042$	$.73 \pm .041$.07	1.3	1.2	.230
D	62	64	$.81 \pm .049$	$.72 \pm .056$.09	1.3	1.2	.230
\mathbf{F}	324	334	$.72 \pm .024$	$.64 \pm .026$.08	4.7	2.2	.028
G	88	129	$.72 \pm .048$	$.62 \pm .043$.10	2.1	1.5	.134

^{*} A. The Manitoba hibernating sample. B. Specimens from the area of intergradation between v. blanchardi and v. vernalis. D. Opheodrys v. blanchardi. F. O. v. vernalis from the central region of its range. G. O. v. vernalis from the northern part of its range.

The following interpretation may be made from Table III. In sample F, if the number of preoculars were not associated with sex, a difference between the proportions (of males and females with a single preocular) as great as, or greater than, the observed difference (.08) would be expected

only 2.8 per cent of the time solely as a result of random sampling errors. The probable significance of the sexual dimorphism in the remaining samples is less certain. None of these probabilities approaches a level at which a definite statement concerning the sexual dimorphism in the number of preoculars would be justified; however, the repetition of similar differences in the same direction in all the groups tested tends to support some such conclusion. The application of Pearson's "chi squared" test (here χ^2 equals 13.7 with 5 "degrees of freedom") results in a probability figure of .0084 for the combined groups. Therefore, if there were no correlation between sex and the number of preoculars one would expect, on the average, differences as great as or greater than these to be present as the result of errors of random sampling less than once in a hundred trials.

These calculations suggest that about 9 per cent of the variation in the number of preoculars in *Opheodrys vernalis* is associated with sex and that the males are more likely to have the reduced number.

GEOGRAPHIC

Latitudinal

Ventrals.—Although the ranges of the two recognized races are well correlated with the vegetation cover, a comparison of a series of v. blanchardi from the tall grass region with a similar series from the short grass region showed no significant difference in the number of ventrals, which averaged 144.9 in the females from the Great Plains and 144.4 in those from the prairies.

The statement of Van Denburgh and Slevin (1919: 200) about *Pitu-ophis*: "While individual variation is great in any one locality, it may be said that, in a general way, the warmer and dryer the climate of a given locality the greater the number of gastrosteges," apparently is applicable to *Opheodrys vernalis*, for the southwestern race (blanchardi) has a greater number of ventrals than has the northeastern race (vernalis) (see Table I).

Caudals.—There is a geographic gradient⁶ in the number of caudals with the number decreasing from south to north. A comparison of specimens of v. vernalis from the northern (New Brunswick, Nova Scotia, and Quebec), middle (New England, Michigan, New York, Ontario, and northeastern Wisconsin), and southern (Maryland, New Jersey, North Carolina, northeastern Ohio, Pennsylvania, and West Virginia) parts of its range demonstrates this gradient (Table IV).

Since the area used embraces a wide range of physiographic and vegetation conditions besides the latitudinal variation, individuals from the northern part (Maine) and the southern part (Massachusetts) of the seaboard lowland section of the New England (physiographic) Province in the

⁶ This is the same as Huxley's (1940: 31) cline.

TABLE IV

Number of Caudals in *Opheodrys v. vernalis* from the Northern, Middle, and Southern Parts of Its Range

	Ma	les	Females		
Region	Average	Number of Specimens	Average	Number of Specimens	
Northern Middle Southern	78.2 84.7 ± .38 86.5 ± .62	6 136 39	67.7 ± 1.24 72.8 ± .41 75.7 ± .54	15 138 57	

northeastern hardwoods (vegetation) region have been compared as a control. The number of caudals is summarized in Table V.

TABLE V $\label{thm:local_problem} \text{Number of Caudals in } \textit{Opheodrys v. vernalis } \text{from the Seacoast Counties of Maine } \\ \text{and Massachusetts}$

	M	ales	Fei	males
Area	Average	Number of Specimens	Average	Number of Specimens
Maine	83.7 ± 1.6 86.9 ± .9	7 13	73.3 ± .9 75.6 ± .7	13 12

Despite the slight latitudinal range (less than 225 miles) these variations are probably reliable as trend indicators for, on the average, differences as great as or greater than these would be expected only 4.6 per cent (females) or 9 per cent (males) of the time as a result of errors of random sampling from a homogeneous population.

It seems evident from the preceding tables that the number of caudals in O. v. vernalis decreases from south to north.

According to data given by Stull (1940), Ruthven (1908b), and Gloyd (1940), the same decrease in number of caudals from south to north is found in *Pituophis melanoleucus mugitus*, *P. catenifer annectens*, *P. c. deserticola* (in part—Utah and Idaho), *Thamnophis ordinoides*, and *Crotalus triseriatus*, but the trend is apparently reversed in *P. d. deppei*, *T. megalops*, and *T. sauritus proximus*, in which the number of caudals is increased from south to north. Klauber (1940: 111) reported that there is no significant geographical trend in *Leptotyphlops d. dulcis*.

Insular

Caudals.—The specimens available from several marine islands (Appledore Island, Maine; an island in Penobscot Bay, Maine; Orr's Island, Maine; and Dutch Island, Rhode Island) possess a lesser number of caudals

than do the snakes from the adjacent mainland. The counts in question are summarized in Table VI.

TABLE VI Number of Caudals in $O.\ v.\ vernalis$ from Certain New England Islands and from the Adjacent Mainland

	Mai	nland	Island		
Area	Average	Number of Specimens	Average	Number of Specimens	
Maine males Maine females S. New England males S. New England females	83.7 73.6 87.8 75.1	10 15 21 21	82.7 71.6 84.4 74.2	8 5 15 11	

The number of specimens is too few to justify statistical treatment of the apparent differences between the average number of caudals of the mainland and of the insular samples. Nevertheless, it hardly seems likely that this arrangement is a result of chance grouping of a homogeneous series. Thompson (1913: 158) found that the island specimens of Natrix vibakari had more vertebrae than those from the mainland and that the increase was due solely to the lengthening of the tail. Later, Van Denburgh (1923: 3) was able to separate the insular from the mainland race solely on the basis of the greater number of caudals in the former.

Since the island *vernalis* were undoubtedly derived from the mainland fauna, it seems evident that the change in the number of caudals was by reduction. If this has been the direction of evolution of the number of caudals in the species, those snakes illustrating the most primitive condition with respect to this character are, at present, to be found in the southwest.

Posterior chin shields.—The posterior chin shields may be in contact along the midventral line or they may be separated by one or more small scales. They were in contact in .151 of 608 specimens. There seem to be no significant differences between the frequencies of these alternatives in the two subspecies (the difference is contained in the error of difference several times), nor between the sexes, nor between northern and southern snakes of the eastern race. The *vernalis* from Dutch Island, Rhode Island, however, have a quite different frequency from that of the mainland specimens (Table VII).

TABLE VII

PERCENTAGE OF SPECIMENS HAVING THE POSTERIOR CHIN SHIELDS SEPARATED BY
SMALL SCALES

Area	Number of Specimens	Percentage Separated
Dutch Island vernalis	29	48.3
Mainland vernalis	337	16.3

As the difference (32.0 ± 7.4) contains its error 4.3 times there is undoubtedly (P = .00002) a real difference between these two groups in this character.

C. C. Branson, of the Department of Geology of Brown University, has furnished some information (in a letter, April 20, 1939) on the geological history of the island which is of interest in regard to the general problem of the relation of isolation to differentiation. Dr. Branson wrote: "The Wisconsin ice sheet passed over Dutch Island and wiped out all life within the last hundred thousand years. . . . The island may then have been connected to the mainland for a short time by outwash deposits and it is then that migration over land surface by natural means would have had to take place. This connection if it ever existed could have lasted but a few thousand years." He also suggested that accidental dispersal is possible, for the island is within two miles of land in several directions. This indicates that the snakes may have been isolated from the mainland forms after the glacial retreat and that pollution by mainland individuals may have occurred an indefinite number of times thereafter.

Uncorrelated Scutellation

Ventrals plus caudals.—As the males have more caudals than the females and the latter have more ventrals than the males, a compensation is apparent in the production of a lower coefficient of divergence for the combined counts than for either series separately. In O. v. vernalis, the coefficients are .147 for the caudals, .066 for the ventrals, and only .017 for the ventrals plus caudals. (The mean ventral plus caudal count for 181 males is 208.4; for 213 females 204.8.)

The totals obtained by adding the number of ventrals to the number of caudals show significant geographic variation (they are higher in the southern part of the range than they are in the northern) and significant racial difference (they are higher in v. blanchardi than in v. vernalis). Analysis of these counts into their component series, however, shows that the geographic variation is due to the change in the number of caudals and the racial difference to the number of ventrals.

Ventrals minus caudals.—When both series in the combination are variable, a result opposite from that of the ventral plus caudal union is obtained. A greater degree of sexual dimorphism manifests itself in the comparison of this index figure for male *vernalis* with that for female *vernalis*. This is shown in the coefficient of divergence, which is .403 (181 males averaged 39.0; 208 females 58.7) for the ventral minus caudal counts as compared with .017 for the ventral plus caudal series.

Since the lesser ventral series reduced by the greater caudal series in males is compared with the greater ventral series reduced by the lesser caudal series in females, the coefficient of divergence is greater than that of either series used separately. Thus the coefficient for the index number is .403 as compared with that of .147 for the caudals and that of .066 for the ventrals.

Dorsal scale rows.—Except for a greater number of dorsals in the neck region of a few specimens the dorsal scale row formula has not been found to vary from 15–15–15.

Supralabials.—Although data for both the right and left supralabial series were kept separated and specimens were segregated according to sex, race, and locality, no significant differences in dispersions of the number of labials were discerned. The frequencies of occurrence of any given number of supralabials, regardless of side, sex, race, or locality, are combined in Table VIII.

TABLE VIII

Number of Supralabials in Opheodrys	vernalis
Number of Supralabials	Frequency
4	1
5	3
6	56
7	1360
Q.	19

It is apparent from these data that a change in the number of supralabials from the modal or normal number, 7, to a reduced number (by fusion) is three times more common than an increase in the number (by splitting).

In the most exhaustive description of the scutellation of *Opheodrys ver-nalis* that has yet appeared, Cope (1900: 782) recorded the fourth supralabial as the largest in the series. Any supralabial from the third to the eighth, however, may be the largest; Table IX lists the disposition of this character.

TABLE IX

FREQUENCIES OF OCCURRENCE OF THE LARGEST SUPRALABIAL IN Opheodrys vernalis

Supralabial	F'requency as Largest Supralabi
3	3
4	37
5	53
6	1111
7	17
8	1

As in the number of supralabials, the distribution of the largest supralabial in the series seems to be independent of sex, side, locality, or race.

Infralabials.—The interpretation of the variation in the infralabials is the same as that in the supralabials. The number of infralabials varies independently of sex, race, locality, and side of the head. Variation as a reduction from the modal number (8) is ten times as frequent as an increase. The numbers for both sexes of Opheodrys vernalis are brought together in Table X.

TABLE X

NUMBER OF INFRALABIALS IN Opheodrys vernalis

Number of Infralabials	Frequency
5	5
6	30
7	242
8	1123
9	31

Postoculars.—The number of postoculars varies fortuitously from the modal number, two; there are rare occurrences of one and three (Table XI).

TABLE XI

NUMBER OF POSTOCULARS IN Opheodrys vernalis

Number of Postoculars	Frequency
1	17
2	1411
3	17

Anterior temporals.—The number of anterior temporals is almost invariably one (1432 specimens). Eight exceptions of two anterior temporals have no apparent correlation with other characters.

Posterior temporals.—Two posterior temporals are usually present (1340 cases); a reduction from this modal number to one is more common (seventy times) than the increase to three (twenty-three times). The observed variation seems to be independent of other characters.

SUMMARY

During the initial stages of this variational study it became apparent that there are at least two well-differentiated races (one of which is herein described) of *O. vernalis* with, perhaps, an incipient (incipient either in actual development or in our knowledge) race in the Black Hills. An attempt has been made to correlate the normal ranges of the recognized forms with the vegetation, physiography, and glacial history of the areas in which they occur. Several literature records have been rejected. A brief résumé of the published habitat notes, a synonymy, and an historical summary are included.

It is suggested that the green color of O. vernalis is the result of a mixture of blue, gray, and alcohol-soluble yellow.

The ventrals vary both racially and sexually. The caudals, besides varying with sex, reduce in number from south to north and from mainland to island. The character indices in *vernalis* formed by adding caudals to ventrals and by subtracting caudals from ventrals indicate no new phenomena that cannot be seen in the study of the individual series independently.

The labials, both upper and lower, the temporals, both anterior and posterior, and the preoculars have variations that do not seem to be correlated with either sex, race, locality, or side of head.

The loreal is more frequently elongated in v. blanchardi than in v. vernalis.

The number of dorsal rows is practically invariable.

The males tend to have a reduced number of preoculars.

The posterior chin shields are more frequently separated by small scales in a particular insular population than they are in the adjacent mainland population.

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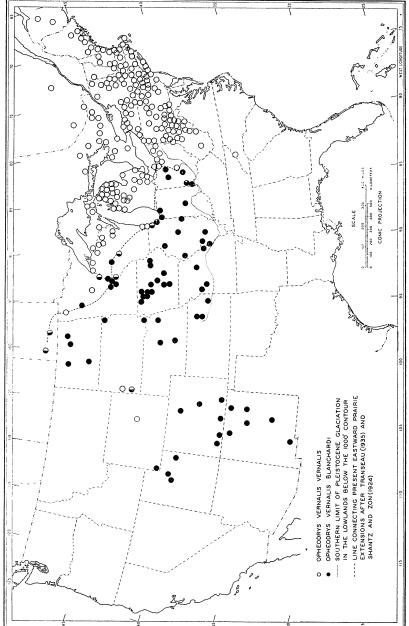
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