

**BULLETIN**  
**OF THE**  
**FLORIDA STATE MUSEUM**

**BIOLOGICAL SCIENCES**

**Volume 6**

**Number 3**

**REVISION OF NORTH AMERICAN SALAMANDERS  
OF THE GENUS PLETHODON**

**Richard Highton**



**UNIVERSITY OF FLORIDA**  
**Gainesville**  
**1962**

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

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Published 31 December 1962

Price for this issue \$1.55

# REVISION OF NORTH AMERICAN SALAMANDERS OF THE GENUS *PLETHODON*

RICHARD HIGHTON<sup>1</sup>

**SYNOPSIS:** Systematic study of the North American salamander genus *Plethodon* reveals three major groups in the genus, designated the western plethodons, the eastern small plethodons, and the eastern large plethodons. The western plethodons occur in the northwestern United States and adjacent Canada and include five species (*vandykei*, *larselli*, *dunni*, *vehiculum*, and *elongatus*) in three species groups. Five species in three species groups also comprise the eastern small plethodons. Four of these (*wellerti*, *dorsalis*, *cinereus*, and *richmondi*) occur in eastern North America; the fifth (*neomexicanus*) is known only from the Jemez Mountains of New Mexico. The eastern large plethodons include six species (*wehrlei*, *yonahlossee*, *ouachitae*, *caddoensis*, *jordani*, and *glutinosus*) in three species groups and occur only east of the Rocky Mountains. The eastern large and small plethodons are more closely related to each other than either is to the western plethodons, but of the two, the small group appears to be closer to the western plethodons.

Special emphasis has been placed on a study of geographic variation in pigmentation and segmentation characteristics of the eastern species. The use of the trinomen to describe geographic variation has been found unsatisfactory because of nonconcordance of geographically variable characters in species formerly considered polytypic. Seven isolated allopatric populations are still recognized as subspecies because of their apparent close relationship to the nominotypical subspecies, but the taxonomic status of each is still uncertain. Some of these forms are weakly differentiated and all are in need of further study.

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<sup>1</sup> The author is Associate Professor of Zoology at the University of Maryland. He did much of the work reported here while a graduate student at the University of Florida, and an earlier version was accepted as a doctoral dissertation in 1956. Although primarily a student of salamanders, the author contributed a paper in this journal on the snake genus *Stilosoma* (1956). Manuscript submitted 2 April 1961.—Ed.

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## INTRODUCTION

The North American salamander genus *Plethodon* is the type genus of the lungless family Plethodontidae, today the most successful group of salamanders, for it contains more than half of the known living species of the Order Caudata. The family's center of distribution is North America; one genus, *Hydromantes*, also occurs in southern Europe, and representatives of several genera enter the Neotropical Region. Plethodontid salamanders occupy widely varied habitats. Some are strictly aquatic cavernicoles (*Typhlomolge* and *Haideotriton*); others live only in mountain streams (*Leurognathus*); and still others, like *Plethodon*, are terrestrial even to the extent of depositing their eggs on land and dispensing with the aquatic larval stage.

Here recognized in the genus *Plethodon* are 16 species. Most live on the forest floor in the leaf mold and under stones and rotting logs; ten occur in wooded areas of eastern North America, five more in the Pacific Northwest, and one is known only from the Jemez Mountains of New Mexico. Of the 25 genera in the family Plethodontidae, only two others show as great or greater disjunctions in their distribution: *Hydromantes*, with two species in Europe and three in California, and *Aneides*, with four species in western North America and one in the Appalachian Mountains of the eastern United States.

The last revision of the entire genus was that of Dunn (1926), when only a fraction of the presently known forms and material was available. His review of the family led him to consider *Plethodon* the most primitive existing genus in the attached-tongue branch of the Plethodontidae. He considered *Hemidactylum*, *Ensatina*, *Batrachoseps*, and *Aneides* as more specialized derivatives of a *Plethodon*-like ancestor.

Grobman (1944) studied the distribution and systematics of the eastern species and divided them into two groups, the large plethodons and the small plethodons. He suggested that these groups might actually represent distinct genera or subgenera, but he reserved judgment until their relationships with the western species could be determined. Since the revisions of Dunn and Grobman, many new species and subspecies have been described. A review of these forms offers a valuable opportunity to study speciation in this important group of North American salamanders and to clarify the relationships of the eastern and western species.

An earlier draft of this paper based mainly on material in the University of Florida Collections was presented to the University of Florida as a degree requirement in 1956. Since then I have studied

the *Plethodon* material in all of the major eastern museums, and have borrowed additional material from a number of other collections. It thus has been possible to expand the study into a more nearly complete generic revision. Several changes have been made in the systematic conclusions and nomenclature of the earlier draft, particularly in the treatment of infraspecific variation.

Most recent workers have emphasized the importance of studying the pigmentation characters of plethodons in life. Many species, particularly the large eastern forms, are extremely difficult to identify after years of preservation. Few other vertebrates exhibit after preservation so few differentiating characters. Living specimens of all 16 species have been examined, plus representatives from many geographic areas for most of the widely ranging eastern forms. Living specimens representing all of the previously recognized geographic races have also been studied.

#### ACKNOWLEDGMENTS

More than 100 persons contributed living and preserved materials for this study. To each of these individuals I express sincere thanks. Most of the material is deposited in the University of Florida Collections. The remainder is retained for further study (listed as RH), but eventually will be placed in permanent museum collections.

A list of abbreviations used in the text follows. For the loan of personal materials or specimens in their care, and for all courtesies extended, I wish to thank the following institutions and individuals:

- AMNH, American Museum of Natural History, Charles M. Bogert and Richard Zweifel  
ANSP, Academy of Natural Sciences of Philadelphia, James M. Böhlke  
BCB, Bryce C. Brown  
BDV, Barry D. Valentine  
CA, Chicago Academy of Sciences, Howard K. Gloyd and Laura Brödie  
CAS, California Academy of Sciences, Alan E. Leviton  
ChM, Charleston Museum, Albert Schwartz  
CJS, Charles J. Stine  
CM, Carnegie Museum, Neil D. Richmond and Graham Netting  
CNHM, Chicago Natural History Museum, Robert Inger and Hymen Marx  
CSNH, Cincinnati Society of Natural History, Ralph Dury and Jack L. Gottschang  
CU, Cornell University, Edward Raney, Bruce Collette, and Frederick Gehlbach  
CWM, Charles W. Myers  
DC, Donald Cooper  
DMB, Douglas M. Burns  
DMNH, Dayton Museum of Natural History, James MacMahon  
DR, Douglas Rossman  
ERA-WTN, Ross Allen Reptile Institute, Wilfred T. Neill

- GSMNP, Great Smoky Mountains National Park, Arthur Stupka  
 HAD, Harold A. Dundee  
 HB, Herbert Barden  
 HCM, Henry C. Moski  
 INHS, Illinois Natural History Survey, Philip W. Smith  
 JAF, James A. Fowler  
 JSM, John S. Mechem  
 JWC-FC, John W. Crenshaw, Jr.  
 KNH, Ken N. Hovde  
 MCZ, Museum of Comparative Zoology, Arthur Loveridge and Ernest Williams  
 MMNH, Minnesota Museum of Natural History, William J. Breckenridge  
 MUOZ, Museum of the University of Oklahoma, Zoology, Arthur N. Bragg  
 MVZ, Museum of Vertebrate Zoology, University of California, Robert C. Stebbins  
 NMC, National Museum of Canada, A. W. F. Banfield and Francis R. Cook  
 OC, Oberlin College, Warren F. Walker, Jr.  
 OS, Ottys Sanders  
 PLC, Pacific Lutheran College, Jens W. Knudsen  
 PSM, Paul S. Martin  
 RC, Roger Conant  
 ROMZ, Royal Ontario Museum of Zoology, E. B. S. Logier  
 SAM, Sherman A. Minton, Jr.  
 SM, Strecker Museum, Baylor University, Bryce C. Brown  
 SRT, Sam R. Telford, Jr.  
 TNHC, University of Texas Natural History Collection, W. Frank Blair  
 TU, Tulane University, Fred R. Cagle and Harold Dundee  
 UA, University of Arkansas, Herndon G. Dowling  
 UF, University of Florida Collections, William J. Riemer  
 UG, University of Georgia, Bernard Martof  
 UIMNH, University of Illinois Museum of Natural History, Hobart M. Smith  
 UKMNH, University of Kansas Museum of Natural History, Edward H. Taylor  
 and John M. Legler  
 UKy, University of Kentucky, Roger W. Barbour  
 UMMZ, University of Michigan Museum of Zoology, Charles F. Walker, Norman  
 Hartweg, Thomas M. Uzzell, Jr., and James A. Organ  
 USC, University of Southern California, Jay M. Savage and David Wake  
 USNM, United States National Museum, Doris M. Cochran  
 WVBS, West Virginia Biological Survey, N. Bayard Green

Cornelius Barry aided by counting the vomerine teeth of some specimens. Clifford H. Pope lent his original data on vomerine tooth counts from his three published studies. Vincent Schultz contributed valuable statistical advice. My wife, Anne, contributed by collecting specimens, typing and proofreading parts of the manuscript, and especially by taking color notes on geographic variation in *P. glutinosus* and *P. jordani*. The Chairman of my Graduate Supervisory Committee, Arnold B. Grobman, has been a constant source of intellectual stimulation, encouragement, helpful advice, and criticism.

Part of this work was supported by grants from the National Science

Foundation, the General Research Board of the University of Maryland, the Florida State Museum and the Graduate School of the University of Florida, and the Highlands Biological Station. Collecting in the Great Smoky Mountains National Park, in the Shenandoah National Park, and along the Blue Ridge Parkway was permitted through the cooperation of the National Park Service.

## METHODS

The necessity of studying living material made a considerable amount of field work imperative, particularly on the eastern large plethodons. Specimens were kept alive in the laboratory at low temperatures for long periods for later comparison with other living material.

Detailed descriptions of many living and preserved specimens were made during the course of this study. Similar data for many forms are available in Bishop (1943), Stebbins (1951), or in the original descriptions. These are not repeated here as the concern is with variation in populations, not detailed descriptions of individual specimens.

Many recent workers have given considerable weight to variation in the number of costal grooves. Analysis of published data often reveals lack of agreement in the number of grooves in some forms. A method for determining body segmentation by counting costal grooves consistently has been suggested (Highton, 1957).

Snout-vent length is measured always from the tip of the snout to the anterior end of the vent.

The distribution maps are based on literature records (hollow symbols) and specimens examined by the writer (solid symbols, unless otherwise noted). Many new records and several range extensions are included.

During the course of this study I examined more than 40,000 specimens, about 25 percent of them of my own collecting. I have seen all type specimens known to exist with the exception of the holotype of *P. neomexicanus*.

## PIGMENTATION IN THE GENUS PLETHODON

The pigmentation of living specimens of all previously recognized forms in the genus was studied under a dissecting microscope. The great variety of coloration in these salamanders is produced by only three different types of pigment cells. Following Hertzler (1958), these are referred to as melanophores, iridophores, and red or yellow chromatophores. In his histological and biochemical study of the pigmentation of *Plethodon cinereus*, Hertzler identified black melanophores,



iridophores, and red chromatophores. He presents evidence that the black pigment cells in the red-backed salamander contain melanin, and that the white or brassy pigmentation is produced by pigment cells that contain no guanine, although herpetologists have long referred to these cells as "guanophores." As the granule-bearing cells responsible for the white pigment of these salamanders have not yet been analyzed chemically, Hertzler prefers the nonspecific term, iridophore. Finally, the red chromatophores, usually referred to in the literature as "lipophores," are not lipid in nature, but are chemically related to melanin, although they differ from melanin in having smaller amounts of the elements magnesium, calcium, and iron.

Although no biochemical studies have yet been conducted on the pigmentation of other species of the genus, their pigments as compared under a dissecting microscope show no significant difference from those of *Plethodon cinereus*, other than in distribution of the cells. Color and black and white photographs, and drawings of most of the forms of the genus are available in the literature (see especially Bishop, 1943; Conant, 1958; and Stebbins, 1951 and 1954).

Melanophores are present in all members of the genus and are responsible for the dark ground color of these salamanders. The other pigments generally occur in gaps in the melanophore background. Partial albinos of five species, *glutinosus*, *jordani*, *cinereus*, *dorsalis*, and *vehiculum* have been reported (literature summarized by Hensley, 1959).

Iridophores are responsible for the white spotting and brassy flecking present on the dorsum, sides, and belly of most species. Little difference is apparent in the structure of the differently colored iridophores, though the amount of light reflected by the spots varies considerably. Hertzler (1958) finds that small brassy iridophores lie deeper in the dermis than do the larger white ones and suggests that the color is altered because light must pass through the pigmented corium twice. Possessing iridophores is a condition that has been described as "brassy flecking," "metallic golden spotting," "golden blotching," "bronzy mottling," and "frosting." Brassy iridophore pigmentation is present in the iris of most species, though it is often reduced in the eastern large plethodons. It is responsible for the small brassy flecks of some *glutinosus*, *jordani*, *ouachitae*, *caddoensis*, *wehrlei*, *cinereus*, *richmondi*, *welleri*, *dorsalis*, *neomexicanus*, *larselli*, and *vehiculum*. The larger white spots are present on the dorsum of at least some populations of most of the forms in the genus, but in some, especially *welleri*, *hubrichti*, *caddoensis*, and some *glutinosus*, even the largest spots have

a brassy appearance. The dorsum of a single *glutinosus* may show every type of intermediate between the brassy and the white type. Lateral and ventral iridophore pigmentation, when present, is almost never of the brassy type.

"Red chromatophores" of Hertzler may vary from yellow to red, but red is the prevailing hue. They are present in *yonahlossee*, *ouachitae*, *cinereus*, *dorsalis*, *elongatus*, *vehiculum*, *dunni*, *vandykei*, *larselli*, and in some populations of *richmondi*, *jordani*, and *wehrlei*.

The variety of coloration in the genus seems due entirely to variation in the presence, location, and abundance of these three pigments. Some forms lack the red chromatophores or iridophores or both. Pigmentation characters may vary widely within a species—individually, ontogenetically, and geographically—but are constant enough within most populations so that a person familiar with the variations can identify most living specimens easily by color pattern alone. The phylogenetic significance of the distribution of these pigments is discussed in the accounts of the various groups.

#### VARIATION IN NUMBER OF VOMERINE TEETH

The number of vomerine teeth is often used as a systematic character in the genus *Plethodon*. In a series of three papers on *glutinosus*, *yonahlossee*, and *ouachitae* published in 1949, 1950, and 1951, Clifford and Sarah Pope demonstrate that the total number of vomerine teeth of all three species is correlated with size. The study of variation in the number of vomerine teeth within and among species of *Plethodon* must therefore consider the rate of ontogenetic change in number of teeth as well as the absolute number of teeth at any given body length.

The Popes fitted rectilinear regression lines to their data on the three species of eastern large plethodons. The teeth of the specimens of *glutinosus* counted by Pope and Pope (1949:253) were recounted and it is found that our counts are comparable. The data for *yonahlossee* and *ouachitae* are taken directly from the Popes' original data sheets. Using the same statistical technique, I have fitted regression lines to data on the relationship between the total number of vomerine teeth and snout-vent length for every species in the genus. Geographic variation in the number of vomerine teeth was studied in seven species previously considered polytypic, *vandykei*, *dorsalis*, *cinereus*, *richmondi*, *wehrlei*, *jordani*, and *glutinosus*. Significant geographic variation occurs only in *glutinosus*.

Two values must be calculated to obtain a regression line, the Y-intercept and the slope of the line. The slope estimates the rate of

increase in the teeth-size relationship; the Y-intercept is an estimate of the initial number of teeth the animal possesses early in development. Rectilinear regressions are used rather than curvilinear regressions because graphical plots of the data show that linear regressions describe the variation adequately. No species shows significant sexual dimorphism in vomerine tooth counts. The number of teeth is considered the dependent variate and the snout-vent length the independent variate.

The ontogenetic change in the relationship of vomerine teeth and snout-vent length in different species is often similar, particularly in closely related forms. The rate of increase tends to be greater in the larger species, with the exception of *wehrlei*, *elongatus*, and *neomexicanus*. The last species has a negative slope, but it does not differ significantly from zero. (A real negative slope would be produced by a loss of teeth in old individuals.) The eastern small plethodons have the lowest rate of increase in the number of vomerine teeth during growth.

Regression lines for each species are calculated by the method of least squares. The data for the several geographic samples of each of the seven polytypic species listed above are combined to obtain a single regression line for each species. Several factors may lead to bias. Geographic samples of each species were not chosen at random, but were often selected because of availability of material, and in some instances because of indications of geographic variation in other characters. Sizes of the various geographic samples were seldom equal. *P. glutinosus* shows such significant geographic variation that the pooling of the 12 geographic samples does not reflect the vomerine teeth-snout-vent length relationship in any one region. In spite of these shortcomings, the estimates of the slopes and Y-intercepts of the regression lines, together with their 95 percent confidence intervals, have value in illustrating patterns of variation in the genus and are included in table 1.

## TREATMENT OF INFRASPECIFIC VARIATION

Several types of geographic variation occur in the genus *Plethodon*. The gradual clinal type occurs in some species. In others abrupt changes are apparent over short distances where the ranges of two nominal subspecies meet. Some populations are isolated from their nearest relatives by unoccupied regions. In this event the nature of intergradation cannot be used to determine whether or not the species level of differentiation is attained.

TABLE 1. Slopes and Y-intercepts of regression lines for number of vomerine teeth on snout-vent length in the species of *Plethodon*.

Species	Sample Size	Slope			Y-intercept		
		Estimate	95% confidence interval		Estimate	95% confidence interval	
			Lower limit	Upper limit		Lower limit	Upper limit
<i>vandykei</i>	51	.237	.156	.318	5.22	1.87	8.57
<i>larselli</i>	25	.292	.142	.442	0.54	-5.14	6.23
<i>dunni</i>	49	.146	.067	.224	5.43	1.27	9.59
<i>vehiculum</i>	68	.151	.058	.243	3.18	-0.83	7.19
<i>elongatus</i>	49	.028	-.024	.080	9.42	6.73	12.12
<i>neomexicanus</i>	20	-.027	-.235	.180	14.78	4.17	25.39
<i>dorsalis</i>	182	.057	-.005	.118	9.10	6.83	11.37
<i>welleri</i>	31	-.054	-.221	.113	11.18	5.09	17.28
<i>cinereus</i>	398	.054	.025	.084	8.10	7.01	9.18
<i>richmondi</i>	237	.101	.069	.134	7.16	5.82	8.50
<i>wehrlei</i>	183	.065	.029	.101	10.27	8.52	12.02
<i>yonahlossee</i>	125	.410	.372	.447	0.88	-1.49	3.25
<i>ouachitae</i>	125	.267	.213	.321	6.67	3.83	9.52
<i>caddoensis</i>	43	.168	.011	.326	13.00	6.66	19.34
<i>jordani</i>	683	.232	.214	.251	4.97	4.08	5.87
<i>glutinosus</i>	1117	.197	.184	.210	6.25	5.56	6.94

All three types of geographic variation have been used in the past as a basis for naming subspecies of *Plethodon*. The large amount of material now available permits more detailed analysis of geographic trends than have heretofore been possible. Results indicate that independent characters in *Plethodon* often do not show concordance in their geographic variation. This is probably because environmental factors modifying the phenotype directly or modifying the genotype through natural selection rarely affect the independent characters of the organism in the same way.

Systematic literature reflects considerable controversy about the usefulness of the trinomen (see Wilson and Brown, 1953, and Mayr, 1942, for opposing viewpoints).

Nomenclatural recognition of geographic subspecies based on characters showing nonconcordant variations has little objective value because the use of different sets or combinations of characters results in different infraspecific classifications. Geographic variation in *Plethodon* is sometimes great; spectacular examples occur. Even so it is necessary to be so arbitrary in the choice of characters used to demarcate subspecies that I fail to see the advantage of their continued use. Therefore I have not used subspecies to describe geographic variation.

The treatment of isolated populations I still recognize as subspecies remains to be considered. It is not known whether reproductive isolation would be established or maintained if the area between the disjunct ranges became habitable and isolated forms came into contact. Seven forms presently recognized as subspecies—*P. v. idahoensis*, *P. r. hubrichti*, *P. r. nettingi*, *P. d. angusticlavius*, *P. c. polycentratus*, *P. c. serratus*, and *P. g. albagula*—are clearly more closely related to the species with which they are associated nomenclaturally than to any other form. In all there is morphological overlap in the systematic characters used to differentiate the two subspecies. However, this may also occur between full species of *Plethodon*. As each isolated form is apparently closely related to its nominotypical subspecies and was probably isolated from it relatively recently, I think that the recognition of these forms as subspecies should be continued. An alternative some herpetologists might choose would be to recognize some or all as full species, but this would not reflect their relationships so well. Further research on each of these cases is greatly needed.

## SYSTEMATICS

### *Plethodon* Tschudi

*Plethodon* Tschudi (1838:58). Generic type by original designation: *Salamandra glutinosa* Green.

*Phatnomatorhina* Bibron in Bonaparte (1839:256). Substitute name.  
*Sauropsis* Fitzinger (1843:33). *Non Sauropsis* Agassiz, 1832, *Jahrb. f. Min.*, p. 142. Generic type by original designation: *Salamandra erythronotus* Rafinesque.

**DIAGNOSIS.** Plethodontidae with tongue attached in front, premaxillae separate, teeth on posterior portion of maxillae, tail not constricted at base, five toes on hind feet, no palmar tubercles, terminal phalanges normal, and no aquatic larval stage.

**REMARKS.** According to Dunn (1926), the closest relatives of *Plethodon* are *Batrachoseps*, *Ensatina*, *Aneides*, and *Hemidactylium*. All four of these genera differ from *Plethodon* in important characteristics. *Batrachoseps* and *Hemidactylium* have only four toes on the hind feet. *Ensatina* and *Hemidactylium* have a basal constriction of the tail, a provision for urotomy. *Ensatina* has palmar tubercles. The premaxillae are fused in *Aneides* and *Batrachoseps* (except *B. wrighti*). *Hemidactylium* is the only genus in the group with an aquatic larval state, but this may not represent a primitive condition for its larvae differ

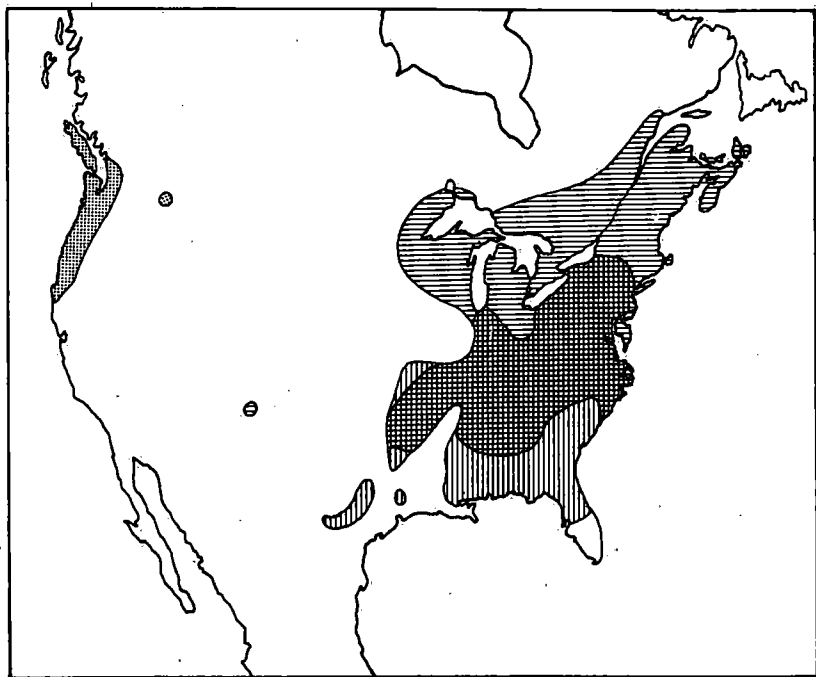


FIGURE 1. Distribution of the western plethodonts (stippling), the eastern large plethodonts (vertical lines), and the eastern small plethodonts (horizontal lines) in North America.

from those of most other plethodontids. *Aneides* lacks teeth on the posterior portion of the maxilla and has expanded terminal phalanges. Most of the characters by which these genera differ from *Plethodon* appear to be specializations. For this reason Dunn (1926:22) considers *Plethodon* the most primitive of this group of genera, with the possible exception of *Ensatina*. *Plethodon* is the largest genus in number of species, and shows within itself more divergence than most related genera.

The genus *Plethodon* has three major natural subdivisions: the western plethodons, eastern small plethodons, and eastern large plethodons. The distribution of these groups is shown in figure 1. These might be considered subgenera in some animal groups, but herpetologists have rarely used subgenera in their classifications, so only common names are given them in keeping with current herpetological practices. Each of these subdivisions is further divided into groups of closely related species. A few species are distinct enough to warrant monotypic grouping.

Grobman (1944:266) suggests that the relationship between the eastern large and small plethodons is not close and lists size and costal groove differences between the two groups. Actually variations in these characters overlap somewhat, but there are other important differences. The mental gland of the adult male is usually better developed in the eastern large plethodons (fig. 2). Most eastern small plethodons have characteristically more elongated bodies and shorter legs; they have fewer vomerine teeth; and the number of their trunk vertebrae

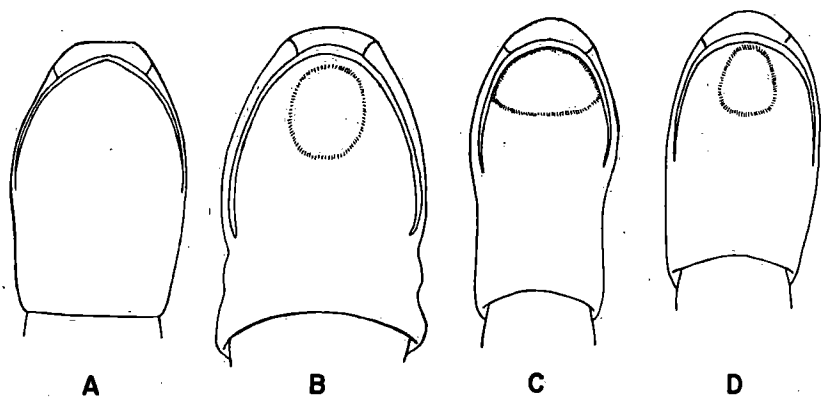


FIGURE 2. Chins of adult male *Plethodon* showing variation in the presence and shape of the mental gland. (A) *P. larselli*, (B) *P. glutinosus*, (C) *P. richmondi*, (D) *P. dorsalis*. Drawings not to same scale.

varies greatly within the group (16-24), whereas the eastern large plethodons show little variation (16-19, usually 17-18). The small forms usually have more webbing on the toes than the large ones. Eastern large plethodons usually have an unpigmented parietal peritoneum; in the small ones the peritoneum is pigmented with melanophores. Premaxillary teeth of adult males of some eastern small plethodons are highly modified (fig. 3).

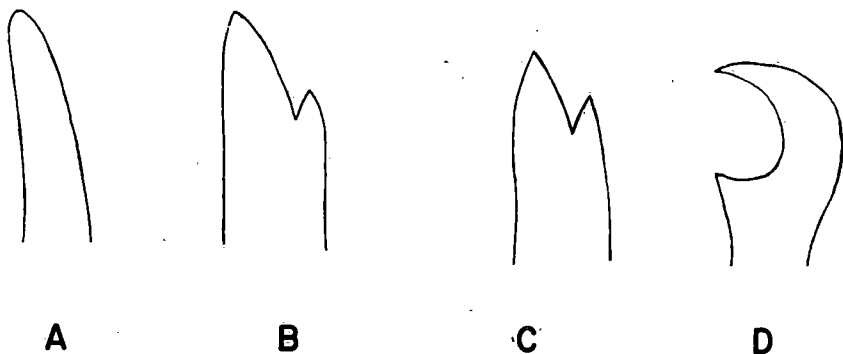


FIGURE 3. Modifications of premaxillary teeth of adult male *Plethodon*. (A) *P. vehiculum*, typical of western plethodons. (B) *P. glutinosus*, typical of eastern large plethodons. (C) *P. dorsalis*; *P. welleri* similar. (D) *P. cinereus*; *P. richmondi* similar. Anterior cusp shown at right, posterior cusp at left.

*Plethodon wehrlei*, usually included with the eastern large plethodons on the basis of size, is intermediate between the two groups in several ways. It has more costal grooves and fewer vomerine teeth than other eastern large plethodons. Its toes are webbed between the proximal phalanges, as in the eastern small plethodons, and the peritoneum has some melanophore pigmentation. The intermediacy of this species suggests the two groups have not become sufficiently distinct to justify taxonomic separation and shows their close relationship. Despite the characters linking it with the eastern small plethodons, *P. wehrlei* is probably more closely related to the larger species, and is therefore listed as a separate species group under the eastern large plethodons.

Series of skeletons are available for most forms, and the vertebrae of all the species of the genus have been examined. The two eastern groups show differences in their body vertebrae. The height of the trunk vertebrae is proportionately less in the eastern small plethodons and their vertebrae usually lack the neural spines present on those of the large eastern species (fig. 4). *P. wehrlei* closely resembles the other eastern large plethodons in this regard.



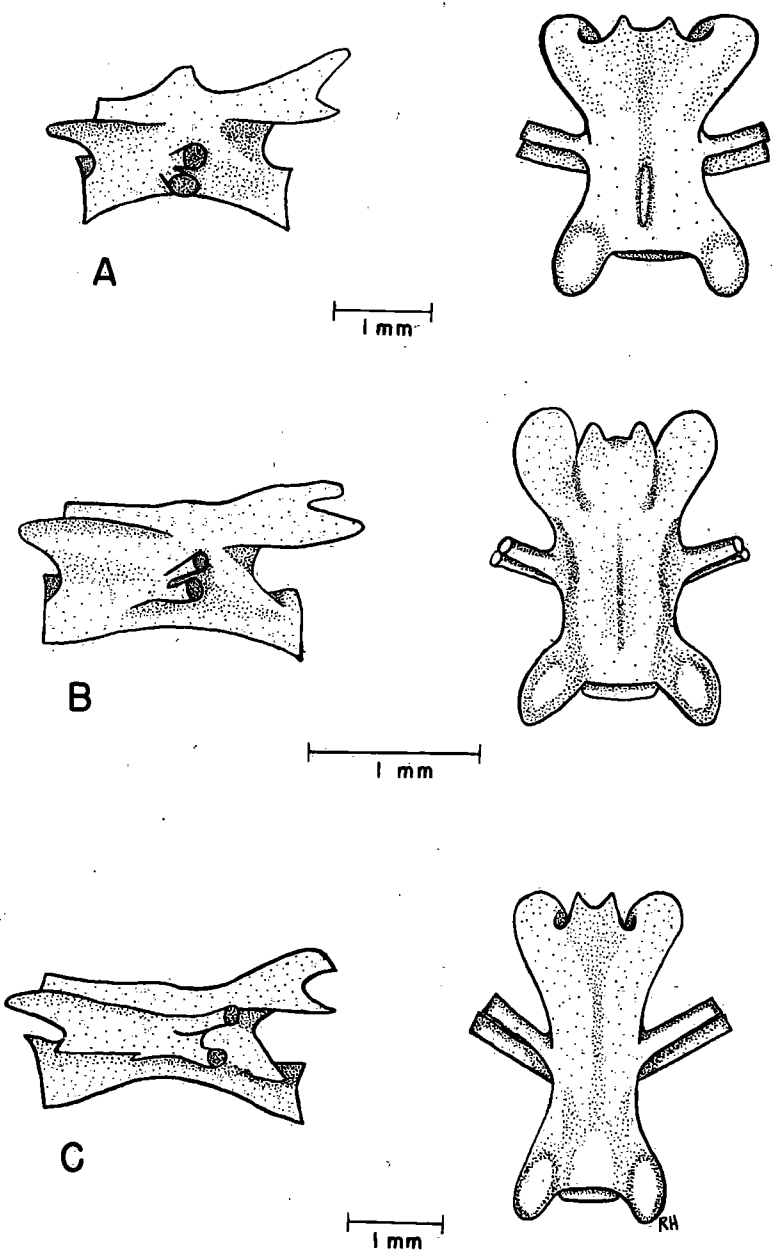


FIGURE 4. Variation in the trunk vertebrae of *Plethodon*. (A) *P. glutinosus*, (B) *P. welleri*, (C) *P. dunni*, representing large eastern, small eastern and western groups respectively.

Comparison of these differential characters also clarifies the relationship of the western to the eastern species. As in the eastern forms, size varies within the western group, but 4 (*vandykei*, *dunni*, *elongatus*, and *neomexicanus*) of the 6 western species are as large as most eastern large plethodons. The number of their trunk vertebrae varies considerably (14-20). Vertebrae of the 5 species from the Pacific Northwest are proportionately lower and longer and have longer transverse processes than any of the eastern species (fig. 4). The vertebrae of *neomexicanus* are like those of the eastern small plethodons. The peritoneum of all western plethodons is pigmented with melanophores, and the mental gland is absent or poorly developed in all adult males. Body form varies from short and stout in *vandykei* to elongate in *elongatus* and *neomexicanus*. The vomerine teeth are few in number, and the premaxillary teeth of males are unmodified except in *neomexicanus*. The toes of *dunni* and *vehiculum* are slightly webbed, while the other 4 species have webbing between the proximal phalanges. Two, *larselli* and *neomexicanus*, have the number of phalanges in the fifth hind toe reduced, presumably a first step in its evolutionary loss, a characteristic of some related genera.

As a group the western species vary morphologically more than either of the eastern groups. In vertebral structure the 5 species from the Pacific Northwest are distinct from the rest of the genus. Although the eastern and western groups probably share a common ancestor, their degree of differentiation suggests they have been separated a long time. In assessing the relationships of these salamanders I place more weight on vertebral differences than on other characters. As they are more stable evolutionarily, vertebrae are more reliable indicators of phylogenetic relationship.

*P. neomexicanus*, known only from the Jemez Mountains of New Mexico, is the most geographically isolated species. In their original description Stebbins and Riemer (1950:77) consider the species probably close to *P. cinereus*, an eastern small plethodon. Blair (1958:450) postulates a late Pleistocene connection between the New Mexican species and the nearest *cinereus* localities in eastern Oklahoma. Though this hypothesis appears more plausible than a recent connection with the *Plethodon* populations in the Pacific Northwest, the amount of differentiation in *neomexicanus* suggests it has been isolated much longer than since the Wisconsin stage of the Pleistocene. Still, resemblances in structure of the trunk vertebrae and in body proportions support the contention that *neomexicanus* is most closely related to the eastern small plethodons. It is not possible to say which eastern

species it most closely resembles, as it has differentiated greatly from them all. It is larger and has a reduced fifth toe. In some adult *neomexicanus* males the premaxillary teeth have two cusps as in the eastern plethodons, but the mental gland is poorly developed as in the western plethodons.

In several ways the eastern small plethodons resemble the western group more closely than do the eastern large plethodons. The red or yellow dorsal stripe is more frequent. Both show greater variation in the number of trunk vertebrae and degree of body elongation. Both have low counts of vomerine teeth and a pigmented parietal peritoneum. The common ancestor of the genus probably resembled these two groups more closely than it did the eastern large plethodons. It is unlikely that convergence can account for so many similarities between the two. The eastern large plethodons therefore have diverged most radically from the ancestral type, becoming specialized by an increase in size, increase in number of vomerine teeth, development of the mental gland, and in the loss of pigmentation in the peritoneum. Yet similar vertebral structure in the two eastern groups, as well as the intermediate position of *wehrlei*, suggests that both are more closely related to each other than either is to the western plethodons. Dunn (1926:23) suggests that *yonahlossee*, one of the eastern large plethodons, is the

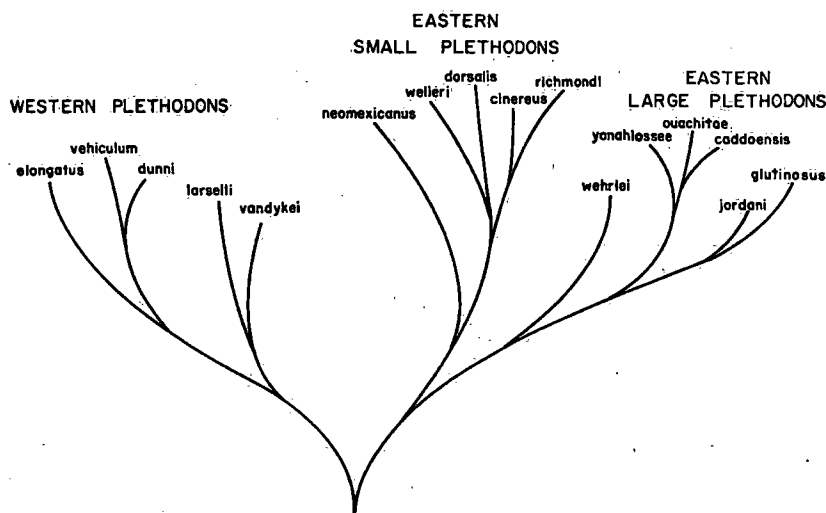


FIGURE 5. Dendrogram showing the suggested phylogeny of the species of *Plethodon*.

most primitive member of the genus, but I consider it one of the most highly specialized. Morphological relationships suggest the phylogeny shown in figure 5.

The relationships of the western plethodons with the other plethodontid genera in western North America need further study. Western plethodons may be more closely related to *Batrachoseps*, *Ensatina*, or western *Aneides* than to any of the eastern plethodons. The western genera probably have been isolated from their eastern relatives for a long time. The two geographic groups now included in the genus *Plethodon*, one in eastern and one in western North America, both retain many primitive characteristics. This does not necessarily mean that they are congeneric. Each group has more species displaying more diversity than any other plethodontid genus in its region. A review of this entire problem is needed, especially an investigation of the relationships of each group to the genera *Aneides*, *Batrachoseps*, *Ensatina*,

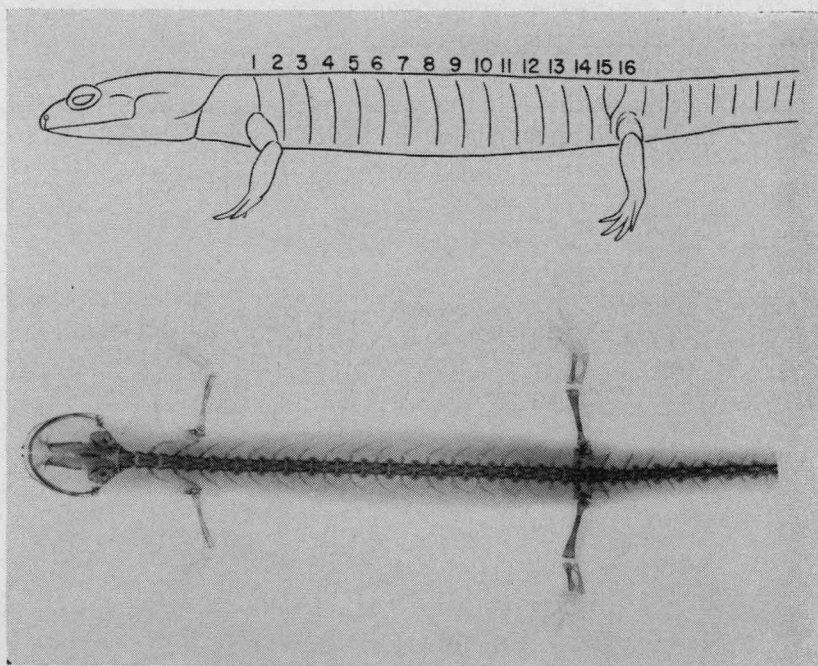


FIGURE 6. Relationship between trunk vertebrae and costal grooves. Radio-graph of a specimen of *P. glutinosus* from Florida with 17 trunk vertebrae, and a lateral view of the same individual showing its 16 costal grooves including two that run together on the groin.

and *Hemidactylum*. Such an inquiry, which is beyond the scope of this study, should be completed before erecting a new genus for the western plethodons, a course which seems indicated by the present data.

The systematic arrangement I propose for the genus *Plethodon* is shown in the table of contents.

## KEY TO SALAMANDERS OF THE GENUS *PLETHODON*

The following key is based mainly on the average number of costal grooves in each form of the genus. The number of costal grooves is one less than the number of trunk vertebrae if counted to include the groove over the front limb (even if it is not well developed) and all dorsolateral grooves anterior to the hind limb (even when two of the grooves join ventrally on the groin). See figure 6. A small percentage of some forms may not be correctly identifiable by the number of costal grooves, but a small series usually suffices to key out correctly. Ranges are included because locality data may prove more helpful in identifying preserved specimens than pigmentation characters, which often disappear after preservation.

1. Costal grooves usually 14; parotoid gland well developed ..... 2  
    Costal grooves usually 15 or more; no parotoid gland ..... 3
2. Proximal segment of limbs dark in color (northern Idaho) .. *P. v. idahoensis*  
    Proximal segment of limbs red or yellow, similar to pigment in dorsal  
    stripe (western Washington) ..... *P. v. vandykei*
3. Costal grooves usually 15 ..... 4  
    Costal grooves usually 16 or more ..... 5
4. One phalanx in fifth toe of hind foot; belly reddish (Multnomah and  
    Hood River Cos., Oregon, and Skamania Co., Washington) .... *P. larselli*  
    Two phalanges in fifth toe of hind foot; belly without red pigment (west-  
    ern Oregon and southwestern Washington) ..... *P. dunni*
5. Costal grooves usually 16 ..... 6  
    Costal grooves usually 17 or more ..... 15
6. Belly mottled with yellow or red, and white and black; adult size small,  
    usually less than 50 mm. snout-vent length; often a red, tan, or yellow  
    dorsal stripe (southwestern British Columbia, including Vancouver  
    Island, western Washington and western Oregon) ..... *P. vehiculum*  
    Belly usually dark, at least posteriorly, or with scattered small white  
    spots; adult size usually greater than 50 mm. (except *welleri* and *cad-*  
    *doensis*); dorsal stripe usually absent (except *yonahlossee* and *oua-*  
    *chitae*) (eastern United States) ..... 7
7. Red pigment on back, legs, or cheeks ..... 8  
    No red pigment ..... 10
8. Red pigment on legs or cheeks; on dorsum only in very young individuals  
    (southern Appalachian Mountains) ..... *P. jordani*

- Red pigment largely restricted to dorsum ..... 9
9. White pigment lacking in dorsal chestnut-colored stripe (Blue Ridge Mountains of southwestern Virginia, northeastern Tennessee, and northwestern North Carolina) ..... *P. yonahlossee*  
Abundant white pigment occurring within the dorsal stripe (Ouachita Mountains of Arkansas and Oklahoma) ..... *P. ouachitae*
10. Size small, adults not over 50 mm. snout-vent length; dorsum with large coalescing brassy spots usually covering at least half the dorsum; dark parietal peritoneum (Blue Ridge Province of southwestern Virginia, northeastern Tennessee, and northwestern North Carolina) ... *P. welleri*  
Back without brassy spots, or if present, small in size and occupying less than one-quarter of the dorsum; parietal peritoneum with a slight amount of melanophore pigmentation or none ..... 11
11. Body entirely black, completely lacking iridophores; chin usually lighter than belly (Blue Ridge Mountains of western North Carolina and adjacent portions of Tennessee and Virginia) ..... *P. jordani*  
Dorsum or sides or both with white or yellow spotting; chin as dark as belly, sometimes lighter ..... 12
12. Dorsum with large conspicuous white or brassy spots ..... 13  
Back usually without such spotting; spots present are of very small size ..... *P. jordani*
13. Melanophore pigmentation on chin much less than on belly ..... 14  
Melanophore pigmentation on chin similar to that on belly (eastern United States from southwestern Connecticut to northern Florida, west to Louisiana, Missouri, and Illinois, also eastern Oklahoma and eastern Texas ..... *P. g. glutinosus*
14. Dorsum with small white spots (central Texas) ..... *P. g. albagula*  
Dorsum with large white spots and smaller more numerous brassy flecks (Caddo Mountains of Arkansas) ..... *P. caddoensis*
15. Costal grooves usually 17 (Cattaraugus County, New York, south through western Pennsylvania, adjacent Ohio, West Virginia, and southwestern Virginia) ..... *P. wehrlei*  
Costal grooves usually 18 or more ..... 16
16. Costal grooves usually 18 ..... 17  
Costal grooves usually 19 or more ..... 21
17. Size large, to 70 mm. snout-vent length (northwestern California and southwestern Oregon) ..... *P. elongatus*  
Size small, to 50 mm. snout-vent length (eastern United States) ..... 18
18. Belly mottled with black and yellow or white; or belly with red, black, and yellow or white pigment ..... 19  
Belly black with small white spots (Cheat Mountains of West Virginia) ..... *P. r. nettingi*
19. Red pigment abundantly present on belly ..... 20  
No red pigment on belly except occasionally between front limbs (Missouri, Appalachian Plateaus, and Catskill Mountains, New York) *P. cinereus*
20. Dorsal stripe narrow, less than one-third the width of the body (southwestern Missouri, northwestern Arkansas, and adjacent Oklahoma) ..... *P. d. angusticlavius*  
Dorsal stripe much wider than one-third the width of the body, edges

- of stripe usually irregular except in individuals from Georgia and southwestern Illinois (southern Illinois, Indiana and southern Ohio, south through Kentucky and Tennessee to northeastern Mississippi, northern Alabama and northwestern Georgia) ..... *P. d. dorsalis*
21. Costal grooves usually 19 ..... 22  
 Costal grooves usually 20 or more ..... 25
22. Fifth toe of hind foot usually with one phalanx (Jemez Mountains, New Mexico) ..... *P. neomexicanus*  
 Fifth toe of hind foot with two phalanges (eastern North America) .... 23
23. Belly black with small white spots (Peaks of Otter region of Virginia Blue Ridge Mountains) ..... *P. r. hubrichti*  
 Belly mottled with equal amounts of black and yellow or white pigment ..... 24
24. Dorsal red stripe with straight edges (southeastern Canada south to North Carolina, eastern Tennessee, Ohio, Indiana, southeastern Illinois, and eastern Missouri) ..... *P. c. cinereus*  
 Dorsal red stripe with regular serrations associated with costal grooves (western Arkansas and eastern Oklahoma) ..... *P. c. serratus*
25. No stripe or a red dorsal stripe present; belly mottled with equal amounts of black and white or yellow pigment ..... 26  
 No stripe present; belly dark with small white spots (Pennsylvania and Ohio south to North Carolina and Tennessee) ..... *P. r. richmondi*
26. Red striped, or if unstriped (lead backed color phase), red pigment present on sides and dorsum (northwestern Georgia) .. *P. c. polycentratus*  
 Red striped, or if unstriped, no red pigment on the sides and dorsum (Coastal Plain and Piedmont from Long Island to North Carolina) ..... *P. c. cinereus*

## THE WESTERN PLETHODONS

The five species of western plethodons are well differentiated except for *dunni* and *vehiculum*, which appear to be fairly closely related. *P. vandykei* has two isolated races, *vandykei* in western Washington, and *idahoensis* in northern Idaho. *P. larselli* is known only from Multnomah and Hood River Counties, Oregon, and Skamania County, Washington. *P. dunni* occurs in southwestern Washington and coastal Oregon. *P. vehiculum* ranges along the coast from central Oregon to southern British Columbia, including Vancouver Island. *P. elongatus* occurs in a small area in northwestern California and southwestern Oregon.

In his recent summation of knowledge of the amphibians of western North America, Stebbins (1951) gives detailed descriptions of four of the five species in life. I have had no field experience with these animals and can offer little new information on individual or geographic variation. The modal number of trunk vertebrae differs in each of

the species (table 2) except *dunni* and *larselli*. None of the known forms has a modal number of 18 trunk vertebrae, and they show less vertebral variation within species than do the eastern forms. Each species has a mean number of vertebrae close to a whole number, indicating that strong selection restricts variation from the modal number.

TABLE 2. Number of trunk vertebrae in western forms of the genus *Plethodon*.

Form	Number of trunk vertebrae														Mean
	14	14/15	15	15/16	16	16/17	17	17/18	18	18/19	19	19/20	20		
<i>P. v.</i>															
<i>vandykei</i>	1	—	54	1	4									15.06	
<i>P. v.</i>															
<i>idahoensis</i>			29	1	4									15.13	
<i>P. larselli</i>			3		22	1	4							16.05	
<i>P. dunni</i>					56	1	3							16.06	
<i>P. vehiculum</i>					17	2	116	2	17					17.00	
<i>P. elongatus</i>									4	—	41	—	3	18.98	

All the western plethodons except *vehiculum* and *larselli* are fairly large. All have a striped phase, although in *larselli*, *dunni*, *vehiculum*, and *elongatus* some individuals of some populations are unstriped. All but *dunni* and *vehiculum* have webbed toes, and their vomerine tooth counts are low compared to most eastern large plethodons of similar size; *vehiculum* and *elongatus* have especially low vomerine counts. *P. vandykei* is unusual in having a parotoid gland and the fewest vertebrae in the genus. *P. larselli* is the only one with reduced fifth hind toes, a character shared by *P. neomexicanus*.

Of the closely related pair *P. dunni* and *P. vehiculum*, the former attains a larger size, has more vomerine teeth, and is more aquatic. *P. vehiculum* usually has one more trunk vertebra than *dunni*. The dorsal stripe in *dunni* is usually greenish yellow, while that of *vehiculum* varies from reddish tan to yellow. The toes are slightly webbed in both; the other western plethodons have more webbing. Increase in webbing does not appear to be associated with aquatic habits, as the most aquatic form, *dunni*, has the least webbing, and *vehiculum* and *elongatus*, both less aquatic, differ greatly in the amount of webbing. Some eastern forms have webbed toes while others do not, yet all are terrestrial.

As *dunni* and *vehiculum* occur sympatrically over an extensive area with no evidence of interbreeding, they must be regarded as distinct



species. A study of possible differences in the niches of the two forms, as Stebbins (1951:65) suggested, is much needed.

Burns (1954) considers the form *larselli* a geographic race of *vandykei*. I agree with the unpublished conclusions of Douglas Burns and David Wake (in letters) that *larselli* be considered a full species. The differences between it and *vandykei* are so great that it is doubtful that the two would interbreed if they were sympatric. In addition to the pigmentation characters noted in the original description, it differs from *vandykei* in having a smaller parotoid gland, 1 instead of 2 phalanges on the fifth hind toe, and 16 instead of 15 trunk vertebrae. While I place *larselli* tentatively in the same species group as *vandykei*, its relationships with the other western plethodons need further study.

*P. elongatus* differs from the other western plethodons in pigmentation characters and in having more trunk vertebrae than the other forms. It has no close affinities with any of the others and is placed in a separate species group.

#### VANDYKEI GROUP

##### *Plethodon vandykei vandykei* Van Denburgh Washington Salamander

*Plethodon vandykei* Van Denburgh (1906:61). Dunn (1926:151-3); Slevin (1928:57-9); Bishop (1943:275-8).

*Plethodon vandykei vandykei*, Lowe (1950:93); Stebbins (1951:80-4), (1954:56-7).

**HOLOTYPE.** CAS 6910 (destroyed in the San Francisco fire of 1906), collected at Paradise Valley, Mount Ranier National Park, Washington, by E. C. Van Dyke, July 1905.

Slevin and Leviton (1956:535) designate a neotype, CAS 47495, from Forks, Clallam County, Washington, more than 130 miles from the type locality and at the extreme opposite end of the known range of *P. v. vandykei*. According to the International Rules of Zoological Nomenclature, a neotype should be designated only when required for stability or for solving a confused zoological problem, and it should come from as near as possible to the place at which the holotype was collected. As the neotype was not properly selected in this case, later workers do not have to recognize it.

**DIAGNOSIS.** A western plethodon with a parotoid gland and a modal number of 15 trunk vertebrae. It differs from *idahoensis* in having a wider dorsal stripe, lighter ground color, and yellow pigment on the

proximal segments of the limbs similar to that in the dorsal stripe.

**DISTRIBUTION.** Western Washington from Clallam County south to Pacific County, east to Pierce County (fig. 7). The populations in the Olympic Mountains, the Cascades, and the Willapa Hills may now be isolated from one another.

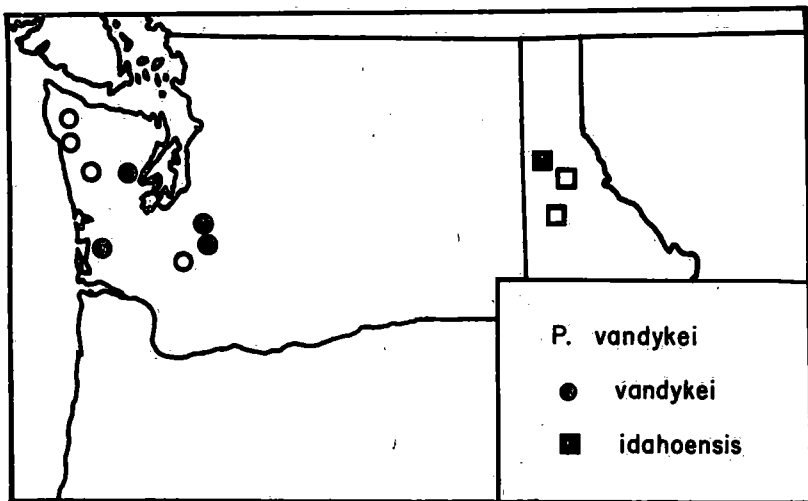


FIGURE 7. Distribution of *P. vandykei* in Washington and Idaho

**DESCRIPTION.** Specimens from Lewis County, Washington, have pale yellow dorsal stripes in life. The chromatophores vary from reddish yellow to yellow. Those in the dorsal stripe are unusual in having small dark granular inclusions. Similar yellow pigment also occurs on the legs, head, sides, and belly, but is greatly reduced on the chin. Melanophores are plentiful on the sides, but less so in the stripe region and on the legs. Melanophore pigmentation on the belly varies; it is heavy in some black-bellied individuals, while in others it is greatly reduced. White iridophore spots occur on the head, legs, dorsum, belly, and sides, and are largest and most abundant on the sides. Brassy flecking is heavy in the iris, both above and below the pupil. This is the only species examined that has silvery white pigment in the iris. It occurs above the pupil. Usually a large area including most of the chin is almost pigmentless. The dorsal stripe in adults has straight edges, but often in young specimens its borders are irregular. Probably the remnants of embryonic dorsolateral spots similar to those

found in the young of some of the eastern species cause this irregularity.

Costal grooves usually number 14 and trunk vertebrae 15; vomerine tooth counts range from 8 to 19 (fig. 8). The largest individual examined is 56 mm. in snout-vent length.

*Plethodon vandykei idahoensis* Slater and Slipp  
Coeur d'Alene Salamander

*Plethodon idahoensis* Slater and Slipp (1940:38). Bishop (1943:259-61).

*Plethodon vandykei idahoensis*, Lowe (1950:93); Stebbins (1951:80-4), (1954:56-7).

**HOLOTYPE.** USNM 110504, adult male, collected at the northeast corner of Coeur d'Alene Lake, Kootenai County, Idaho, elevation 2160 feet, by James R. Slater, 13 September 1939.

**DIAGNOSIS.** A race in which the yellow or orange dorsal stripe is narrower than in *P. v. vandykei* and contrasts sharply with the lateral black ground color. The proximal segments of the limbs are dark.

**DISTRIBUTION.** Known only from Benewah and Kootenai Counties in northern Idaho (fig. 7).

**DESCRIPTION.** The dorsal stripe contains orange or yellow chromatophores. The remainder of the body is pigmented with melanophores, except for gaps on the chin where there are yellow chromatophores. The iris has brassy iridophores, and the belly and sides have a few scattered white ones.

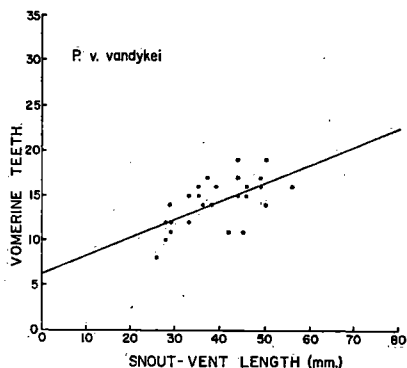


FIGURE 8. Variation in the number of vomerine teeth of *P. v. vandykei*.

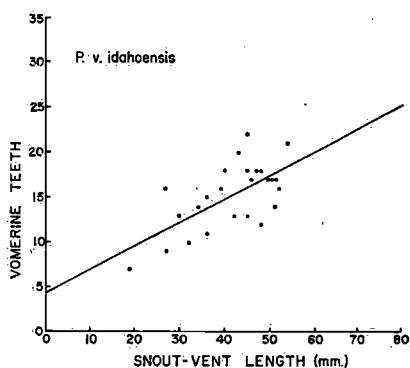


FIGURE 9. Variation in the number of vomerine teeth of *P. v. idahoensis*.

Costal grooves usually number 14, the trunk vertebrae 15. Vomerine teeth range from 7 to 22 (fig. 9). The largest specimen examined is 54 mm. in snout-vent length.

\* \* \* \* \*

*P. v. vandykei* is known from the Willapa Hills, Olympic Mountains, and west central Cascade Mountains of western Washington; a disjunct population, *P. v. idahoensis* occurs in northern Idaho. The three populations in western Washington now appear to be isolated from one another. The Idaho population was originally described as a distinct species, *idahoensis*, by Slater and Slipp (1940), but Lowe (1950:93) and more recent workers consider it a subspecies of *vandykei*. Although the Idaho form is usually believed to be isolated from the Washington populations, Savage (1952) suggests that they may be connected by a corridor of high humid country along the international boundary between Washington and British Columbia. The forms *idahoensis* and *vandykei* apparently differ mainly in pigmentation.

Stebbins (1951:80-1) points out the presence of two color phases of *P. v. vandykei*. The light phase is rather uniform in color with slight contrast between the dorsal stripe and the belly and sides; the dark phase has a greater concentration of melanophores on the belly and sides closely resembling the pattern in *idahoensis*. A third color phase recently discovered in the Willapa Hills is similar to the light phase, except that the ground color is pinkish rose. Although freshly preserved specimens of all three color phases have been examined, only specimens of the light phase of *P. v. vandykei* have been studied in life. Therefore detailed pigmentation comparisons cannot be given.

One specimen, PLC 626, appears to have only one phalanx in each fifth hind toe, thus resembling the normal condition in *neomexicanus* and *larselli*.

This species usually lives in damp places according to Stebbins (1951:75, 82), and may replace *P. dunni* ecologically as well as geographically. However, Storm (1955) shows that their ranges do overlap slightly in Pacific County, Washington.

*Plethodon larselli* Burns  
Larch Mountain Salamander

*Plethodon vandykei larselli* Burns (1954:83-7).

**HOLOTYPE.** USNM 134129, adult male, collected on the north slope of Larch Mountain, 3 miles from the summit on the Multnomah Falls

Trail, Multnomah County, Oregon, 24 May 1953, by Douglas M. Burns.

**DIAGNOSIS.** A western plethodon with only one phalanx in the fifth hind toe, a modal number of 16 trunk vertebrae, reduced parotoid glands, and a cardinal red to reddish-orange venter.

**DISTRIBUTION.** Known from the type locality and from Wyeth, Hood River County, Oregon; Wahkeena Falls, Multnomah County, Oregon, and from Archer Falls, Skamania County, Washington (fig. 10). This recently discovered species may have a wider range; it should be looked for in adjacent areas of both Washington and Oregon.

**DESCRIPTION.** The dorsal stripe varies from bright red to yellow, and in some specimens is almost completely obscured by melanophores. Many specimens show a concentration of melanophores in the middorsal region forming a dark black line. Small brassy iridophores are present on the dorsum of some specimens, particularly those with a heavy diffusion of melanophores in the dorsal stripe region. Red or yellow chromatophores similar to those on the dorsum occur on the sides. On the belly and the ventral side of the tail these chromatophores are bright red, even in specimens with a yellow or dull-red dorsal stripe. Large white iridophore spots are present on the lower sides, limbs, and to a variable extent on the chin, but they are absent from the belly. Most of the iridophore pigment on the upper sides is of the brassy type, contrasting with the white pigment of the lower sides. Brassy iridophores are abundant in the iris.

Costal grooves usually number 15 and trunk vertebrae 16; vomerine teeth range from 5 to 17 (fig. 11). The largest individual examined is 49 mm. in snout-vent length.

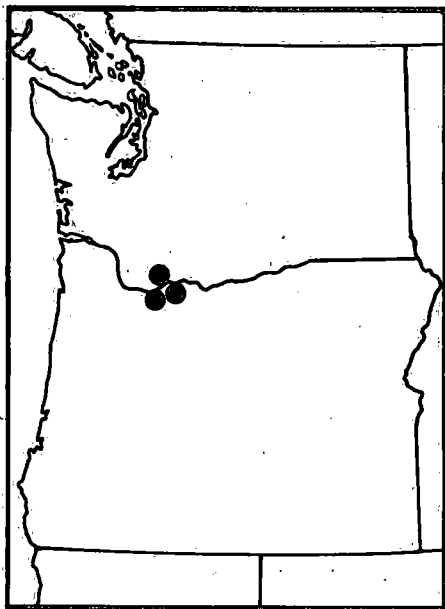


FIGURE 10. Distribution of *P. larselli* in Washington and Oregon.

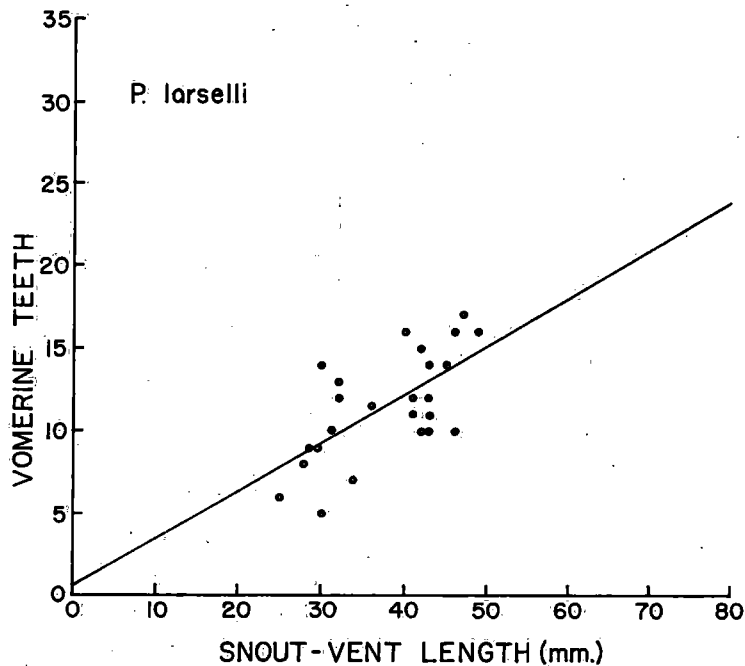


FIGURE 11. Variation in the number of vomerine teeth of *P. larselli*.

## VEHICULUM GROUP

*Plethodon dunni* Bishop  
Dunn's Salamander

*Plethodon dunni* Bishop (1934:169-71). Bishop (1943:242-6); Stebbins (1951: 68-72), (1954:54-5).

**HOLOTYPE.** USNM 95196, adult female, collected just outside the city limits of Portland, Clackamas County, Oregon, by Stanley G. Jewett, Jr., 13 January 1934.

**DIAGNOSIS.** A western plethodon with two phalanges in the fifth hind toe, a modal number of 16 trunk vertebrae, and a greenish-yellow dorsal stripe.

**DISTRIBUTION.** Curry County in southeastern Oregon, north to Pacific County, Washington, east to the western slope of the Cascade Mountains (fig. 12).

**DESCRIPTION.** The dorsal stripe is composed of greenish-yellow chromatophores, in contrast to the red chromatophores usual in *vehiculum*. This pigment also occurs abundantly on the sides, but diminishes on the belly. The lower sides and belly show a few yellowish iridophores, and the brassy type occurs in the iris.

The costal grooves usually number 15, the trunk vertebrae 16. Vomerine teeth range from 8 to 21 (fig. 13). The largest specimen examined is 66 mm. in snout-vent length.

*P. dunni* is closely related to *P. vehiculum*, but differs in size, coloration, average number of vomerine teeth, and number of body segments. This species occurs sympatrically with *P. vandykei* in southwestern Washington, with *P. elongatus* in southwestern Oregon, and with *P. vehiculum* throughout most of its range. *P. dunni* is apparently the most aquatic plethodon; Stebbins (1951:70) states it is almost invariably found in places saturated with water and that it often takes to the water to escape capture.

Most individuals have a greenish-yellow dorsal stripe, but Stebbins (1951:69) reports melanistic specimens from Benton County, Oregon, lacking the stripe.

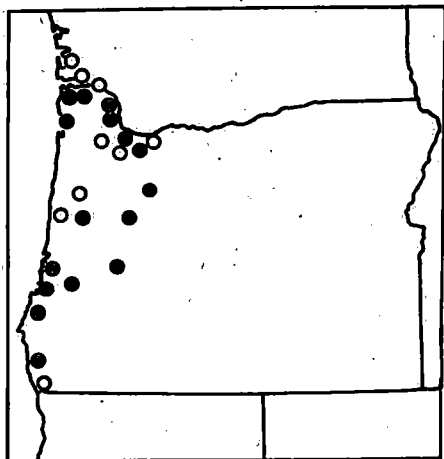


FIGURE 12. Distribution of *P. dunni* in Washington and Oregon.

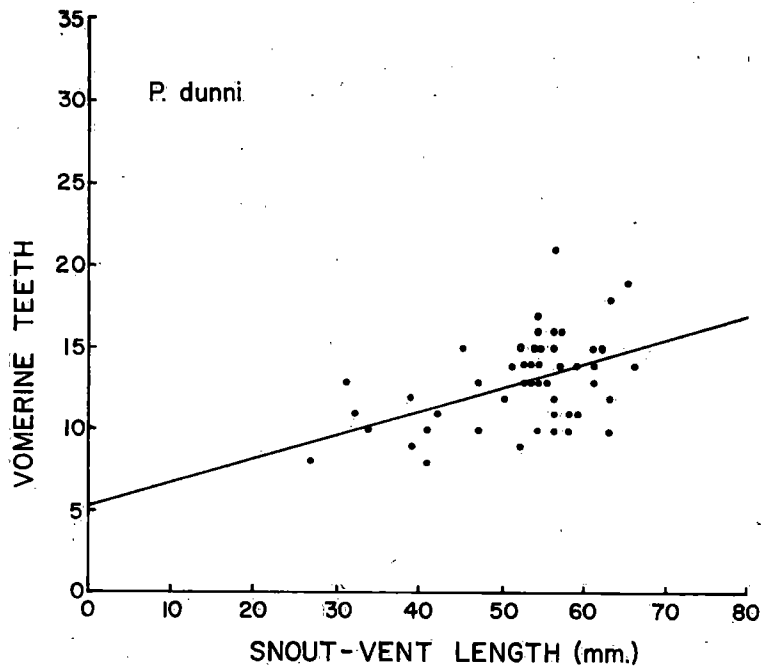


FIGURE 13. Variation in the number of vomerine teeth of *P. dunni*.



*Plethodon vehiculum* (Cooper)  
Western Red-backed Salamander

- Ambystoma vehiculum* Cooper (1860:pl. 31, fig. 4). No description accompanies the figure published by Cooper. The salamander illustrated clearly has the appearance of the western red-backed salamander, and Bishop (1934:171) assigned Cooper's name to this species. However, the salamander Cooper figures has only 13 costal grooves, a lower number than known in this species or in *larselli* or *dunni*. Occasional specimens of *vandykei* may have 13 costal grooves, but Astoria, Oregon, the collection site of Cooper's animal, is outside the known range of *vandykei*. Most likely the specimen figured by Cooper is a western red-backed salamander with the number of costal grooves drawn incorrectly. Thus no change in the current nomenclature is necessary.
- Plethodon intermedius* Cope (1867:209-10). Type locality: Fort Tejon, California; obviously in error. Dunn (1926:154-6); Slevin (1928:51-5).
- Plethodon vehiculum*, Bishop (1934:171).
- Plethodon vehiculum*, Slater (1940:43); Bishop (1943:278-81); Stebbins (1951:84-7), (1954:57-9).

**HOLOTYPE.** Apparently no longer extant. The type locality is Astoria, Oregon.

**DIAGNOSIS.** A western plethodon with a modal number of 17 trunk vertebrae.

**DISTRIBUTION.** From Coos County in southwestern Oregon north to southwestern British Columbia, including Vancouver Island (fig. 14).

**DESCRIPTION.** Two color phases occur, a striped phase and a unicolorous phase. The dorsal stripe varies from light yellow through yellow, orange, and red to brown. It is never greenish yellow as in *dunni*. The chromatophores that color the dorsal stripe are absent from the sides but present on the belly. The sides are black with a few small white iridophore spots. These also occur on the belly, and combined with the melanophores and red chromatophores give it a mottled appearance. Unstriped individuals have small white iridophore spots on the dorsum similar to those on the sides and smaller brassy flecks as well. Brassy iridophores are present in the iris.

Costal grooves usually number 16, trunk vertebrae 17. Vomerine teeth range from 5 to 14; one unusual specimen has 22 vomerine teeth (fig. 15). The largest specimen examined is 53 mm. in snout-vent length.

This species and *P. larselli* are the smallest of the western plethodons. *P. vehiculum* is the most widespread of the western plethodons, and the most abundant member of the genus over much of its range. *P. vehiculum* is superficially similar to the eastern *P. cinereus*;

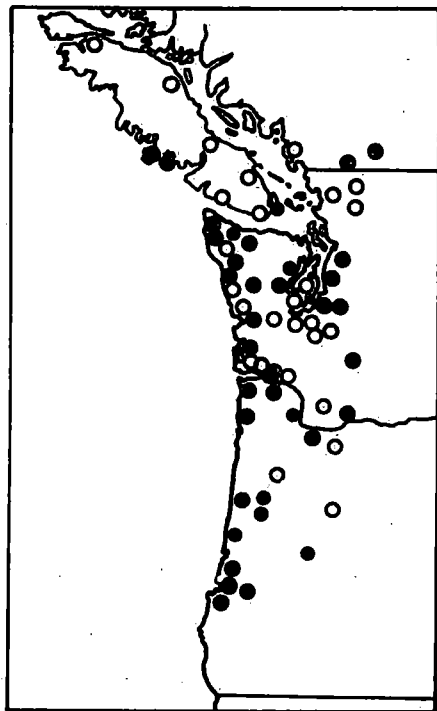


FIGURE 14. Distribution of *P. vehiculum* in British Columbia, Washington, and Oregon.

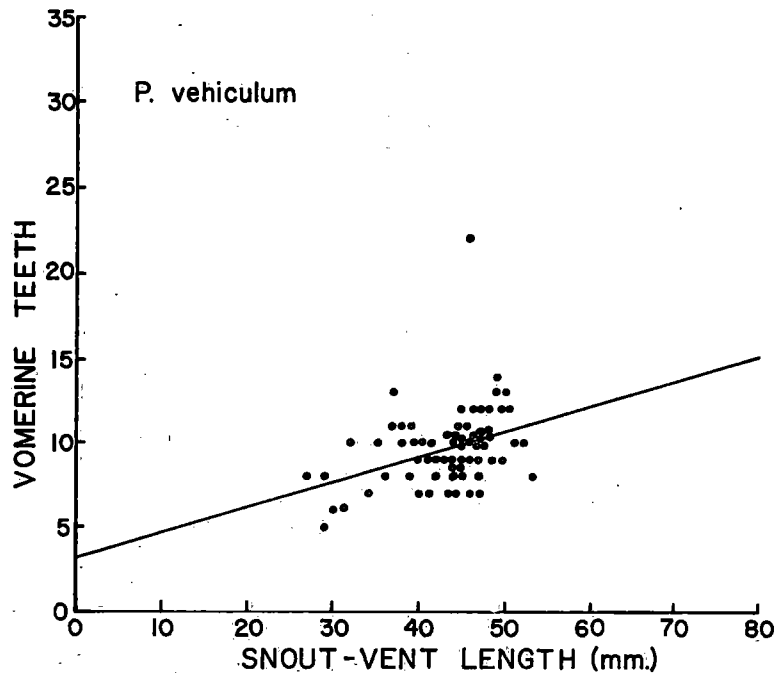


FIGURE 15. Variation in the number of vomerine teeth of *P. vehiculum*.

both have striped and unstriped color phases and mottled bellies. These similarities are probably due to convergent or parallel evolution, because in all other characters *P. vehiculum* is morphologically more similar to the other western plethodons. No characters yet found vary significantly geographically.

#### ELONGATUS GROUP

##### *Plethodon elongatus* Van Denburgh Del Norte Salamander

*Plethodon elongatus* Van Denburgh (1916:216-8). Dunn (1926:156-8); Slevin (1928:55-7); Bishop (1943:246-9); Stebbins (1951:72-6), (1954:55-6).

Dumeril, Bibron, and Bibron (1854:84) first published the name *Salamandra elongata* Valenciennes, which has since appeared in the synonymy of *Plethodon glutinosus* (Dunn, 1926:137). As *elongata* is merely a manuscript name, not proposed validly under the International Rules of Zoological Nomenclature, it is not available for *P. glutinosus*. Thus *Plethodon elongatus* Van Denburgh (1916) is not a junior homonym and can remain the valid name of the Del Norte Salamander.

**HOLOTYPE.** CAS 29096, collected at Requa, Del Norte County, California, by J. R. Slevin, 22-26 May 1911.

**DIAGNOSIS.** A western plethodon with a modal number of 19 trunk vertebrae.

**DISTRIBUTION.** Southwestern Oregon and northwestern California (fig. 16).

**DESCRIPTION.** The belly is very dark with a few scattered white iridophore spots. The orange to reddish-brown dorsal stripe is usually brighter in juveniles than in adults, where it is usually reduced or obliterated by melanophore suffusion. Often medial melanophore pigment divides it into a right and left dorsolateral stripe. The head usually has a few small white iridophore spots, which may occur rarely on the dorsum. Occasional individuals show a few brassy flecks in the iris, but most have none.

Costal grooves usually number 18, trunk vertebrae 19. Vomerine teeth range from 8 to 15 (fig. 17). The largest specimen examined is 70 mm. in snout-vent length.

This species is the most elongated of the western plethodons. Its greater number of body segments distinguishes it from *vandykei*, *larselli*, *dunni*, and *vehiculum*; its webbed toes distinguish it from the last two also. Known only from Trinity, Humboldt, and Del Norte Counties, California, and Curry County, Oregon, its distribution is

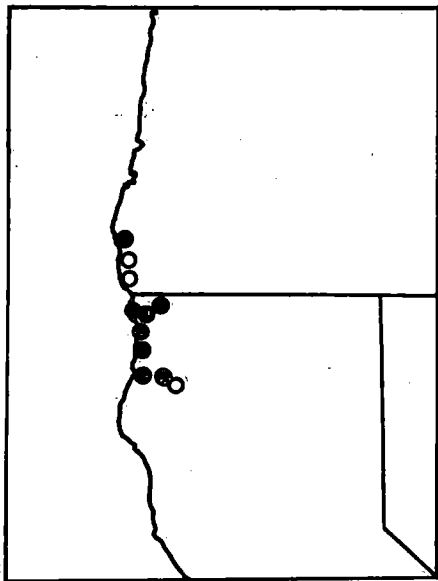


FIGURE 16. Distribution of *P. elongatus* in Oregon and California.

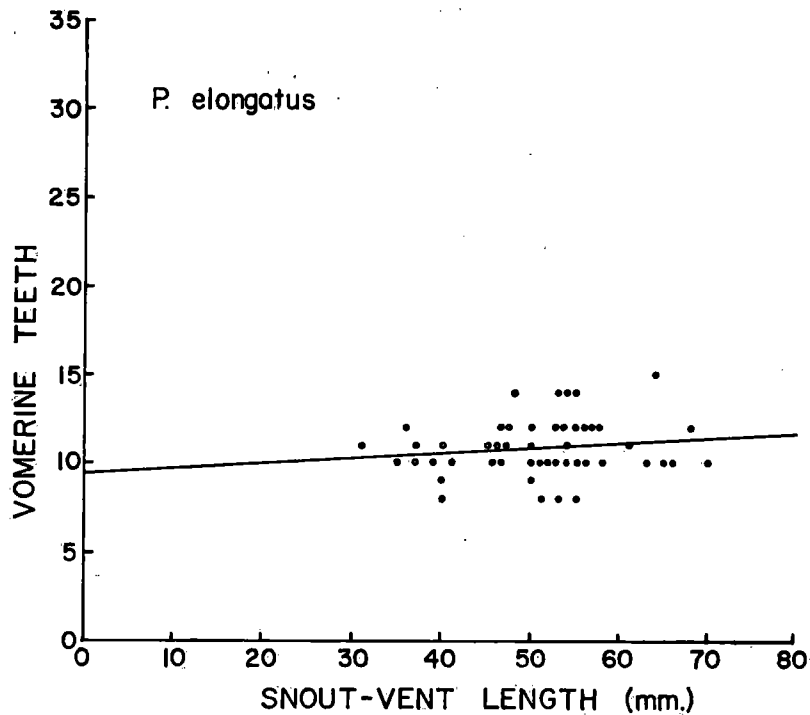


FIGURE 17. Variation in the number of vomerine teeth of *P. elongatus*.

rather limited. Stebbins (1951:76) believes that specimens from the interior of the range differ in several respects from those on the coast.

### THE EASTERN SMALL PLETHODONS

As the relationships of *P. neomexicanus* to the four other species of eastern small plethodons are not clear, it is considered as a separate species group. The remaining eastern small plethodons are characterized by their small size. With the exception of *welleri*, they have more trunk vertebrae and are relatively more elongated than the eastern large plethodons. *P. welleri* has a restricted range in the southern Blue Ridge Mountains, and is known only from a few counties in northwestern North Carolina and adjacent Tennessee and Virginia.

*P. richmondi* is an elongated species whose range centers in the Appalachian Plateaus Physiographic Province of western Pennsylvania, Ohio, eastern Kentucky, and West Virginia. It also occurs in adjacent physiographic provinces in parts of Pennsylvania, Maryland, Virginia, North Carolina, Tennessee, Kentucky, Indiana, and Ohio. *P. r. hubrichti* occurs in the Blue Ridge Province of Virginia, and *P. r. nettingi* in the Cheat Mountains of West Virginia. The range of the latter subspecies is surrounded by that of *P. r. richmondi*, and thus apparently represents a Rassenkreis overlap.

*P. c. cinereus* is widely distributed over most of the eastern United States and southeastern Canada, except for the region occupied by *dorsalis*. Two disjunct populations are recognized as subspecies, *P. c. polycentratus* in the Piedmont of western Georgia, and *P. c. serratus* in Arkansas and Oklahoma. A third disjunct population in southeastern Missouri is distinct from the nearest *cinereus* populations, but is similar to certain other populations in the central part of the range of *P. c. cinereus*.

The range of *P. d. dorsalis* is centered in the Interior Low Plateaus Physiographic Province, and an isolated subspecies, *P. d. angusticlavius*, occurs in the Ozark Plateau.

The four species *welleri*, *dorsalis*, *cinereus*, and *richmondi* form a natural group of rather closely allied forms. All have webbed toes, a pigmented peritoneum, low vomerine tooth counts, brassy flecks on the dorsum, and white iridophore spots on the belly and sides. Both *cinereus* and *dorsalis* typically show at least as much white as black pigment on their bellies, and both have two color phases, a unicolored dark or unstriped phase and a striped phase with a dorsal band of red or yellow on the body and tail. Both *richmondi* and *welleri*

resemble the unstriped phase of the other two species dorsally, but possess much more black pigment ventrally; the white pigment of the belly is usually limited to small spots. The mental glands of mature male *cinereus* and *richmondi* differ in shape from those of all other *Plethodon* including the other eastern small plethodons (fig. 2). The premaxillary teeth of mature males of these two species are highly modified (fig. 3), another characteristic they share with no other species of *Plethodon*. They have the greatest number of trunk vertebrae in the genus, and significant geographic variation in this character occurs only in these two species. Doubtless they are closely related. The two are sympatric over more than half of the range of *richmondi*, and character displacement occurs in color pattern over much of the area of sympatry.

*P. welleri* is the least elongated and has the fewest trunk vertebrae of the eastern small species. It is unusual in having melanophore pigmentation in the ovaries and an extremely dark parietal peritoneum. The brassy flecks on the dorsum of *welleri* coalesce to form large patches, giving it an exceptional appearance found only in one other form, *P. r. hubrichti*.

Throughout most of their ranges *cinereus* and *dorsalis* are allopatric, but they overlap in several areas. As they apparently do not hybridize, they are usually considered distinct species. They differ in several pigmentation characters, in the shape of the premaxillary teeth and mental glands of adult males, and usually in the average number of trunk vertebrae. Dunn (1926:24) suggests that the striped pattern of *dorsalis* is more primitive than that of *cinereus*, as the paired dorsal spots of a primitive plethodontid probably pass through a zigzag phase similar to that of *dorsalis* before evolving into a straight-edged stripe as in *cinereus*.

The elongation and increased trunk vertebrae in *richmondi* and *cinereus* appear as a marked departure from the usual plethodontid condition. The forms *welleri* and *dorsalis*, therefore, have retained more primitive characteristics.

With mammalian gonadotropic hormone injections I have induced gravid female *cinereus*, *richmondi*, *nettingi*, *hubrichti*, and *welleri* to deposit eggs in the laboratory. Embryos and newly hatched young of *dorsalis* are available in museum collections. Embryonic *welleri*, *richmondi*, *hubrichti*, and *nettingi* have abundant red pigment on the dorsum. In *richmondi* and *nettingi* the red remains after hatching. The young have a straight-edged stripe, though it is less well defined than in striped *cinereus* and *dorsalis*. Embryos of *welleri* have a series

TABLE 3. Number of trunk vertebrae in eastern small plethodons. (See tables 4, 5, and 7 for geographic variation in *dorsalis*, *cinereus*, and *richmondi*.)

Species	16	16/17	17	17/18	18	18/19	19	19/20	20	20/21	21	21/22	22	22/23	23	23/24	24	Mean
<i>Plethodon</i>																		
<i>neomexicanus</i>							2	3	16		1							19.89
<i>welleri</i>	4	1	154	4	14													17.06
<i>dorsalis</i>					25	16	905	34	327	3	4							19.25
<i>cinereus</i>				2	114	41	4591	674	18335	672	4571	34	163	2	7	1		20.00
<i>richmondi</i>					119	32	592	30	516	25	731	39	839	25	174	7	12	20.71

of alternating dorsolateral red spots, similar to those found in embryonic *dorsalis*. In *welleri* these spots disappear. In *dorsalis* they enlarge and coalesce to form a stripe in which the original spots apparently produce the lobular edges characteristic of most populations of *dorsalis*. Similarities in embryonic dorsal color patterns, mental glands, and premaxillary teeth of males are the basis for placing *welleri* and *dorsalis* in a single species group.

Grobman (1944) divides the eastern small plethodons into two species groups, the "cinereus group" including *cinereus* and *dorsalis*, and the "welleri group" including *richmondi*, *nettingi* (then considered a full species), and *welleri*. This grouping is based mainly on the presence of the red or yellow dorsal stripe in *cinereus* and *dorsalis* and its absence in the other species, and on the presence of dorsal brassy flecks in the "welleri group." Rabb (1955) and Muchmore (1955) correctly point out that the brassy flecks characteristically present in *richmondi* and *welleri* also occur in the unstriped phase of *cinereus*. Indeed they occur in many species of *Plethodon*. Moreover, *richmondi*, *nettingi*, *welleri*, and *hubrichti* as embryos have considerable red pigment on the dorsum. As pattern dimorphism (stripe or no stripe) is rather widespread in this genus and occurs in other genera as well, it is not particularly useful in evaluating relationships. The presence of two color phases in some western as well as eastern species suggests that the dorsal stripe has probably been present in the genus for a long time or has reappeared repeatedly. The two color phases of *cinereus* may be due to a single pair of alleles (Highton, 1959).

#### NEOMEXICANUS GROUP

##### *Plethodon neomexicanus* Stebbins and Riemer Jemez Mountains Salamander

*Eurycea multiplicata*, Dunn (1926:313-6; part).

*Plethodon neomexicanus* Stebbins and Riemer (1950:73-80). Stebbins (1951: 76-9), (1954:56).

**HOLOTYPE.** MVZ 49033, adult male, collected 12 miles west and 4 miles south of Los Alamos, Sandoval County, New Mexico, altitude about 8750 feet, by Robert C. Stebbins, 14 August 1949.

**DIAGNOSIS.** A *Plethodon* with a modal number of 20 trunk vertebrae and with a single phalanx in the fifth hind toe.

**DISTRIBUTION.** Known only from the Jemez Mountains of New Mexico (fig. 18).



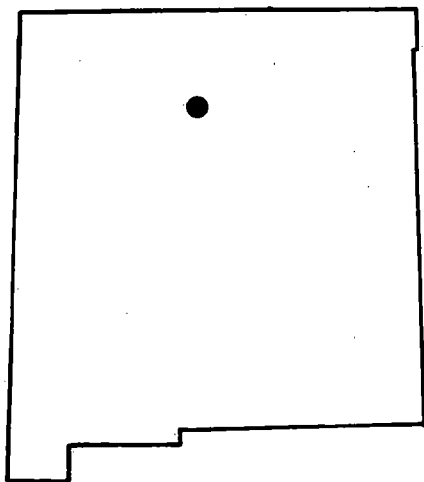


FIGURE 18. Distribution of *P. neomexicanus* in New Mexico.

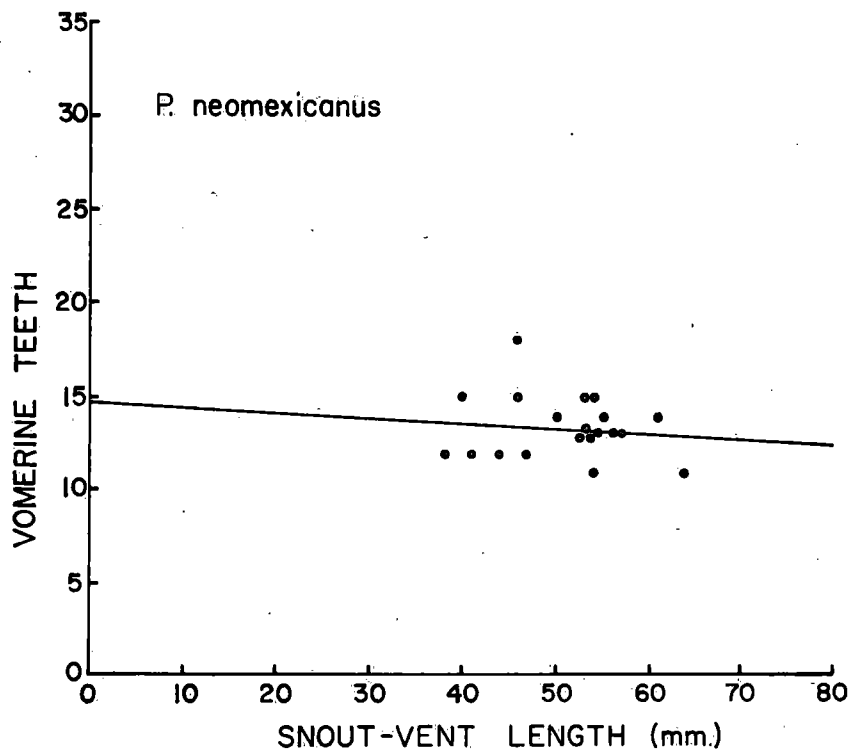


FIGURE 19. Variation in the number of vomerine teeth of *P. neomexicanus*

DESCRIPTION. Dorsal and lateral melanophore pigmentation is reduced so that the ground color appears brown, rather than black as in most other species. Pigmentation is so reduced on the belly that the internal organs are visible through the belly wall. Brassy iridophore flecking is heavy on the dorsum of the body and tail, particularly in gaps in the melanophore background. These gaps are more numerous in young animals and often occur most abundantly in two dorso-lateral longitudinal lines. Brassy flecking is so heavy here that some young specimens appear to have a brassy dorsal stripe. Lateral iridophore spots are yellow and small, not much larger than the dorsal brassy flecks. A few of these small yellow spots occur on the belly also. The iris contains abundant brassy pigmentation.

Costal grooves usually number 19, trunk vertebrae 20 (range, 19-21, mean 19.9). Vomerine teeth range from 11 to 18 (fig. 19). The type is more than 70 mm. in snout-vent length. According to Stebbins and Rierner (1950:75), sexual maturity is attained at approximately 50 mm. snout-vent length.

#### WELLERI GROUP

##### *Plethodon welleri* Walker Weller's Salamander

*Plethodon welleri* Walker (1931:48-51). Bishop (1943:285-7); Grobman (1944:313).

*Plethodon welleri welleri*, Thurow (1956a:343-56).

*Plethodon welleri ventromaculatum* Thurow (1956a:344). Type locality: Mt. Rogers, Grayson County, Virginia.

HOLOTYPE. USNM 84135, adult male, collected at an altitude above 5000 feet on Grandfather Mountain, near Linville, North Carolina, by W. H. Weller and Ralph Dury, 27 August 1930.

DIAGNOSIS. A dark-bellied eastern small plethodon with 17 trunk vertebrae and abundant dorsal brassy spotting. In adult males the mental gland is round and the premaxillary teeth have small anterior cusps.

DISTRIBUTION. From Yancey County, North Carolina, northeastward in Tennessee and North Carolina to Mt. Rogers and White Top Mountain, Virginia (fig. 20).

DESCRIPTION. The dorsal pattern consists of large anastomosing patches of brassy spots almost entirely made up of brassy iridophores. Brassy pigment is more abundant in *welleri* than in any other *Plethodon*; in some specimens it occupies more than two-thirds of the

dorsum. White iridophore pigmentation present on the dorsum of most plethodons is lacking in *welleri* except on the sides and belly. Small white spots (0.1-0.2 mm.) are scattered over the belly. Lateral iridophore spots (to 1 mm.) are white with an occasional slight brassy flecking. Four of eight specimens from Mt. Rogers, Virginia, in life had small red spots on the proximal segment and at the base of the front legs.

Costal grooves usually number 16, trunk vertebrae 17. Vomerine teeth range from 7 to 12 (fig. 21). Maximum snout-vent length is between 45 and 50 mm. Sexual maturity is reached at about 35 mm. snout-vent length.

*P. welleri* has the same modal number of trunk vertebrae (17) as most of the eastern large plethodons and resembles them more in body form than does any other eastern small plethodon. Yet its small size, vertebral structure, webbed toes, pigmented parietal peritoneum, and other pigmentation characters associate it most closely with the small eastern forms.

This species, long thought to be restricted to high elevations, may occur in suitable habitats at lower altitudes throughout its range. Hoffman (1953) collected it at 2500 feet in Johnson County, Tennessee.

*P. welleri* has pigmented ovaries. Its closest relative is probably *dorsalis*, whose ovaries also are occasionally pigmented. The coloring of *welleri* is similar to that of adult *P. r. hubrichti*, which is not far separated geographically from *welleri* and occurs in similar habitats. Only *P. r. nettingi* is closer to *welleri* in number of body segments than is *P. r. hubrichti*.

Thurrow (1956a) describes geographic variation in the amount of ventral white spotting in *welleri*. He shows, as previously noted by Walker (1934), that individuals from Grandfather Mountain, North Carolina, the type locality of *welleri*, have less white spotting on the belly than those from White Top Mountain and adjacent Mt. Rogers, Virginia. Thurrow examined few specimens from other localities, for little material is available. It seems wise to await additional information on geographic and individual variation before recognizing races on the basis of such limited material. One specimen from Flat Top Mountain, Yancey County, North Carolina (CU 4768) has a dark belly and chin without white mottling, but Snyder (1946) describes a specimen with conspicuous mottling on the belly from this locality. Specimens from 5.3 miles north of Carderview, Johnson County,

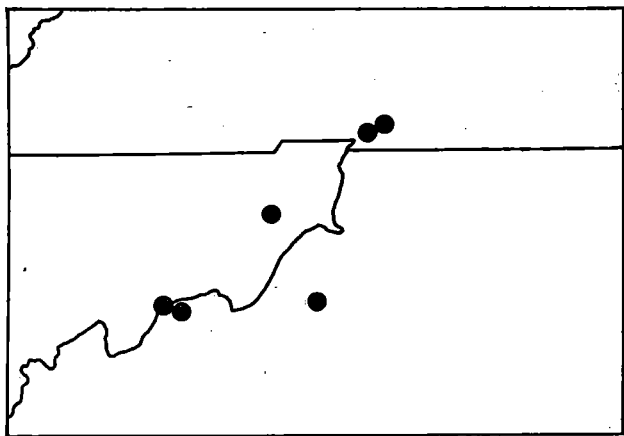


FIGURE 20. Distribution of *P. welleri* in Virginia, North Carolina, and Tennessee.

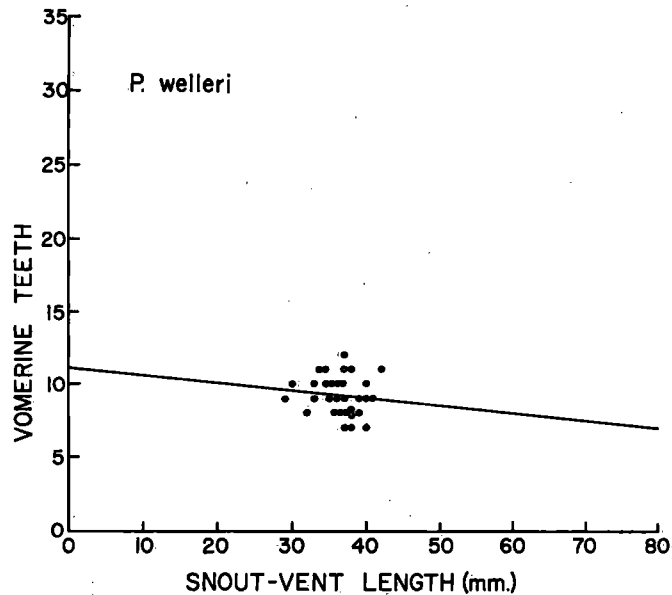


FIGURE 21. Variation in the number of vomerine teeth of *P. welleri*.

Tennessee, have a moderate amount of ventral spotting. Specimens from Mt. Rogers average much more dorsal brassy spotting than those from Grandfather Mountain. I have not examined living material from other localities, except for a young salamander from near Carder-view. Description of a juvenile from this locality by Hoffman (1953) actually is based on a *richmondi* (USNM 132325).

*Plethodon dorsalis dorsalis* Cope  
Zigzag Salamander

*Plethodon cinereus dorsalis* Cope (1889:138-9). Blanchard (1926:269-70); Bishop (1943:236-9).

*Plethodon erythronotus*, Garman (1894:38).

*Plethodon dorsalis*, Stejneger and Barbour (1917:15); Dunn (1926:158-62); Grobman (1944:308-11).

*Plethodon dorsalis dorsalis*, Thurnow (1956b:177-82), (1957b:91-9).

LECTOTYPE. USNM 3776A (one of four syntypes listed in the original description, here designated as the lectotype), collected at Louisville, Jefferson County, Kentucky.

DIAGNOSIS. An eastern small plethodon with the modal number of trunk vertebrae 19, usually with a wide dorsal stripe with irregular borders, a round mental gland in mature males, premaxillary teeth with small anterior cusps in both sexes, and red chromatophores on the belly in addition to black melanophores and white iridophores. It differs from *P. d. angusticlavius* in having a wider dorsal stripe.

DISTRIBUTION. From southern Illinois, Indiana, and southeastern Ohio, south through Kentucky and Tennessee to northeastern Mississippi, northern and central Alabama, the Piedmont of western Georgia and the French Broad River Valley of North Carolina (fig. 22).

DESCRIPTION. The dorsum of both color phases of *P. d. dorsalis* has small white spots (0.2-0.4 mm.) as well as smaller brassy flecks. The red-backed phase has abundant red chromatophore pigment in the stripe region and on the sides and belly. All the chromatophores are similar to those of *P. cinereus*. Color differences between the two species involve mainly the abundance and distribution of the three pigments. The melanophore background in *dorsalis* is somewhat reduced, giving the animal a lighter appearance over-all than *cinereus*. On the belly an increase in the number of red chromatophores produces a mottling of red, black, and white, instead of black and white alone as in *cinereus*. On the head of *dorsalis* red pigment is concentrated in front of the eyes. Lateral iridophore pigment is often yellow.

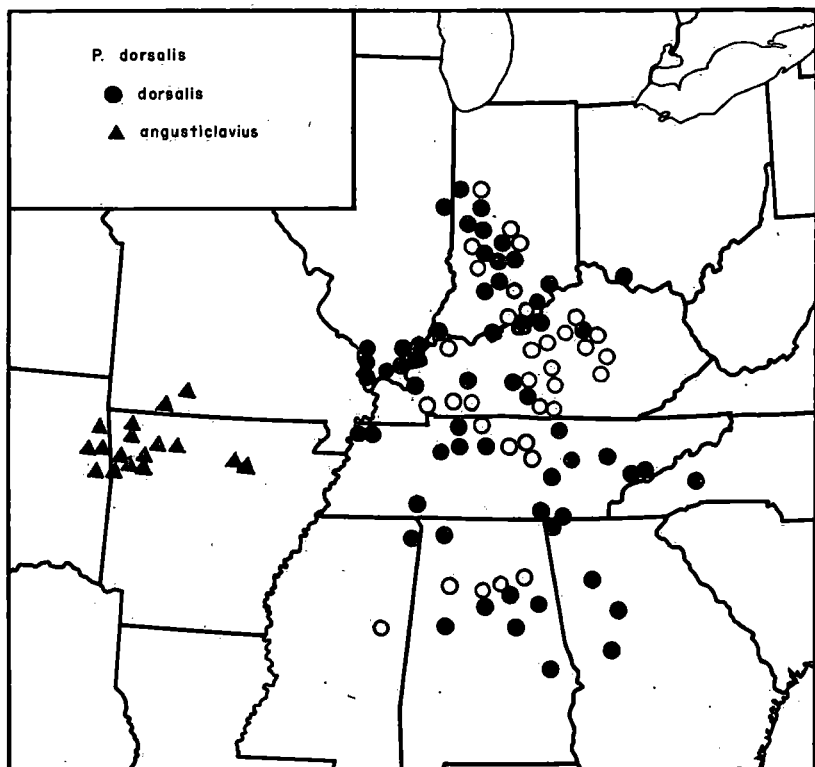


FIGURE 22. Distribution of *P. dorsalis* in the eastern United States.

The dorsal red stripe varies in the amount of melanophore encroachment and in the degree of irregularity of its edges. Brassy pigment is present in the iris.

Costal grooves usually number 18, trunk vertebrae 19. Vomerine teeth range from 5 to 18 (fig. 23). This is a small species; sexual maturity is reached at about 30 mm. snout-vent length. The largest specimen measured is 50 mm. in snout-vent length.

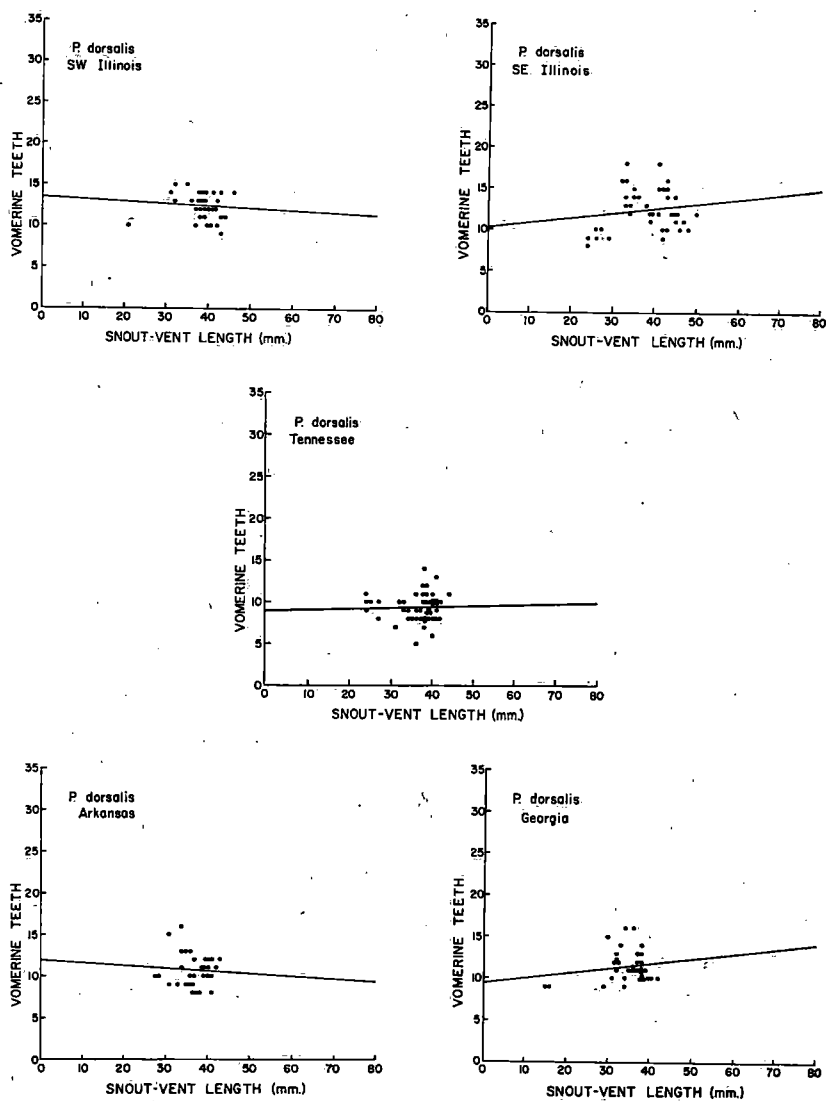


FIGURE 23. Variation in the number of vomerine teeth in 5 geographic samples of *P. dorsalis*.

*Plethodon dorsalis angusticlavius* Grobman  
Ozark Red-backed Salamander

*Plethodon dorsalis*, Black and Dellinger (1938:7).

*Plethodon cinereus*, Black and Dellinger (1938:7; part).

*Plethodon cinereus angusticlavius* Grobman (1944:302).

*Plethodon dorsalis angusticlavius*, Thurow (1956b:177), (1957b:99).

**HOLOTYPE.** AMNH 40366, adult male, collected at Mud Cave, near Fairy Cave, Stone County, Missouri, by B. C. Marshall, 1 October 1927.

**DIAGNOSIS.** A race of *Plethodon dorsalis* in which the width of the dorsal stripe is usually less than one-third the width of the body.

**DISTRIBUTION.** Southwestern Missouri, northwestern Arkansas and adjacent Oklahoma, north of the Arkansas River (fig. 22).

**DESCRIPTION.** More than 50 percent of the individuals in some localities lack the dorsal stripe. The narrow dorsal stripe of the striped phase may be yellow or red, and it usually widens on the tail. Sometimes the stripe becomes completely suffused with melanophores in the body region and remains visible only on the tail. The stripe is sometimes irregular anteriorly as in *dorsalis*. Pigmentation of the belly and sides is also similar to *dorsalis*. Red lateral and ventral pigment is reduced or absent.

Costal grooves usually number 18, trunk vertebrae 19. Vomerine teeth range from 8 to 16 (fig. 23). The largest specimen measured is 43 mm. in snout-vent length.

\* \* \* \* \*

The distribution of *P. dorsalis* centers in the Interior Low Plateaus Physiographic Province, but the species ranges various distances into every adjoining physiographic province. It occurs in the Coastal Plain of Mississippi and western Tennessee, the Piedmont of western Georgia, the Cumberland Plateau of Alabama and Tennessee, the Blue Ridge Province of North Carolina, and the glaciated region to the north in Indiana and Illinois. A disjunct subspecies, *P. d. angusticlavius*, occurs in the southern section of the Ozark Plateau of southwestern Missouri, northwestern Arkansas, and adjacent Oklahoma.

Grobman (1944) originally described *angusticlavius* as a race of *P. cinereus*, but all available evidence supports its transfer to *dorsalis* by Thurow (1956b, 1957b). Number of trunk vertebrae, male secondary sexual characteristics, ventral red pigmentation, and habitat all



associate it closely with *dorsalis*. Thurow (MSb) found that *dorsalis* in Indiana is usually associated with wetter habitats than *cinereus*, an animal of the forest floor. *P. dorsalis* is usually associated with canyons, ravines, and escarpments, in exposures of naked rock around springs and seepage areas. Both subspecies of *dorsalis* often are found in caves.

The species *cinereus* and *dorsalis* are so similar in appearance individual specimens are often difficult to identify, particularly after preservation. Thurow (1956b) lists a number of differences between them, but most differential characters show some overlap. The two species are sympatric in Georgia, eastern Tennessee, Indiana, Illinois, and Oklahoma. Though hybridization is not reported, studies to determine whether it occurs in these areas are desirable. In Georgia the stripe of *dorsalis* often has straight edges, resembling that of the local *cinereus*, but a similar condition also occurs in southwestern Illinois, where *cinereus* is absent. Differences in number of trunk vertebrae between the two species are greater in Georgia than in other areas of sympatry.

In some areas of sympatry ecological differences may isolate *cinereus* and *dorsalis*. The two are generally separated altitudinally where they occur together in the Great Smoky Mountains of Tennessee, with *cinereus* at higher elevations (1600 to 5000 feet) and *dorsalis* restricted to lower elevations (below 2200 feet) (King, 1939:551, and Grobman, 1944:310-1). The two species occur together at White Oak Sinks and Little River Sinks. They also occur sympatrically in the Piedmont of western Georgia in at least two localities—3.8 miles north of McDonough, Henry County and 8.5 miles south of Thomaston, Upson County. Bragg (1955) reports specimens of *P. c. serratus* and *P. d. angusticlavius* from about 4 miles east of Eldon, Cherokee County, Oklahoma. This is the only record of sympatric occurrence and of *P. c. serratus* north of the Arkansas River. Thurow (MSb) reports that near Bloomington, Indiana, the two species differ markedly in seasonal activity, in habitat, moisture, and temperature preferences. Apparently where the two species are geographically sympatric, they are usually ecologically isolated.

The most useful character for distinguishing between striped individuals of the two species is the nature of the stripe border. It is straight in *cinereus*, but lobular or zigzag in *dorsalis*. The unstriped phase of *dorsalis* differs from that of *cinereus* in having small amounts of red pigment on the dorsum, sides, and belly, often enough to outline the characteristic dorsal lobular stripe. Unstriped *cinereus* rarely

have red pigment except in the subspecies *polycentratus* and *serratus*. Adult male *cinereus* and *dorsalis* usually show two striking differences, the shape of the mental gland (fig. 2), and the modification of the premaxillary teeth (fig. 3), but these characters are of no use in distinguishing females and immatures.

The modal number of trunk vertebrae in *dorsalis* is 19; that in adjacent and sympatric populations of *cinereus* is 20, except in Georgia where it is 21 or 22. Some populations of *cinereus* also have a modal number of 19 trunk vertebrae, but none of these occurs in areas of overlap. As a small percentage of specimens in most *cinereus* populations have 19 trunk vertebrae and a similar percentage of *dorsalis* have 20 (tables 4 and 5), this character often is not definitive for individual specimens.

Red chromatophores are present on the belly of living *dorsalis*, but absent in living *cinereus* except occasionally in the pectoral area between the front limbs. As the red pigment is soluble in preservatives, this valuable character cannot be used to identify museum specimens. Other differences Thurow (1956b) lists are of little value in identifying individual specimens because of the great variation within both species.

Dunn (1926:162) states that the unstriped dark phase of *dorsalis* is confined to adults and is lighter than the dark phase of *cinereus*. Apparently the dark phase is due to the suffusion of melanophores into the dorsal stripe. In *dorsalis* this invasion may occur at a very early age. Five juveniles from Van Buren County, Tennessee (UF 8394) that are only 16 to 18 mm. in snout-vent length have very dark stripes in contrast to other young and adults of the same series. I have seen similar young from Monroe County, Indiana (AMNH 52433-6). I previously classified similar specimens of *cinereus* as striped (Highton, 1959:34). If the unstriped dark phase of *dorsalis* is homologous to the indistinctly striped *cinereus*, then no truly unstriped phase occurs in *dorsalis* corresponding to the lead-backed phase of *cinereus*.

Geographic variation in the number of trunk vertebrae is slight in different populations of *dorsalis* (table 4). Samples from the southern part of the range (Alabama, Mississippi, and Georgia) have a slightly lower average vertebral count than those from the northern parts of the range (Kentucky and Indiana). The difference appears attributable to a gradual clinal increase from south to north rather than to hybridization of *dorsalis* and *cinereus* in Indiana.

Neill (1957:44) reports *dorsalis* from Dade County, Georgia, in

TABLE 4. Geographic variation in the number of trunk vertebrae in *P. dorsalis*.

Subspecies and State	Number of trunk vertebrae							Mean
	18	18/19	19	19/20	20	20/21	21	
<i>P. d. dorsalis</i>								
Mississippi			8					19.00
Alabama	4		36	1	2			18.97
Georgia	2	1	53	1	3			19.02
North Carolina			6					19.00
Tennessee	7	3	226	5	49	1		19.15
Kentucky		1	57	1	33			19.35
Ohio		1						—
Indiana	5	6	261	22	196	2	4	19.42
Illinois	6	3	164	3	34			19.13
<i>P. d. angusticlavius</i>								
Arkansas		1	77	1	10			19.11
Oklahoma		1	10					18.95
Missouri			7					19.00

the Appalachian Plateau region of the extreme northwestern part of the state. The species also occurs in the Piedmont of western Georgia, but in this area most specimens have a rather straight-edged dorsal stripe at least posteriorly, similar to that of *cinereus*. Only in this character do they show an approach to *cinereus*. Georgia material of the two forms is easily distinguishable by the costal groove counts, ranging from 17 to 19 in *dorsalis* and 20 to 22 in *cinereus*. Living specimens of *dorsalis* have much red pigment on the venter, and the bellies of preserved specimens are usually lighter than those of *cinereus* because fewer melanophores are present. Georgia *dorsalis* are unusual in having few melanophores in the dorsal stripe at the base of the tail, so the stripe is much brighter there than in the body region. In this character they resemble many *P. d. angusticlavius*. A series of 18 specimens from near Oxford, Cleburne County, Alabama (BDV) approach the dorsal stripe condition of Georgia *dorsalis*.

In southeastern Illinois most *dorsalis* have a typical lobular stripe, but those in southwestern Illinois usually have a straight-edged stripe, as in *cinereus*. Many workers familiar with the typical striped patterns of *dorsalis* and *cinereus* would assign southwestern Illinois material to *cinereus*, as did Smith and Minton (1957:347). However, Thurow's (1957b) analysis of specimens from the area and my own study of additional living and preserved material indicate that these salamanders resemble *dorsalis* in all other characters and should be assigned

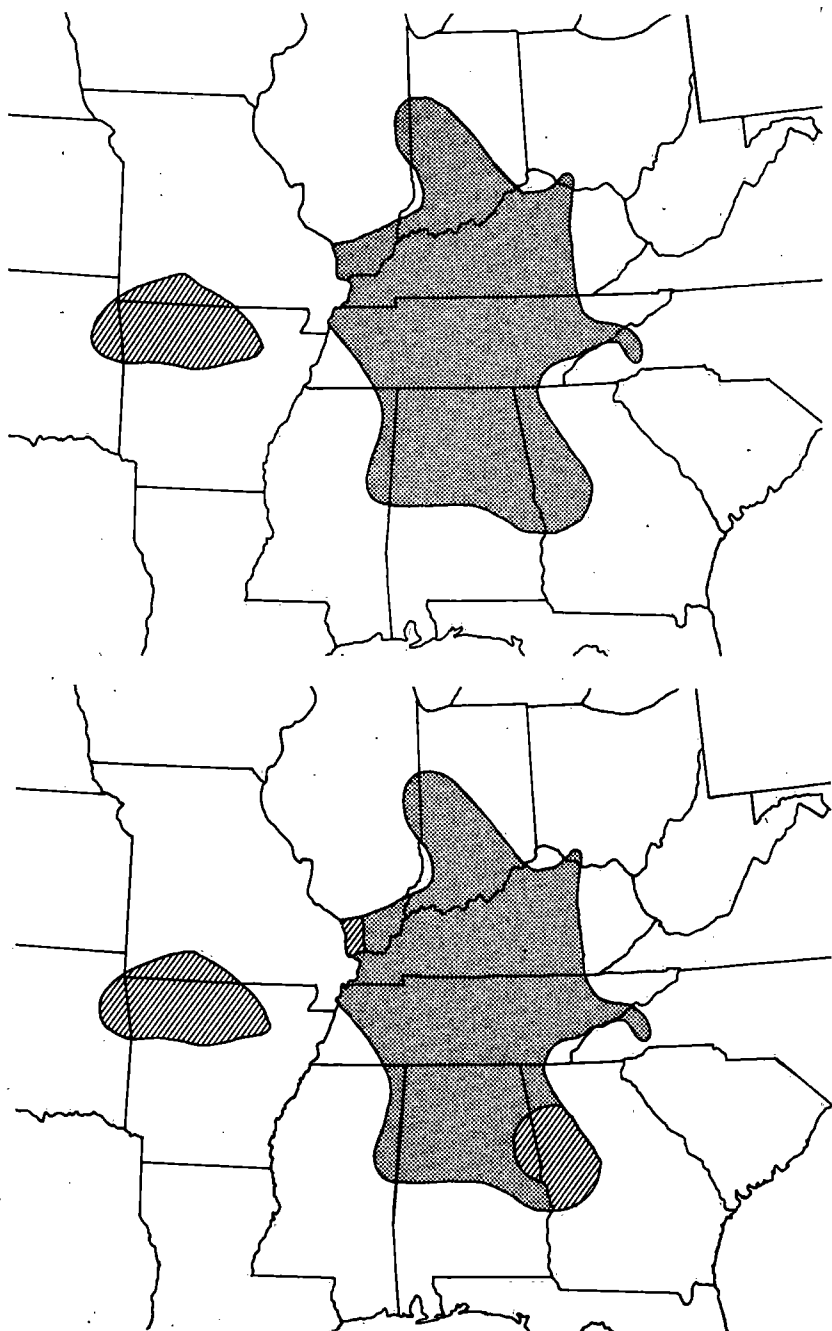


FIGURE 24. Geographic variation in *P. dorsalis*. (Upper) Hatched area represents region where species has a narrow dorsal stripe. (Lower) Hatched areas represent regions where species has a straight-edged dorsal stripe.

to that species. Thurow (1957b:94) regards most of these populations as *P. c. angusticlavius*. Others from southern Union County, Illinois, he considers intergrades between the races *angusticlavius* and *dorsalis* because they have wider stripes than those from farther north. They also have what he calls "semi-lobed" borders to the dorsal stripe. Rossman (1960:211) reports the average width of the stripe in a series from the Pine Hills of Union County, Illinois, to be closer to *P. d. angusticlavius* as defined in the original description by Grobman, but he compares the stripe to the width in *cinereus* rather than in *dorsalis*. The average width of the dorsal stripe when measured between the lobes is less in *P. dorsalis* than in *P. cinereus*.

The southwestern Illinois populations have a straight-edged wide stripe. Georgia *dorsalis* material also has a wide straight-edged dorsal stripe (fig. 24). It seems reasonable to conclude that the straight-edged stripe has evolved separately in southwestern Illinois and in Georgia, and that the subspecies *angusticlavius* developed through an increase in the frequency of the narrow striped pattern from a population similar to that now existing in southwestern Illinois. Geographically the two races are closest in southwestern Illinois and western Tennessee. Southeastern Missouri and northeastern Arkansas may yield additional intergrade material between the two races. Lack of specimens rather than real isolation is possibly responsible for the apparent disjunct distribution of the two forms.

#### CINEREUS GROUP

##### *Plethodon cinereus cinereus* (Green) Red-backed Salamander

*Salamandra erythronota* Rafinesque (1818:4). Type locality: Hudson Highlands of New York. Green (1818:356).

*Salamandra cinerea* Green (1818:356-7). Type locality not listed, but presumably the vicinity of Princeton, New Jersey.

*Salamandra erythronota*, Smith in Hitchcock (1833:552).

*Plethodon cinereus*, Tschudi (1838:58); Dunn (1926:163-80).

*Salamandra agilis* Sager (1839:322-3). Type locality not listed, but presumably Detroit, Michigan.

*Sauropsis erythronota*, Fitzinger (1843:33).

*Plethodon erythronota*, Baird (1850:285).

*Ambystoma erythronotum*, Gray (1850:37-8).

*Plethodon erythronotus*, Storer (1852:138).

*Plethodon erythronotum*, Duméril, Bibron, and Duméril (1854:86).

*Salamandra puncticulata* Valenciennes in Duméril, Bibron, and Duméril (1854:87). *Nomen nudum*.

*Plethodon erythronotus cinereus*, Cope (1869:100).

*Plethodon erythronotus erythronotus*, Cope (1869:100).

*Plethodon cinereus cinereus*, Davis and Rice (1883:12); Bishop (1941a:196-219), (1943:232-6); Grobman (1944:330-2).

*Plethodon cinereus erythronotus*, Davis and Rice (1883:12).

*Plethodon cinereus erythronota*, Britcher (1903:120).

*Plethodon huldae* Grobman (1949:136). Type locality: Hawksbill Mountain, Madison County, Virginia.

Many think the names *Salamandra cinerea* and *Salamandra erythronota*, based on the unstriped and striped color phases of this species respectively, were simultaneously proposed by Green (1818:356). During the 19th century the two color phases were considered variously as species, subspecies, and varieties, but Stejneger and Barbour (1917:15) conclude that *cinereus* should be the valid name for both, as the first revisor (Tschudi, 1838:58) used this name. Since 1917 *cinereus* has been regarded as the valid name of the species, and a large literature has accumulated using this name. Reed (1960) and Goodwin (1960) have shown that the name *erythronota* has clear priority over the name *cinerea*. Green (1818) clearly stated that Rafinesque (1818:4) had already validly described the species as *erythronota*. Though the name *cinereus* is thus a junior synonym, a change in this long established name would be extremely undesirable and an appeal has been submitted to the International Commission on Zoological Nomenclature to validate *cinereus* and suppress *erythronotus* (Highton, 1960b). Pending a decision by the Commission, it is suggested that zoologists continue to use *P. cinereus* for this species.

**HOLOTYPE.** Dunn (1926:165) states that the type is not known to exist. He refers, of course, to the type series of Green's species, *Salamandra cinerea*. In the Academy of Natural Sciences of Philadelphia collection are 12 specimens from the Green collection (ANSP 1227-38), among them one that is probably *Eurycea bislineata* (ANSP 1238) and another *Desmognathus fuscus* (ANSP 1228). A third specimen (ANSP 1229) is in such poor condition I cannot identify it. The other 9 are red-backed salamanders, 5 of the striped phase and 4 of the unstriped phase. I propose that the unstriped specimens (ANSP 1232, 1233, 1234 and 1237) be considered the syntypes of *Salamandra cinerea*, and here designate ANSP 1232 as the lectotype. The types of Rafinesque's *Salamandra erythronota*, originally supposed to be in the Lyceum Collection, are probably no longer extant.

**DIAGNOSIS.** An eastern small plethodon with a black and white mottled belly; a modal number of 19, 20, or 21 trunk vertebrae, depending on geographic locality (fig. 27); and a straight-edged dorsal stripe in the striped phase.

**DISTRIBUTION.** In eastern Canada, from Nova Scotia including Cape Breton Island, Prince Edward Island, New Brunswick, southern Quebec and Ontario, southward through the eastern United States to

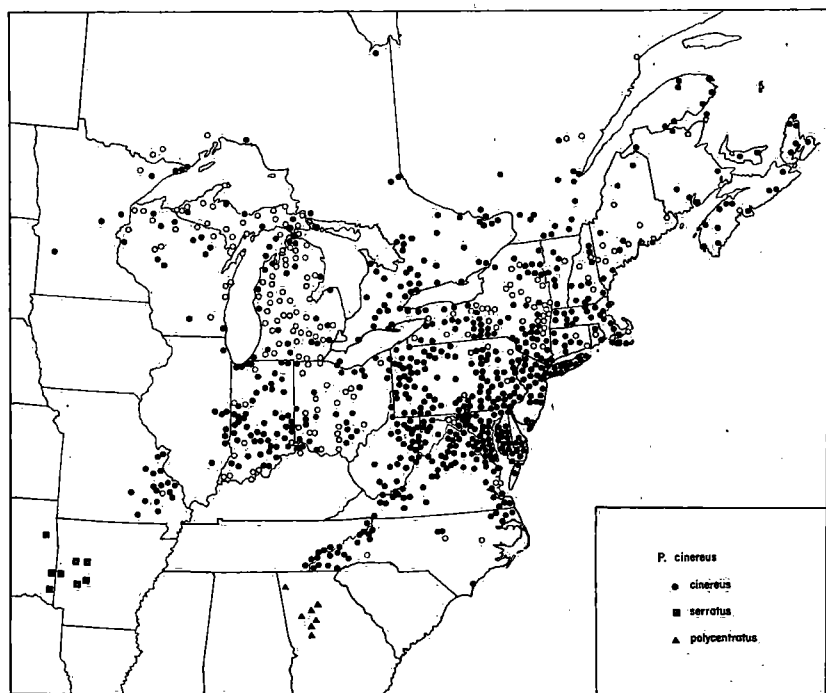


FIGURE 25. Distribution of *P. cinereus* in eastern North America.

North Carolina and eastern Tennessee, Ohio, Indiana, and southeastern Illinois; southeastern Missouri (fig. 25).

**DESCRIPTION.** The dark lead-backed or unstriped phase is characterized by the absence of red chromatophores, the presence of small white spots on the dorsum (0.07-0.2 mm. diameter), and numerous smaller brassy flecks on the head, back, and tail. The belly is mottled with black melanophores and yellow or white iridophores. Lateral iridophore pigment is similar to that on the belly and contrasts sharply with the brassy pigment on the dorsum.

The red-backed or striped phase has sides and belly similar to the unstriped phase. The white spots and brassy flecks are reduced in the dorsal stripe region, but not on the head and tail. Chromatophores in the dorsal stripe are somewhat variable in color. Some specimens lack red in the stripe. Abundant brassy pigment is present in the iris of both color phases.

The modal costal groove count varies geographically from 18 to 20, and the number of trunk vertebrae from 19 to 21. Vomerine teeth

range from 5 to 20 (fig. 26). Maximum size is 52 mm. snout-vent length. Sexual maturity is reached at about 35 mm. snout-vent length.

*Plethodon cinereus serratus* Grobman  
Ouachita Red-backed Salamander

*Plethodon cinereus serratus* Grobman (1944:306-8). Thurn (1957b:91-9).

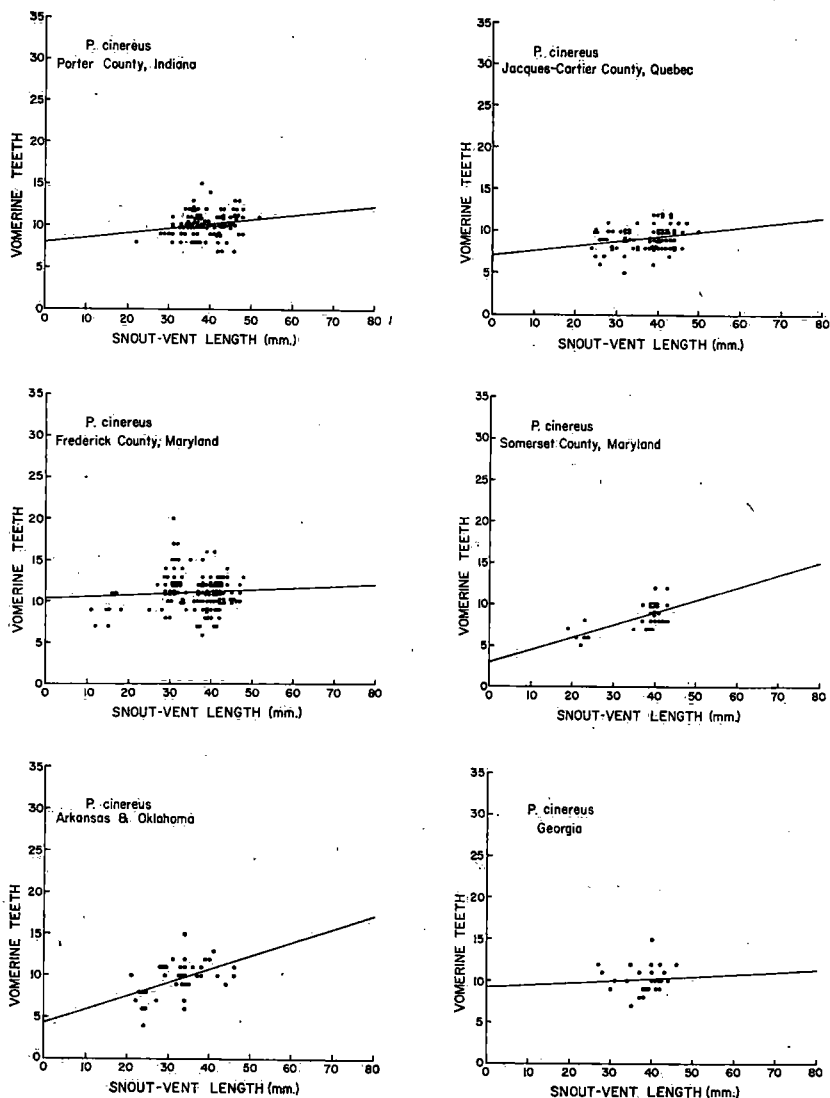


FIGURE 26. Variation in the number of vomerine teeth in 6 geographic samples of *P. cinereus*.



**HOLOTYPE.** CNHM 39464, female, collected on Rich Mountain, Polk County, Arkansas, at 2500 feet, by Karl P. Schmidt and C. M. Barber, 23 March 1938.

**DIAGNOSIS.** A race of *Plethodon cinereus* in which the edges of the dorsal stripe have a serration at each costal groove. In the unstriped phase red pigment is present on the body and sides. The modal number of trunk vertebrae is 20.

**DISTRIBUTION.** West-central uplands of Arkansas and adjacent Oklahoma south of the Arkansas River (fig. 25). Also reported by Bragg (1955:28) north of the Arkansas River in Cherokee County, Oklahoma.

**DESCRIPTION.** In striped individuals the serrations of the dorsal stripe are present on the body, but not on the tail. Serrations are produced by the red pigment in the dorsal stripe extending ventrolaterally at the top of each costal furrow. Absence of melanophores in these extensions makes the saw-tooth edge of the stripe conspicuous. In all other ways this form resembles *P. c. cinereus* except for the presence of red pigment on the sides and dorsum in the unstriped phase. This statement is based on preserved specimens; I have examined no living unstriped *P. c. serratus*.

Costal grooves usually number 19, trunk vertebrae 20. Vomerine teeth range from 4 to 15 (fig. 26). The largest specimen examined is 46 mm. in snout-vent length.

*Plethodon cinereus polycentratus* Highton and Grobman  
Georgia Red-backed Salamander

*Plethodon cinereus polycentratus* Highton and Grobman (1956:185-7).

**HOLOTYPE.** UF 8376, adult male, collected 2 miles northeast of Palmetto, Fulton County, Georgia, by Albert H. Highton and Richard Highton, 2 February 1954.

**DIAGNOSIS.** A race of *Plethodon cinereus* in which the usual number of trunk vertebrae is 21 or 22, and with red pigment on the sides of unstriped specimens.

**DISTRIBUTION.** The Piedmont of western Georgia (fig. 25).

**DESCRIPTION.** This subspecies is similar to the nominate subspecies in color, but usually has more red pigment on the anterior part of the belly, especially between the front limbs, than do the other two subspecies. Unstriped specimens have red pigment, unlike unstriped *P. c. cinereus*. Trunk vertebrae range from 21 to 23, vomerine teeth

from 7 to 15 (fig. 26). The largest specimen is 46 mm. in snout-vent length. Sexual maturity is reached at about 35 mm. snout-vent length.

\* \* \* \* \*

Throughout much of its extensive range the red-backed salamander is the commonest terrestrial urodele. Two distinct color phases occur in many populations, one with a prominent dorsal stripe (usually red, but sometimes yellow or colorless), the other unstriped. Geographic variation in color phase frequencies is discussed below. Recent evidence (Highton, 1959) shows that the difference between the striped and the unstriped phases may be due to one pair of alleles with the gene for striped pattern dominant.

An erythristic color phase, similar to the striped phase except for a reduction of melanophore pigmentation, is reported from several localities in the northern part of the species' range (Thurrow, MSb, summarizes literature records). In most areas this "scarlet phase" appears only as a rare variant, but is abundant in some populations in Litchfield County, Connecticut (Matthews, 1952; Reed, 1955).

Another color variant is a rare spotted phase. This type is similar to the unstriped phase except that it has small red spots scattered over the dorsum. In one specimen from Frederick County, Maryland, these spots vary from 0.3 to 0.8 mm. in diameter. Specimens from some other localities have larger spots. This phase appears infrequently in populations sampled so far.

Grobman (1944) recognizes the Arkansas and Oklahoma populations as a separate subspecies, *P. c. serratus*. This form differs from other red-backed salamanders by the presence of regular serrations at each costal groove along the borders of the dorsal stripe. The unstriped phase is rather rare in *serratus* populations, so most specimens can be identified readily. Occasionally a specimen from outside the range of *serratus* exhibits a slightly serrated dorsal stripe, but the serrations are usually irregular.

Highton and Grobman (1956) point out that Georgia populations of *P. cinereus* differ from others in having a greater number of trunk vertebrae and describe them as a separate subspecies, *P. c. polycentratus*. It was not known then that many other populations of *P. cinereus* have a high vertebral count. Such populations occur in the Piedmont and Coastal Plain of Virginia and North Carolina, the lower Coastal Plain of Maryland, the eastern part of Long Island, and probably also on Staten Island. The average number of trunk vertebrae in most of these populations is less than in Georgia (table 5). The original

TABLE 5. Geographic variation in the number of trunk vertebrae in *Plethodon cinereus*. (Refer to figure 27 for boundaries of the regions).

	Number of trunk vertebrae													Mean
	17/18	18	18/19	19	19/20	20	20/21	21	21/22	22	22/23	23	23/24	
19-vertebrae areas														
Catskill Mts., New York		1		56	6	24								19.30
Appalachian Plateaus		96	28	1389	47	324	4	4						19.13
Missouri				61	5	41	1	2						19.45
Arkansas				14		5								19.26
20-vertebrae areas														
east of Mississippi River	2	17	12	3056	612	17416	604	3692	20	32		1	1	20.03
Arkansas and Oklahoma				14	2	122	4	5						19.95
21 to 22-vertebrae areas														
eastern Long Island, New York					1	48	11	124	1	2				20.72
Staten Island, New York						2		4		1				20.86
eastern Maryland, Virginia, and North Carolina			1	1	1	353	48	707	10	92	2	4		20.77
Georgia								33	3	36		2		21.56

description of *P. c. polycentratus* notes that considerable red pigment is present on the legs and the sides of the head and body of unstriped specimens. These red spots are usually lacking on unstriped specimens from all parts of the range except Arkansas and Oklahoma. The basic diagnostic character of *P. c. polycentratus*—number of vertebrae—therefore fails to separate the Georgia populations from those of several other areas. Another characteristic present only in the unstriped color phase—red spots—can be used to distinguish Georgia populations from all others except those in Oklahoma and Arkansas. The recognition of *polycentratus* as a valid subspecies is therefore open to serious question, but it is retained here tentatively as there is no question that the Georgia populations have differentiated significantly from the nearest *cinereus* populations in North Carolina and Tennessee.

Red pigment in the unstriped phase of *cinereus* from two isolated populations southwest and southeast of the main body of the range is of interest as this character may likely be a primitive one. Red chromatophores occur regularly in the unstriped phase of *P. dorsalis*. The races *polycentratus* and *serratus* may be relict populations at the periphery of the range of a successful species (see Brown, 1957, for a discussion of centrifugal speciation), though they differ from each other in number of trunk vertebrae and dorsal stripe shape. Probably a long period of isolation has permitted their differentiation from the parent stock.

**GEOGRAPHIC VARIATION IN COLOR PHASE FREQUENCIES.** Thurow analyzes geographic variation in the frequency of the striped and unstriped color phases and summarizes the results in a distribution map (MSb:217). His data consist mostly of museum specimens and literature reports. Many published records are unreliable because *P. richmondi* is often wrongly identified as unstriped *P. cinereus*. Grouping data from large areas prevented Thurow from evaluating variation among populations within each region. My field studies on color phase frequencies in the Chesapeake Bay area show much variation within single physiographic regions. One extreme example illustrates the type of microgeographic variation that may occur: of 81 specimens from a single wood lot near Skipton, Talbot County, Maryland, 80 (99%) were striped. Only 5 of 49 specimens (10%) collected 14 miles away (2.3 miles north of Trappe, Talbot County, Maryland) were striped. The average for the entire Chesapeake Bay region is about 50 percent of each color phase. About half of approximately 100 series, each of

more than 25 specimens, differ significantly from a 50 : 50 ratio, ranging from 0 to 100 percent striped individuals. Obviously the averaging of data from museum material and literature reports for several localities within a physiographic region cannot reflect accurately the color phase frequencies in that region.

Series in collections indicate that the unstriped phase is scarce in parts of Canada, New England, eastern New York, Georgia, Arkansas, and Oklahoma. Large samples of *P. cinereus* from many localities consist entirely of striped specimens. Test (1952) reports this for upper Michigan, Bogert (1952) for southwestern Virginia. Except for those few noted, all available individuals from the following areas are striped: Missouri (115), Minnesota (16), Wisconsin (65), western North Carolina (438), Tennessee (55), West Virginia except for the extreme eastern and northern parts (1366), western Maryland (93), western Pennsylvania except the southwest section from Lawrence, Butler and Westmoreland Counties southward (505), eastern and southern Ohio (259), southwestern New York (460). The only unstriped individuals from these areas are from Yancey County, North Carolina (AMNH 2212, which may be a young *richmondi*, but is too young to be identified with certainty), Trumbull County, Ohio (USNM 57023, a J. Hurter specimen); and Allegany State Park, Cattaraugus County, New York (CU 3515 and CNHM 91807). Also 6 of 19 specimens from the French Broad River, North Carolina, (ANSP 1167-86) are unstriped, but the data are questionable. So few specimens are available from some parts of these regions that large series from many more localities are needed to confirm the rarity of the unstriped phase the above data suggest (fig. 27).

The unstriped phase is known to be abundant in only a few scattered areas. From 1½ miles southwest of Hutsonville, Crawford County, Illinois (INHS 5553-73, and others), 32 of 33 specimens are unstriped. From South Bass Island in Lake Erie, Ottawa County, Ohio (UMMZ 95998), all of 40 are unstriped, as are 41 of 44 specimens (UMMZ 95994, 98745) from nearby Catawba Island. The unstriped phase is also common in eastern Long Island (Weber, 1928:108, and unpublished data of Ernest E. Williams and Donald Cooper) and in parts of the southern Coastal Plain of Maryland (Prince Georges, Anne Arundel, Charles, and St. Marys Counties). High frequencies of unstriped specimens also occur near Ottawa (Carleton and Russell Counties, Ontario), and Montreal (Montagnes County, Quebec) (Patch, 1918; Paul S. Martin, personal communication).

In some areas the frequency of the striped phase is less than 5 per-

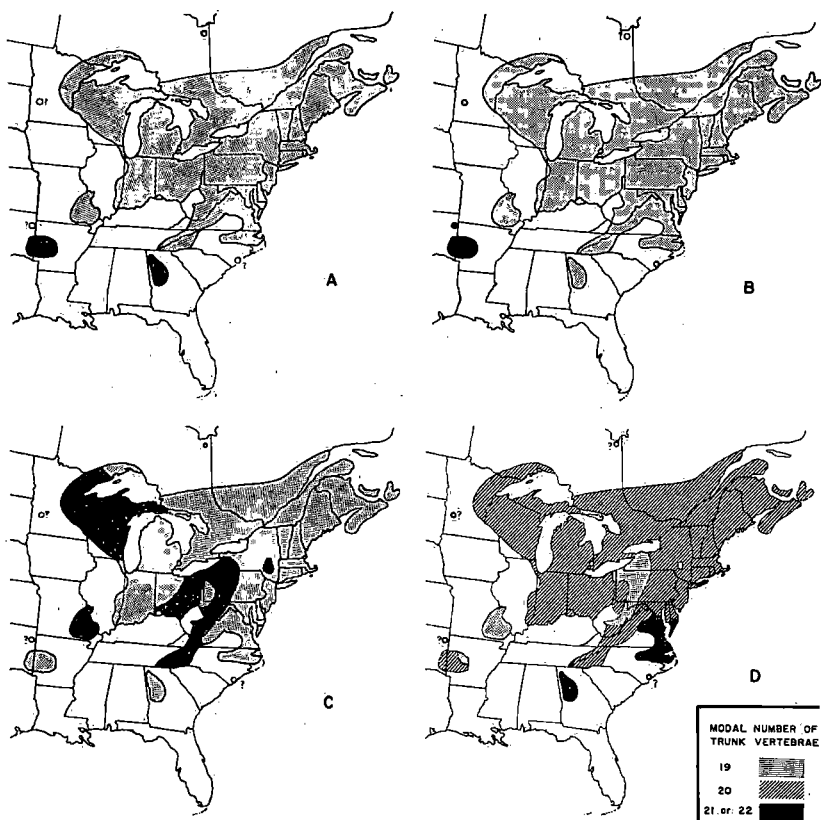


FIGURE 27. Geographic variation in *P. cinereus*. Darkened area represents regions where species has: (A) red pigment in unstriped specimens, (B) a serrated dorsal stripe, (C) absence of the unstriped color phase, (D) variation in the number of trunk vertebrae.

cent. By some current taxonomic procedures these could be recognized as racially different from populations more than 99 percent striped. Clearly variation of this type cannot be described best by naming geographic races, for by this interpretation more than half the range of *P. cinereus* becomes a zone of intergradation.

Both color phases occur in most of the range of the red-backed salamander, with the striped phase usually the more plentiful. But the local variation in some areas is so great that the biological significance of the species' pattern dimorphism should be investigated. Certain geographic correlations between color phase frequencies and trunk vertebrae variation will be pointed out later.

Test (1952) suggests that the dark phase is of more recent origin

than the striped phase. He bases this on the frequencies of the two patterns in Michigan populations. It seems unlikely that the unstriped phase is a recent evolutionary development as it occurs in so many species of *Plethodon*. Moreover, some populations in the center of the range of *cinereus* lack the dark phase, while others on the periphery do not. The unstriped phase seems poorly adapted to some areas, as in the Allegheny Plateau region, although it occurs on both sides of the area.

The closely related species, *P. richmondi*, occupies a large part of the area from southwestern New York southward through Pennsylvania and western Maryland and eastern Ohio into West Virginia where the unstriped phase of *P. cinereus* is apparently almost absent. *P. richmondi* is known only in the unstriped phase. Probably some interaction between the two species in this area of sympatry results in increased pattern divergence. Whether color pattern is an isolating mechanism cannot be determined at present, as nothing is known of its role in these species' reproductive biology. Character displacement (Brown and Wilson, 1956) in a zone of geographic overlap between two closely related species is often due to reinforcement of species barriers to prevent gametic wastage through hybridization. In many areas where *richmondi* and *cinereus* are sympatric they are ecologically segregated; where the two occur together in the same habitat, the rarity or absence of the unstriped phase of *cinereus* is striking. This relationship greatly needs quantitative study in the area of species overlap.

**GEOGRAPHIC VARIATION IN NUMBER OF TRUNK VERTEBRAE.** In my recent study of the heritability of the number of trunk vertebrae in *P. cinereus* (Highton, 1960a), I induced gravid females from different regions to deposit eggs in the laboratory and incubated the embryos under uniform conditions. A significant correlation between the number of vertebrae in the parental populations and the offspring demonstrated that much of the geographic variation is due to genetic differences. Other data obtained from field-collected broods from Giles County, Virginia, indicate a correlation between the number of trunk vertebrae in females and their offspring. An estimate of the percentage of the variance due to heredity in these parent-offspring correlations is 61, indicating that more than half the variation in number of trunk vertebrae within a single population is due to genetic factors.

Variation in the number of trunk vertebrae in *cinereus* is summarized in table 5 and figure 27. There is rarely a variation of more than three vertebrae within any one population, and the class with the medial

TABLE 6. Mean number of trunk vertebrae per county<sup>a</sup> for all counties with eight or more *P. cinereus*.<sup>b</sup>

Mean number of trunk vertebrae	19-vertebrae areas			20-vertebrae areas		21-vertebrae areas	
	Missouri	Appalachian Plateaus	Catskill Mts., N.Y.	Arkansas & Oklahoma	Remainder of range	Eastern Coastal	Georgia
18.8		2					
18.9		1					
19.0		3					
19.1		1					
19.2	2	4					
19.3	1	9	2	1 <sup>d</sup>			
19.4		5			1 <sup>e</sup>		
19.5					8 <sup>e</sup>		
19.6					10		
19.7	1 <sup>c</sup>				23		
19.8					38		
19.9				1	33		
20.0				1	36		
20.1				1	39		
20.2					24	1 <sup>i</sup>	
20.3					22		
20.4					11		
20.5					4 <sup>f</sup>		
20.6					1 <sup>h</sup>	2	
20.7						6	
20.8						6	
20.9						3	
21.0						1	



21.1  
21.2  
21.3  
21.4  
21.5  
21.6

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1

1

1

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- <sup>a</sup> Counties are used rather than samples from single localities in order to reduce geographic bias. If means of samples from all localities were used, some geographic areas would be represented by many series, others by few.
  - <sup>b</sup> Data for 9 counties were divided into two groups because of a significant difference in vertebral counts. Those counties counted twice are: northern and southern Calvert and St. Marys Counties, Maryland; eastern and western Greene, Suffolk, and Ulster Counties, New York; eastern and western Westmoreland County, Pennsylvania; eastern and western Monongalia, Pendleton, and Randolph Counties, West Virginia. Exceptional county means are listed in footnotes.
  - <sup>c</sup> Ste. Genevieve County, Missouri.
  - <sup>d</sup> Logan County, Arkansas.
  - <sup>e</sup> Clark County, Illinois.
  - <sup>f</sup> Emmet and Oakland Counties, Michigan; Franklin County, Ohio; Crawford and Fulton Counties, Pennsylvania; eastern Pendleton County, West Virginia; Victoria County, Nova Scotia; and Brome County, Quebec.
  - <sup>g</sup> Monmouth and Ocean Counties, New Jersey, Clark and Fairfax Counties, Virginia.
  - <sup>h</sup> Crawford County, Illinois.
  - <sup>i</sup> Currituck County, North Carolina.

number of vertebrae usually includes the majority of the sample. Therefore the mean number of vertebrae is close to a whole number in most populations. Grouping all 308 sample means together (table 6) shows three modes, one just above 19 trunk vertebrae, another around 20, and another a little below 21. The 19 and 21 modes are smaller than the mode at 20 because the red-backed salamanders with these counts occupy smaller geographic areas, and a smaller number of series is available. I know no reason why natural selection should favor a population with a high frequency of one particular vertebral number over a population with two equally frequent vertebral numbers. As numerous populations have a high frequency of specimens with 19 trunk vertebrae while many others have specimens mostly with 20, it is surprising that so few populations do exist that have equal numbers of specimens with 19 and 20 vertebrae and a mean around 19.5. The reason for the trimodality might be that three isolates have diverged sufficiently to produce three geographic races each with a mean number of trunk vertebrae close to the whole numbers 19, 20, and 21. This thesis is not supported by the fact that the modal frequency of 19 probably evolved at least three times—in the Catskill region of New York, in the Appalachian plateaus, and in southeastern Missouri (tables 5 and 6 and fig. 27). The 21-vertebrae populations along the eastern coast may have been continuously distributed at a time when sea level was lower, perhaps during the glacial stages of the Pleistocene, so there is no need to postulate a separate derivation for each of the now isolated populations. One exception may be the isolated Georgia race, which probably is derived independently from nearby 20-vertebrae populations. It is difficult to account for the former isolation of 21-vertebrae populations from adjacent ones with 20 vertebrae.

Note that the county means (table 6) are not normally distributed. Many samples are large and a difference of as little as 0.2 of a vertebra is often statistically significant. Distribution of means is not random since adjacent populations usually resemble one another in vertebral counts. Standard deviations of most of the large samples are similar and range from 0.4 to 0.6. No evidence indicates that populations with means midway between 19 and 20 vertebrae show greater variability than those from the centers of the 19-, 20-, or 21-vertebrae areas. For example, at a locality near Fort Littleton, Fulton County, Pennsylvania, 79 of a sample of 176 specimens have 19 trunk vertebrae, 86 have 20, 1 has 21, and 10 are asymmetrical (19 and 20). This locality is near the boundary between areas occupied by 19- and

20-vertebrae populations. Another intermediate sample of 87 specimens from Reddish Knob, on the boundary between Pendleton County, West Virginia, and Augusta County, Virginia, is similar in that 41 have 19 vertebrae, 43 have 20, and 3 are asymmetrical (19 and 20). This series is intermediate between one of 129 specimens with a mean of 20.41 vertebrae, from Natural Chimneys, Augusta County, Virginia (CM 31002-3), and another series of 521 specimens from the Cheat Mountains of Randolph County, West Virginia, which has a mean of 19.05 vertebrae. A study of microgeographic variation in the region where the 20- and 21-vertebrae populations come in contact in southern Maryland and Virginia is now in progress. The three areas with a modal number of 19 trunk vertebrae are widely separated by populations with a modal number of 20 vertebrae.

The mean number of trunk vertebrae in 110 specimens of *cinereus* from southeastern Missouri is 19.45. There appears to be some variation within the area, however. A series of 18 specimens (INHS 8396) from 6 miles southeast of Weingarten, Ste. Genevieve County, has a mean of 19.72 trunk vertebrae. Seven specimens from Meramec State Park, Franklin County (CWM 1306-11; 1443), have a mean of 19.75 trunk vertebrae. The remaining 85 specimens from Bollinger, Butler, Dent, Iron, Jefferson, Oregon, Perry, Reynolds, St. Francois, St. Louis, Washington, and Wayne Counties have a mean of 19.36 trunk vertebrae. The Missouri populations of *cinereus* are geographically situated between the *dorsalis* populations of southwestern Illinois and those of southwestern Missouri (*angusticlavius*). Since their modal vertebral number is 19, the same as that of both *dorsalis* and *angusticlavius*, it might be suggested that they actually represent a population of *dorsalis* rather than *cinereus*. The straight-edged dorsal stripe of the southwestern Illinois *dorsalis* is very similar to that of *cinereus*, so this diagnostic character is of no aid in identification of the Missouri material. All of the southeastern Missouri specimens are of the red-backed phase. There remain only two other good diagnostic characteristics that may be used to differentiate preserved *dorsalis* and *cinereus* and these are present only in mature males. Only 28 of the available specimens from Missouri are mature males, and all of these possess the type of mental gland and modified premaxillary teeth typical of *cinereus*. On this basis, all of the southeastern Missouri specimens are tentatively assigned to *cinereus*. However, the possibility exists that some populations from which no males are presently represented in collections are actually *dorsalis*. Or, *dorsalis* may be present in the area, but may not have been collected yet. A thorough field study of the eastern

small plethodons of southeastern Missouri is greatly needed. Habitat information and belly pigmentation data on living specimens would provide valuable additional information relative to the taxonomic allocation of these Missouri populations. The possibility that the eastern small plethodons of this area represent a primitive relict population should also be considered, for such a population might possess some of the characters of both species. The same might also be true of a population that arose through hybridization of the two species and has since been stabilized with some of the characters of one species and other characters of the other species. Probably both species ranged throughout the entire area during a more favorable climatic period, judging from their present distributions.

In Garland, Yell, and Logan Counties, Arkansas, the mean of 19 specimens of *serratus* is 19.26, while the mean of 95 specimens from Montgomery and Polk Counties is 19.91. The mean of 49 specimens from LeFlore and McCurtain Counties, Oklahoma, is 19.99. The specimen reported by Bragg (1955:28) from Cherokee County, Oklahoma (MUOZ 30678) has 20 costal grooves (probably 21 trunk vertebrae).

Presently available material does not show a good correlation between increasing altitude and a reduction in the number of trunk vertebrae. Almost all samples from the Allegheny Mountains section of the Appalachian Plateaus Physiographic Province have a modal number of 19 trunk vertebrae, but populations from still higher altitudes in the Blue Ridge Province of Virginia, North Carolina, and Tennessee have a modal number of 20. In the Appalachian Plateaus Province of northeastern Pennsylvania the modal number is 20, as it is in the glaciated section of the Allegheny Plateau of New York. In the Catskill Mountains, however, it is 19.

Barden (MS) reports on a study of the zone of contact between the high-altitude populations of *cinereus* in the Catskill Mountains that have a modal number of 19 vertebrae and consist of almost 100 percent striped phase, and the lower altitude populations with a modal number of 20 and both color phases. He finds a narrow zone of intergradation and fair geographic concordance between change in number of vertebrae and color phase frequencies in the east, but not in the south and west. The type of forest vegetation, itself correlated with latitude and altitude, seems to be the most important factor influencing the distribution of this zone. Barden discounts the effects of selection or ecophenotypic variation in influencing the variation in *cinereus* populations of southern New York and attributes the variation to a double invasion and secondary contact of two differentiated populations that

were isolated during the Pleistocene. As there are no nearby populations with a low vertebral count, it seems likely that selection has produced the low-count populations at high elevations in the Catskill Mountains. Whether selection is responsible for variation in color phase frequencies is not yet clear.

There are few available series from the glaciated section of the Allegheny Plateau in Ohio, Pennsylvania, and southwestern New York. A total of 77 specimens from Chautaugua, Erie, Wyoming, Livingston, Ontario, and Steuben Counties, New York have an average of 19.2 trunk vertebrae, while 21 specimens from Ashtabula, Trumbull, and Mahoning Counties, Ohio have a mean of 19.4 trunk vertebrae. The modal number in the Finger Lakes Region of New York is 20, so apparently a rather abrupt change in average number of trunk vertebrae occurs just west of the Finger Lakes. Variation through the remainder of northeastern Ohio is not determined because of the paucity of material.

Populations of red-backed salamanders with a modal number of 21 trunk vertebrae along the Atlantic Coast from Long Island to North Carolina are now discontinuously distributed. They occur on the eastern half of Long Island (187 specimens, mean 20.7) and Staten Island (7 specimens, mean 20.9), but not in the intervening area. Specimens from western Long Island (316) have a modal number of 20 vertebrae (mean, 20.1). Several series from four coastal counties of New Jersey (Monmouth, Ocean, Burlington, and Cape May) have a higher proportion of individuals with 21 trunk vertebrae than other New Jersey material. In the southern Del-Mar-Va Peninsula, in the southern Coastal Plain of Maryland, the Coastal Plain and eastern Piedmont of Virginia, and parts of the Coastal Plain and Piedmont of North Carolina, the modal number is 21.

The species *P. cinereus* and *P. richmondi* exhibit character displacement in color pattern, but a comparison of the number of trunk vertebrae of the two species does not indicate a consistent increase in divergence in areas of sympatry (figs. 27 and 30).

The usual taxonomic treatment of geographic variation of the type found in the number of trunk vertebrae in *P. cinereus* is to separate the populations with different modal numbers of trunk vertebrae into named subspecies. However, the 19-vertebrae populations do not occur in a single continuous geographic area, but in three (or four if the Arkansas populations are included) rather widely separated regions. They do not differ consistently from one another in any other known character and therefore have to be considered as one polytopic sub-

species. Of 2108 specimens from the three areas, 1703 (81%) have fewer than 20 trunk vertebrae; from the regions where the modal number of vertebrae is 20, 21,897 (86%) of 25,612 specimens have 20 or more trunk vertebrae. Separation would be even greater if specimens from near the boundaries of these areas could be called "intergrades" and omitted. No evidence indicates that populations of *cinereus* with a modal number of 19 trunk vertebrae represent a uniform race, but rather that the phenotype has evolved independently in more than one region. The estimate of heritability of variation in trunk vertebrae (Highton, 1960a) indicates that only 61 percent of the variation within one population is due to heredity. If the remainder is due to geographically variable environmental factors, then part of the geographic divergence may be ecophenotypic rather than genetic. Moreover, geographic variation in color phase frequencies is not concordant with that of trunk vertebrae. Though all three areas in which the modal number of trunk vertebrae is 19 are included in regions where the frequency of the striped phase is over 99 percent, the frequency of the striped phase is often equally high in adjoining areas where the modal number of trunk vertebrae is 20. Hence the factors that select for the high frequency of the striped phase must not have the same distribution as those that select for the lower number of vertebrae.

On Long Island, where abrupt change in the color phase frequencies occurs, there is concordance in the variation in vertebral number and color phase frequency. Of 12 specimens from Queens County, 11 (93%) are striped (mean number of trunk vertebrae, 20.4); of 125 from Nassau County, 102 (82%) are striped (mean number of vertebrae, 20.1); and of 173 from western Suffolk County, 167 (97%) are striped (mean number of vertebrae, 20.0). In the eastern part of Suffolk County only 4 of 199 (2%) are striped (mean number of vertebrae 20.7). A sample of 17 (DC 480-496) from Gardiners Island off the eastern end of Long Island is 100 percent striped and has a mean number of trunk vertebrae of 19.6. Thus the concordance between the unstriped populations with 21 trunk vertebrae and the striped populations with 20 trunk vertebrae on Long Island is nearly perfect.

In other areas where the frequency of the unstriped phase is high, as in Crawford County, Illinois, and Catawba Island, Ottawa County, Ohio, the average number of trunk vertebrae is also high (20.6 and 20.5 respectively), but on South Bass Island, Ottawa County, Ohio, the mean number of trunk vertebrae is only 19.7. Though many populations in Maryland and Virginia have a high frequency of the unstriped

phase, these do not occur with any consistently higher frequency in the area where the modal number of trunk vertebrae is 21 than in adjacent areas where the modal number is 20. Canadian samples with a high proportion of dark phase specimens have about the same mean vertebral counts as adjacent mixed populations. Therefore geographic variation exists in the correlation between high frequency of the unstriped phase and presence of a modal number of 21 trunk vertebrae. One area shows a high correlation (Long Island), while in others (Maryland, Virginia, Québec, and Ontario) there is little or no correlation.

**OTHER GEOGRAPHICALLY VARIABLE CHARACTERS.** A series of 30 specimens from Crawford County, Illinois, includes 12 individuals with a type of belly pigmentation not seen in any other *P. cinereus*. This series differs from other Illinois *cinereus* in being 97 percent unstriped and in having a high average vertebral count. Instead of the usual ventral white mottling of *cinereus*, these 12 specimens have a medial pigment-free area on the belly. As the belly is unmottled, I thought at one time they might represent an aberrant isolated population of *P. richmondi*, and Conant's (1958) distribution map plots them as a questionable record of this species. They are probably properly assigned to *cinereus*; however, for one red-backed individual has been found, and the other 18 specimens have typical *cinereus*-type mottled bellies.

In the Blue Ridge Province of Virginia and Maryland and to some extent in adjacent areas (Bogert, 1952), the usual brassy iridophore flecking present on the unstriped phase of *P. cinereus* is highly developed. This led Grobman (1949) to regard these populations as related to *P. richmondi* and he described them as a full species, *P. huldae*. Rabb (1955) and Muchmore (1955) present evidence that *P. huldae* is based on unstriped specimens of *cinereus*. Rabb found both color phases in the offspring of a striped female. These brassy flecked *P. cinereus* resemble *richmondi* dorsally and can be distinguished from that species only by the lower average number of trunk vertebrae and by the greater amount of yellow iridophore mottling on the belly and chin.

Living specimens from Graham, Swain, Haywood, Macon, and Jackson Counties of western North Carolina have red pigment on the sides and belly in front of the forelimbs. This pigment fades in preservatives, so the geographic extent of its occurrence is not yet known.

Specimens from New Kent County, Virginia, and a few in adjacent areas have a median dark band within the dorsal stripe. Some

eastern North Carolina specimens have exceedingly wide stripes.

Sanders and Smith (1949) report a specimen of *P. cinereus* from Fern Lake, near Nacogdoches, Nacogdoches County, Texas. This specimen (OS 556) has 19 trunk vertebrae and lacks the serrated edges of the dorsal stripe present in the nearest populations of *P. c. serratus*. Mr. Sanders writes me that he collected the specimen by dip net from fruiting sphagnum moss near the lake shore, an unusual habitat for this terrestrial species. This record may be the result of an accidental introduction by man and confirmation by additional specimens is necessary before Texas can be included in the natural range of the species.

All eastern small plethodons I examined from southwestern Illinois are clearly referable to *P. dorsalis* except one (UIMNH 16706), an unstriped female from Alto Pass, Union County, Illinois, collected by A. Cahn in 1928. Thurow (1957b:96) reports two other specimens from the same locality (UIMNH 16707-8). Additional material from southwestern Illinois is needed to confirm these records before including this area in the range of the red-backed salamander.

Bleakney (1958:15) cites unconfirmed reports of local residents that *P. cinereus* occurs in the Lake Melville area of Labrador. Since environmental conditions there are similar to those where *cinereus* occurs farther south, further search is desirable. Four unstriped specimens from "Hudson Bay Territory" sent to the National Museum in 1861 (USNM 5963) represent the only record from this northern area. Grobman (1944:281) points out that *cinereus* must have extended its range rather rapidly to penetrate so far north following the retreat of the last Pleistocene glaciers. No records from Newfoundland or Anticosti Island are known.

Most of the literature records of *P. cinereus* from Kentucky are probably based on *P. richmondi*. The only Kentucky specimens of *cinereus* examined are from Boone and Kenton Counties in the extreme northern part of the state. There are no *cinereus* records from western West Virginia; the specimen Grobman (1944:299) records from Mingo County (CM 15998) is a *richmondi*. *P. cinereus* should occur in the mountains of northeastern Georgia and northwestern South Carolina, but it has not yet been found there.

*Plethodon richmondi richmondi* Netting and Mittleman  
Ravine Salamander

*Plethodon richmondi* Netting and Mittleman (1938:288). Bishop (1943:272-5); Grobman (1944:312); Duellman (1954:40-5).



*Plethodon richmondi richmondi*, Highton and Grobman (1956:187-8).

*Plethodon richmondi popei* Highton and Grobman (1956:187-8): Type locality: Comers Rock, Grayson-Wythe County line, Virginia.

**HOLOTYPE.** CM 14189, adult male, collected in Ritter Park, Huntington, Cabell County, West Virginia, elevation 600-700 feet, by Neil D. Richmond and N. Bayard Green, 15 October 1938.

**DIAGNOSIS.** A dark-bellied eastern small plethodon, usually with 21 or more trunk vertebrae, and lacking the striped color phase.

**DISTRIBUTION.** From Centre County, Pennsylvania, south through western Maryland, West Virginia, western Virginia, northwestern North Carolina, and northeastern Tennessee, west to Ohio, southeastern Indiana, and eastern Kentucky (fig. 28).

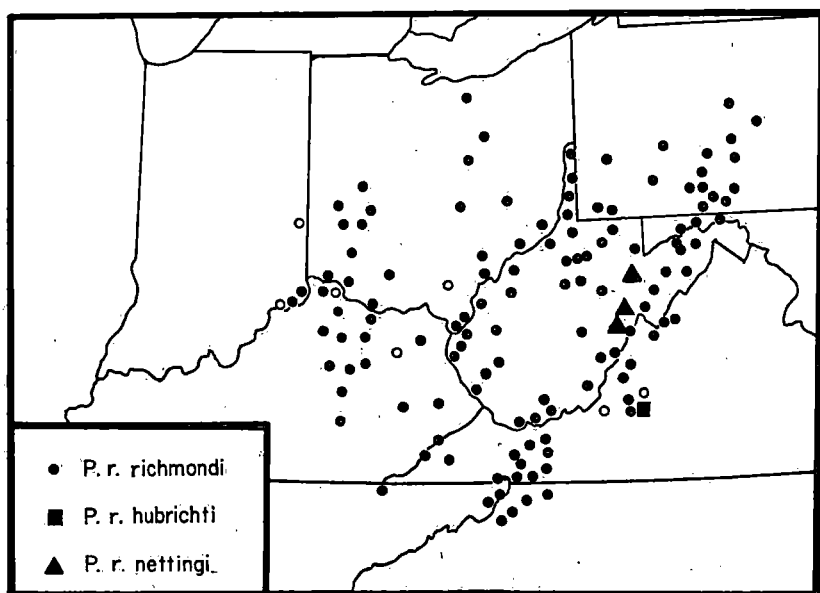


FIGURE 28. Distribution of *P. richmondi* in the eastern United States.

**DESCRIPTION.** The dorsum is covered with small brassy flecks and with larger white spots (0.1-0.3 mm. diameter). Lateral white or yellow iridophore spots are similar in color to those on the belly and chin. The iris has brassy flecking above and below the pupil. Red chromatophores are often present anteriorly on the sides and head of adults of eastern populations, but have not been noted in living material from the western part of the range. Red pigment is present on the dorsum also in young individuals.

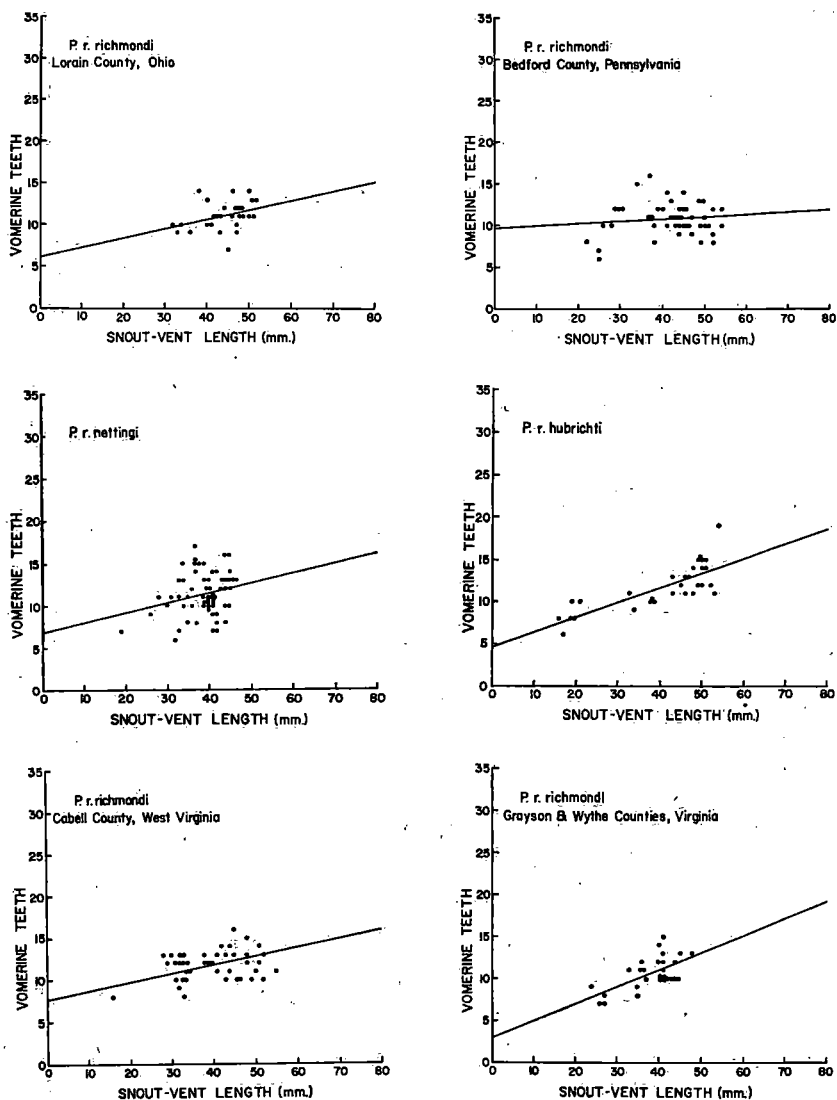


FIGURE 29. Variation in the number of vomerine teeth in 6 geographic samples of *P. richmondii*.

The modal costal groove count varies geographically from 19 to 22, and the modal number of trunk vertebrae from 20 to 23. Vomerine teeth range from 6 to 16 (fig. 29). The largest specimen examined, from Alleghany County, Virginia, is 60 mm. in snout-vent length, but

Duellman (1954) records a 72 mm. specimen from Ohio. Sexual maturity is reached at about 40 mm. snout-vent length.

*Plethodon richmondi hubrichti* Thuirow  
Peaks of Otter Salamander

*Plethodon nettingi*, Thuirow (1955:102-3).  
*Plethodon hubrichti* Thuirow (1957a:59).

**HOLOTYPE.** USNM 139087, adult male, collected at mile 80.9 Blue Ridge Parkway, Bedford County, Virginia, at about 3100 feet, by Gordon R. Thuirow, 9 December 1956.

**DIAGNOSIS.** A race of *P. richmondi* with a modal number of 20 trunk vertebrae, and with more dorsal brassy flecking in the adult than in other populations of *richmondi*.

**DISTRIBUTION.** Known only from the type locality and from Greenlee, southern Rockbridge County, Virginia (fig. 28).

**DESCRIPTION.** More than half the adults and subadults have so much brassy spotting on the dorsum in life that it forms an almost uniform dorsal stripe. In others the brassy areas are separated into spots, though many fuse with adjacent spots. Dorsal brassy flecking is less marked in juveniles, which resemble adults of other *richmondi* populations. Newly hatched young have a reddish dorsal stripe. The amount of white spotting on the belly and chin varies considerably and is sometimes absent. Within the brassy patches are small (0.1-0.3 mm.) white spots. Larger white spots (0.2-0.9 mm. in diameter) are present dorsolaterally. Brassy flecks pattern the iris.

The modal costal groove count is 19, and the number of trunk vertebrae usually 20. Vomerine teeth range from 6 to 19 (fig. 29). The largest specimen examined is 55 mm. in snout-vent length. Sexual maturity is usually reached between 40 and 45 mm. snout-vent length.

*Plethodon richmondi nettingi* Green  
Cheat Mountain Salamander

*Plethodon nettingi* Green (1938:295-9). Bishop (1943:266-9); Grobman (1944:313); Brooks 1948:239-44); Thuirow (1957a:65).  
*Plethodon richmondi nettingi*, Highton and Grobman (1956:187).

**HOLOTYPE.** CM 10279, adult male, collected on Barton Knob, near Cheat Bridge, Randolph County, West Virginia, elevation about 4000 feet, by M. Graham Netting, 29 June 1935.

**DIAGNOSIS.** A race of *P. richmondi* that has a modal number of 19 trunk vertebrae.

DISTRIBUTION. Known from altitudes above 3500 feet in the Cheat Mountains of Randolph and Pocahontas Counties, West Virginia (fig. 28).

DESCRIPTION. Coloration in life is similar to *P. r. richmondi*. Costal grooves usually number 18, trunk vertebrae 19. Vomerine teeth range from 6 to 17 (fig. 29). The largest specimen examined is 46 mm. in snout-vent length. Sexual maturity is reached at about 35 mm. snout-vent length.

\* \* \* \* \*

Netting and Mittleman (1938:288) and Green (1938:295) respectively described *P. richmondi* and *P. nettingi*. Highton and Grobman (1956:187) named a southern race, *P. richmondi popei*, and recognized *nettingi* as a subspecies of *P. richmondi*. Thurow (1957a:59) subsequently described another member of this group, *hubrichti*, as a full species; it is here considered as a subspecies of *P. richmondi*. All *P. richmondi* have brassy dorsal flecking and are characterized by the lack of a striped phase except in the young. Most have dark bellies. These characters show much variation in other eastern small plethodons and they are not diagnostic for *P. richmondi*. Variation in the closely related *P. cinereus* is so great it is impossible to identify all specimens of *cinereus* and *richmondi* without aid of locality data. Where they are sympatric the two species usually differ in color pattern and number of trunk vertebrae. Thus though they cannot always be identified by morphological criteria, they are certainly distinct species. (See discussion of character displacement under *P. cinereus*.)

GEOGRAPHIC VARIATION IN NUMBER OF TRUNK VERTEBRAE. The number of trunk segments is the most easily analyzed geographically variable character of *P. richmondi*. Extremes of variation are found at localities only 100 miles apart in West Virginia. At Bickles Knob in the Cheat Mountains of Randolph County, the mean number of body vertebrae is 18.8 in a sample of 421 *P. r. nettingi*, while 7 miles north-northeast of Sandyville, Jackson County, the mean number is 23.6 in a sample of 9 *P. r. richmondi*, an average difference of almost five vertebrae. Extremes of variation at the two localities are 18 to 20 and 23 to 24. Table 7 summarizes geographic variation in samples from different parts of the range of the species.

Populations from the Cheat Mountains of West Virginia (*P. r. nettingi*) have the lowest number of trunk vertebrae. The modal count of all samples of this form is 19. Leslie Hubricht discovered a high

TABLE 7. Summary of geographic variation in number of trunk vertebrae in *Plethodon richmondi*.

Geographic region	Number of trunk vertebrae														Modal number
	18	18/19	19	19/20	20	20/21	21	21/22	22	22/23	23	23/24	24	Mean	
<i>P. r. nettingi</i>															
Cheat Mountains, W. Virginia	118	30	537	11	23									18.85	19
<i>P. r. hubrichti</i>															
Bedford County, Virginia	1	2	53	18	244	1	8							19.82	20
<i>P. r. richmondi</i>															
Smyth Co. slope of Whitetop Mountain, Virginia			1		24		3							20.07	20
Southwestern Virginia, northwestern North Carolina, northeastern Tennessee, southeastern Kentucky, and southern West Virginia					218	23	581	18	91		2			20.87	21
Paddy and Reddish Knobs, West Virginia—Virginia state line			1		2	1	28		3					20.96	21
Eastern Ohio				1	9	1	46	1	19		1			21.13	21
Western Ohio, southeastern Indiana, northeastern Kentucky, and vicinity of Huntington, West Virginia							103	20	428	11	65	3	3	21.95	22
Ridge and Valley Province of Pennsylvania, Maryland, West Virginia, and Virginia*							19	12	316	4	42	1		22.05	22
Appalachian Plateau of western Pennsylvania									31	3	14		1	22.36	22
Appalachian Plateau of West Virginia									31	7	52	3	8	22.75	23

\* Includes 3 specimens from Mills Gap, Botetourt-Bedford County line, Virginia, in the Blue Ridge Physiographic Province.

altitude population with a modal number of 20 between the James and the Roanoke Rivers in the Blue Ridge Mountains of Virginia. Thurow (1955) reported this find and referred the specimens to *P. r. nettingi*. Thurow (1957a) later described them as *P. hubrichti*.

All southern populations of *P. richmondi*—those in northwestern North Carolina, northeastern Tennessee, southwestern Virginia, and adjacent areas of Kentucky and West Virginia—have a modal number of 21 trunk vertebrae with one exception, a population on the Smyth County slope of Whitetop Mountain, Virginia, with a modal number of 20. All other samples from Whitetop Mountain have a modal number of 21. When describing salamanders from this region as *P. r. popei* (Highton and Grobman, 1956), we were unaware that the modal number of trunk vertebrae is also 21 in at least two other areas, in eastern Ohio, and in the mountains along the Virginia–West Virginia state line—Paddy Knob and Reddish Knob, west and southwest of Harrisonburg, Virginia. The salamanders in each of these regions resemble adjacent 22-vertebrae populations in belly pigmentation, which may be interpreted as evidence against close relationship of these disjunct populations with the same modal vertebral count. Hence I no longer regard *popei* as a valid subspecies. To recognize the three isolated 21-vertebrae populations as the same subspecies would be to ignore differences in belly and chin pigmentation.

The remainder of the range of *P. richmondi* is occupied by populations with modal counts of 22 and 23 trunk vertebrae. The highest numbers occur in the Appalachian Plateau Province of West Virginia (fig. 30).

Data on vertebral variation in *P. richmondi* may suffer from sampling bias. From several regions we have many small samples, but only one or two large ones. Thus the mean value for a region may be unduly influenced by only a few samples. The extent of local variation in many areas is therefore still poorly known.

**GEOGRAPHIC VARIATION IN VENTRAL PIGMENTATION.** Salamanders from the Ridge and Valley Physiographic Province of Pennsylvania, Maryland, West Virginia, and Virginia show more white mottling on the belly and chin than do other *P. richmondi*. This is in sharp contrast to all adjacent populations of *richmondi*, which have the darkest bellies and chins in the species. On belly and chin pigmentation a mixed group of Pennsylvania specimens sorts easily into those from the Ridge and Valley Province and those from the Appalachian Plateaus Province with more than 95 percent accuracy. A similar separation is possible when material from southwestern Virginia (formerly *P. r. popei*)

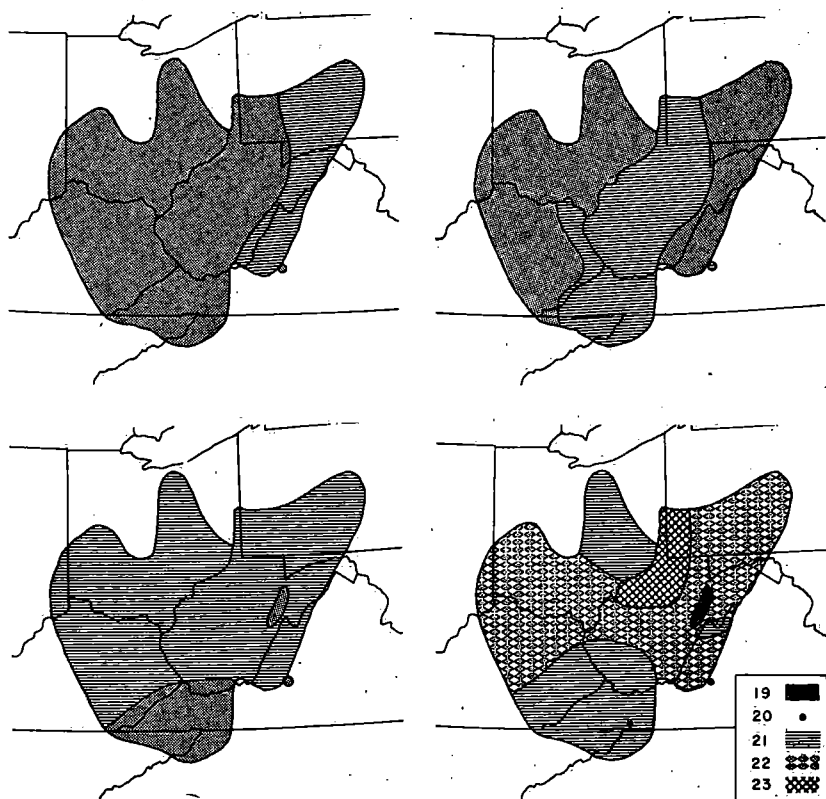


FIGURE 30. Geographic variation in *P. richmondi*. (Upper left) Hatched area represents region where species has a light chin, (upper right) hatched area represents region where species has a dark belly, (lower left) stippled area represents region where species occurs at high elevations and is active at the surface in the summer; (lower right) geographic variation in the modal number of trunk vertebrae.

is compared with *P. r. richmondi* from the Ridge and Valley Province of Virginia. Mottled-bellied *P. richmondi* occur in other parts of the range, but nowhere else is the chin so heavily mottled with white as in the Ridge and Valley Province.

The number and size of the white ventral spots is noticeably greater in Ohio and northern Kentucky populations than in the rest, except for the Ridge and Valley populations which also show much greater contrast between the amount of mottling on the belly and chin. Ontogenetic and individual variation in the amount of belly mottling is so great that it is difficult to measure its geographic variation quantitatively. Further evaluation is warranted.

GEOGRAPHIC VARIATION IN HABITS AND HABITAT REQUIREMENTS. Brooks' (1948) study of the ecological distribution of *P. r. nettingi* shows it to be restricted to spruce forests at high elevations in the Cheat Mountains. The lowest altitudinal record is 3550 feet. *P. r. hubrichti* is also a high altitude form, the elevation at its type locality is 3160 feet. In the southern part of its range—southwestern Virginia, northwestern North Carolina, and northeastern Tennessee—most specimens of *P. r. richmondi* have been collected at high elevations, although the apparent abundance at high altitudes may be due merely to more collecting in mountainous areas. Most records from other regions are from ravine habitats at low elevations.

Few *P. r. richmondi* are recorded for the summer months, except from the mountains in the southern part of the range. Apparently over much of its range this form is not active on the surface in summer. Near the town of Bedford Valley, Bedford County, Pennsylvania, 9 series of *P. glutinosus* and *P. richmondi* were collected each month of the year except during the hibernation period. Table 8 illustrates the relative seasonal abundance of the two species at this locality. Although *glutinosus* was abundant during the entire activity period, *richmondi* was taken infrequently in summer.

TABLE 8. Relative seasonal abundance of *P. glutinosus* and *P. richmondi* at a locality 2.8 miles south, 0.9 miles west of Bedford Valley, Bedford County, Pennsylvania.

Date	Number of <i>P. glutinosus</i>	Number of <i>P. richmondi</i>
27 April, 1957	44	2
25 May, 1958	81	22
14 June, 1958	59	3
19 June, 1959	4	1
8 July, 1959	18	1
3 August, 1958	68	4
1 September, 1959	65	3
21 September, 1958	151	32
25 October, 1958	32	11

*P. r. nettingi* is active during the summer. Little is known about the habits of *hubrichti*. A clinal change in summer activity is apparent from the high-altitude spruce-forest populations (*P. r. nettingi*) to the low-altitude ravine-inhabiting northern *P. r. richmondi*. Southern *P. r. richmondi* are more like *nettingi* in this respect than they are to northern *P. r. richmondi*. This cline corresponds to the variation in the



two geographically variable morphological characters. Number of trunk vertebrae is lowest in *P. r. nettingi* and highest in some northern *P. r. richmondi*. *P. r. hubrichti* and southern *P. r. richmondi* are intermediate. *P. r. nettingi*, *hubrichti*, and southern *P. r. richmondi* have dark bellies, while northern *P. r. richmondi* have mottling on the belly.

It is clear that *nettingi* is most closely related to *hubrichti*, and that *hubrichti* is related to the 21-vertebrae populations of *P. r. richmondi* in the southern part of the range. All three have almost identical belly pigmentation. The dorsal patterns of *nettingi* and southern *P. r. richmondi* are similar, but *hubrichti* has abundant brassy flecking. To recognize *nettingi* and *hubrichti* as full species because of their apparent reproductive isolation from distantly related but sympatric populations of the same stock, would ignore the close morphological similarity and actual morphological overlap in the only characters that differentiate *nettingi*, *hubrichti*, and southern *richmondi*. *P. r. nettingi* and *hubrichti* may be regarded as relict mountain populations surrounded by more specialized derivatives of the same parental stock. *P. r. richmondi* is considered more specialized because of its more elongated body.

Of great interest would be a study of the ecological relationships of *P. richmondi* in the Cheat Mountains of West Virginia and between the James and Roanoke Rivers in the Blue Ridge Mountains where the ends of the *richmondi* Rassenkreis overlap. Reproductive isolation may be established, as no hybrids between *P. r. richmondi* and either *P. r. nettingi* or *P. r. hubrichti* have been found. Records show that *P. r. richmondi* occurs in adjacent areas to the east, west, and north of the Cheat Mountains in West Virginia.

*P. r. richmondi* is recorded from Mills Gap, 2400 feet, on the crest of the Blue Ridge, Bedford-Botetourt County line, Virginia, only 8 miles west of the type locality of *P. r. hubrichti*. Grobman (1949:135) has recorded *P. r. richmondi* from Natural Bridge, Rockbridge County, Virginia, 9½ miles north of the type locality of *P. r. hubrichti*.

I collected eggs and newly hatched young of *P. r. nettingi* near the headwaters of Condon Run on Bickle's Knob, Randolph County, West Virginia, and incubated more than 100 embryos in the laboratory. The dorsum has reduced melanophore pigment and sparsely distributed red chromatophores. These young *P. r. nettingi* differ from newly hatched unstriped *P. cinereus* from Virginia, Maryland, and New Jersey, for the latter lack red pigment in the stripe region. Young *P. r. richmondi* from Fulton County, Pennsylvania, and Washington

County, Maryland, also have red pigment on the dorsum in life. This may be a retention during ontogeny of red chromatophores similar to those found on newly hatched *P. r. nettingi*. Red pigment also occurs in newly hatched *P. r. hubrichti*. Red is not present on adults of the subspecies *nettingi* and *hubrichti*, but is frequently found on the head and anterior sides of *P. r. richmondi* from Pennsylvania, Virginia, and West Virginia. One specimen from Mingo County, West Virginia, (WVBS 615) may have had some dorsal red spots.

The largest specimens of *P. r. richmondi* examined are from the Ridge and Valley Province of Virginia. Populations with the smallest average adult size are from southwestern Virginia and adjacent North Carolina. *P. r. nettingi* is a small animal. Adult *P. r. hubrichti* are heavy bodied, but short in snout-vent length. Geographic variation in size may be similar to the clinal variation in number of body vertebrae, belly pigmentation, and habits.

#### THE EASTERN LARGE PLETHODONS

This group, as defined by Grobman (1944:266) on the basis of its larger size and fewer costal grooves, includes 6 species that inhabit the eastern United States. *Plethodon glutinosus* is the most widely distributed, and all the other species occur within its range. *P. yonahlossee* occurs in the southern section of the Blue Ridge Province north of the French Broad River. *P. ouachitae*, superficially similar to *yonahlossee*, lives in the Ouachita Mountains of Arkansas and Oklahoma. *P. caddoensis* is known from the Caddo Mountains and adjacent areas of Arkansas. *P. jordani* occurs in the southern section of the Blue Ridge Province and enters the adjacent Piedmont Province in North and South Carolina and the Ridge and Valley Province in Virginia. The range of *P. wehrlei* centers in the unglaciated Allegheny Plateau section of the Appalachian Plateaus Physiographic Province. Two recently described species, *P. dixi* and *P. jacksoni*, are local variants of *P. wehrlei* and are here synonymized with it. Grobman (1944) has analyzed the distributional patterns of the eastern large plethodons.

Much speculation exists on relationships within this section of the genus. Dunn (1926:23) considers it the most primitive group, with *P. yonahlossee* the most primitive form. Dunn as well as Grobman (1944:276) think the relationship between *yonahlossee* and *wehrlei* close. Hairston and Pope (1948:276-7) suggest that *yonahlossee* is closely related to *jordani* and that the similarity between some *jordani* and *glutinosus* may be due to parallel evolution. Others think the closest relative of *jordani* is *glutinosus*. Bishop (1941b:19) considers

one geographic race (*P. j. shermani*) a subspecies of *glutinosus* rather than of *jordani*. Grobman (1944) thought that *jordani* and closely related forms (then considered full species, but now known to be conspecific with *jordani*) are different enough to warrant separation as the metcalfi group, distinct from all other eastern large plethodons.

Characters studied in determining the morphological similarities and relationships of these forms include size, number of vomerine teeth, number of costal grooves, degree of sexual dimorphism, and pigmentation. Several characters were found extremely variable and not diagnostic of any one form. For example, Bishop (1941b:18) and Grobman (1944:287) think that those forms now considered *Plethodon jordani* have fewer vomerine teeth than *P. glutinosus*. Comparison of the number of vomerine teeth in large series of each species from several geographic areas (including localities within the ranges of all named subspecies) shows that for a given size, the range of variation is similar, and that greater difference occurs within *glutinosus* than between some populations of *glutinosus* and *jordani* (figs. 39 and 42). As average adult size in some sympatric populations of *glutinosus* and *jordani* differs considerably, the two forms often show a difference in the average number of vomerine teeth. As adults of the same size have a similar average number of vomerine teeth, this character is not definitive. This similarity between the two species probably indicates a close relationship, for the number of vomerine teeth of some of the other eastern large plethodons differs markedly.

Figures 33, 35-37, 39, and 42 illustrate intra- and inter-species differences in the ontogenetic variation in number of vomerine teeth in eastern large plethodons. *P. wehrlei* has the lowest rate of increase in number of vomerine teeth with increasing size, and in this closely resembles some of the eastern small plethodons. The rate is greater in *jordani* and *glutinosus*, and northern samples of *glutinosus* are similar to *jordani*. The highest rates are found in *yonahlossee* and *ouachitae*. In spite of being a small species, *caddoensis* has a high number of vomerine teeth.

Some other supposed differences discussed in the literature are useless in determining relationships of eastern large plethodons. Except for *wehrlei*, all have a similar number of vertebrae (see table 9). Sexual dimorphism in size is present in several forms that have been studied critically, but as females in each average slightly larger than males no species differences exist. The type of lateral pigmentation varies somewhat within each species both individually and geographically, but consistent differences between species are rare. Each species

TABLE 9. Variation in the number of trunk vertebrae in the eastern large plethodons.

Species	Number of trunk vertebrae							Mean
	16	16/17	17	17/18	18	18/19	19	
<i>Plethodon</i>								
<i>wehrlei</i>			16		144	1	5	17.94
<i>yonahlossee</i>			22		2			17.08
<i>ouachitae</i>		1	36					16.99
<i>caddoensis</i>	1		38	2	2			17.05
<i>jordani</i>	41	3	429	1	14			16.94
<i>glutinosus</i>	64	11	855	9	42			16.98

is geographically sympatric and often coexists in the same habitat with one or more of the other species. Each of the sympatric pairs appears to be genetically distinct, with the possible exception of *glutinosus* and *jordani*, and much evidence indicates that different species have different ecological requirements. Preserved specimens that have lost some pigmentation are often extremely difficult to identify because of the morphological similarity among most of these salamanders. Indeed, identification by the field collector familiar with the animals in life is often more valuable than painstaking study of a preserved specimen. The importance of studying these animals in life is readily apparent.

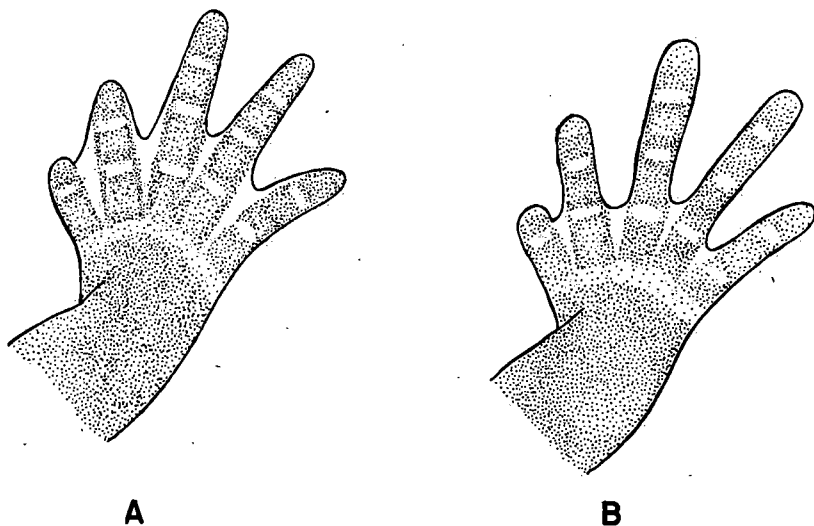


FIGURE 31. Right hind feet of two eastern large plethodons showing variation in amount of webbing on toes. (A) *P. wehrlei*, (B) *P. glutinosus*.

*P. wehrlei* is distinguishable from the rest of the group by having the most webbing on the toes (fig. 31), one more trunk vertebra on the average, a greater development of melanophore pigment in the parietal peritoneum, and the lowest average number of vomerine teeth. *P. yonahlossee*, *P. ouachitae*, and *P. caddoensis* may be recognized by their distinctive color patterns in life. They also differ from the other species in having a larger average number of vomerine teeth. No known character will separate all *glutinosus* and *jordani* consistently. The chin of *glutinosus* is usually darker than that of *jordani*, but not always. The morphological similarity among the forms indicates they are closely related, with only *wehrlei* separated from the others by several characteristics.

The young of *yonahlossee*, some *wehrlei*, and *jordani* from the Great Smoky Mountains and the Nantahala Mountains have dorsal red spots. These usually disappear in *jordani*, and in *wehrlei* too except in the southern part of its range, and become incorporated into the dorsal stripe of *yonahlossee*. No information is available on the very young of *ouachitae*, *caddoensis*, and several geographic populations of *jordani*, but young *ouachitae* may also have red spots (see Pope and Pope, 1951:145). Red dorsal spots are absent in the hatchlings of *P. glutinosus* in Florida (Highton, 1956). Very young specimens from other parts of the range of *glutinosus* also lack red spots. Dunn (1926: 139) records a *glutinosus* from Clayton, Georgia, with tiny paired red dorsal spots, but this may well be a *jordani*, known to occur within 10 miles of Clayton in the Nantahala Mountains. Cope (1889:141) records young specimens of *glutinosus* with red spots from caves in Montgomery County, Virginia, but these were probably *wehrlei*.

Melanophore pigmentation on the chin is less than that on the belly in most species except *P. glutinosus*. Certain populations of *glutinosus* from Texas and the Blue Ridge and Piedmont Provinces south of the Potomac River also have light chins. Most species have dark bellies, but northern populations of *jordani* and southern *wehrlei* are light bellied.

*P. yonahlossee*, and *P. glutinosus* except for its southeastern Coastal Plain populations, attain a larger maximum size than do the other species. *P. caddoensis* is the smallest eastern large plethodon. Individuals of some northern populations of *jordani* are also relatively small.

Red pigment occurs in adult *yonahlossee*, *ouachitae*, *caddoensis*, southern *wehrlei*, and the populations of *jordani* from the Nantahala Mountains and the Great Smoky Mountains. Dorsal iridophores occur abundantly as white spots in most *glutinosus*, *ouachitae*, *caddoensis*,

and *wehrlei*. *P. jordani* from the Snowbird and adjacent mountains of North Carolina have small white spots, while those from Oconee County, South Carolina, have small brassy flecks abundantly scattered on the dorsum. Lateral white iridophores usually are present in all eastern large plethodons except *jordani* in the northern part of its range and southern South Carolina *glutinosus*.

Some *P. caddoensis* and *P. ouachitae* have more toe webbing than is usually present in the glutinosus and yonahlossee groups, thereby resembling *P. wehrlei*. All members of the yonahlossee group average more vomerine teeth than do members of the wehrlei and glutinosus groups. They resemble the glutinosus group in having 17 trunk vertebrae, compared to the 18 of *wehrlei*. It is clear that the glutinosus and yonahlossee groups are more closely related to each other than either is to *wehrlei*, and that *glutinosus* and *wehrlei* are the least closely related.

In summary, *P. wehrlei* is the most distinct species of the eastern large plethodons. The others are morphologically similar to each other. The hypothetical ancestor might have been a moderate-sized animal with a light chin, red dorsal spots, 17 trunk vertebrae, a short vomerine series, and webbed toes. *P. wehrlei* is closest to this hypothetical ancestor, although its body is slightly elongated by the addition of an extra trunk vertebra. The chin is still light in all except some *glutinosus* and a few populations of *jordani*. Red dorsal spots remain only in adult southern *wehrlei* and in the young of several other forms. Large size is attained by *yonahlossee* and *glutinosus*, while dwarfing occurs in *caddoensis* and northern *jordani*. Adult *yonahlossee* have a much longer vomerine series than the others. The suggested phylogenetic relationships are shown in figure 5.

#### WEHRLEI GROUP

##### *Plethodon wehrlei* Fowler and Dunn Wehrle's Salamander

*Plethodon wehrlei* Fowler and Dunn (1917:23-4). Dunn (1926:133-6); Bishop (1941a:232-9); (1943:281-4); Grobman (1944:285-7).

*Plethodon dixi* Pope and Fowler (1949:1-4). Type locality: Dixie Caverns, Roanoke County, Virginia.

*Plethodon jacksoni* Newman (1954:9-14). Type locality: 1 mile east of Blackburg, Montgomery County, Virginia.

*Plethodon wehrlei wehrlei*, Conant (1958:234).

*Plethodon wehrlei dixi*, Conant (1958:234).

**HOLOTYPE.** ANSP 19123, collected in the Two Lick Hills, Indiana County, Pennsylvania, September 1911, by R. W. Wehrle.

**DIAGNOSIS.** An eastern large plethodon with webbing between the toes on the hind foot often extending to the joint between the first and second phalanges (fig. 31), a modal number of 18 trunk vertebrae, and a moderate amount of melanophore pigmentation in the parietal peritoneum.

**DISTRIBUTION.** From Allegany State Park, Cattaraugus County, New York, south in the Allegheny Plateaus section of the Appalachian Plateaus Physiographic Province through western Pennsylvania and West Virginia to southwestern Virginia, where it occurs in the Ridge and Valley, Blue Ridge, and Piedmont Physiographic Provinces (fig. 32). This species also occurs in Monroe and Washington Counties, Ohio (Walker, 1933).

**DESCRIPTION.** The ground color is usually lighter in *wehrlei* than in the other eastern large plethodons; the belly has fewer melanophores. Often large gaps exist between melanophores anteriorly on the belly and chin; yellow iridophores occupy these gaps. Yellow pigment is

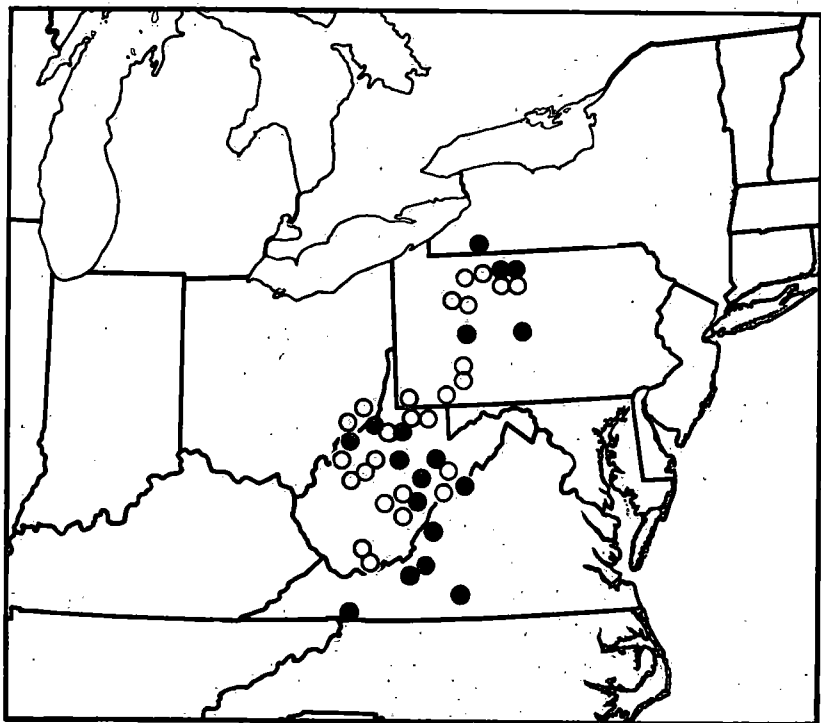


FIGURE 32. Distribution of *P. wehrlei* in the eastern United States.

usually abundant laterally and the yellow often persists in preservatives, unlike that in the other eastern large plethodons. Usually small white iridophore spots occur on the dorsum. In the southern populations numerous brassy flecks occur as well, especially among the red dorsal spots. The red dorsal spots occupy gaps in the melanophore bed. Brassy iridophores are usually present in the iris.

Costal grooves usually number 17, the trunk vertebrae, 18. Vomerine teeth range from 6 to 20 (fig. 33). Moderate in size, the largest specimen examined is 65 mm. in snout-vent length. Sexual maturity is reached between 45 and 50 mm. snout-vent length.

\* \* \* \* \*

*Plethodon wehrlei* inhabits the unglaciated Appalachian Plateaus Physiographic Province in southwestern New York, western Pennsylvania, extreme southeastern Ohio, West Virginia, and adjacent Virginia (where it occurs a short distance outside the Appalachian Plateaus Province). The most distinct of the eastern large plethodons, it appears to occupy an isolated position, differing from the other species in several respects. Webbing on the toes is usually extensive although occasional specimens of other species, particularly *caddoensis* and *ouachitae*, show a similar development. *P. wehrlei* is the only eastern large plethodon that normally has 18 trunk vertebrae; the others usually have 17. *P. wehrlei* has fewer vomerine teeth than any other eastern large plethodon, and it has the greatest development of peritoneal melanophores.

Two populations from southwestern Virginia were described as distinct species by Pope and Fowler (1949) and Newman (1954). *P. dixi* differs from other southern *wehrlei* only in proportions and pigmentation, and occurs only in Dixie Caverns and nearby Blankenship Cave, Roanoke County, Virginia. Differences from adjacent *wehrlei* populations are slight. Certainly *P. dixi* is conspecific with *wehrlei*, and little is gained by retaining this extremely localized population as a named geographic race. One juvenile from Dixie Caverns (UF 8445) had dorsal red spots in life similar to those in other southern *wehrlei*. *P. jacksoni*, named from a population less than 15 miles from the *dixi* locality, differs from other southern *wehrlei* only in retaining the juvenile red spots in the adult. Some adults in West Virginia also retain their red spots (Brooks, 1945). Red dorsal spots are completely absent in juvenile and adult *wehrlei* from New York and Pennsylvania (Bishop, 1941a:238). Geographic differences in the occurrence of red dorsal pigmentation in *wehrlei* are significant and clinal. Detailed data



on the nature of the cline are not available. I have examined living specimens from Cattaraugus County, New York; Lewis, Randolph, and Pendleton Counties, West Virginia; and Alleghany, Roanoke, and Montgomery Counties, Virginia. Populations from each of these localities show striking differences in pigmentation and local variation is marked.

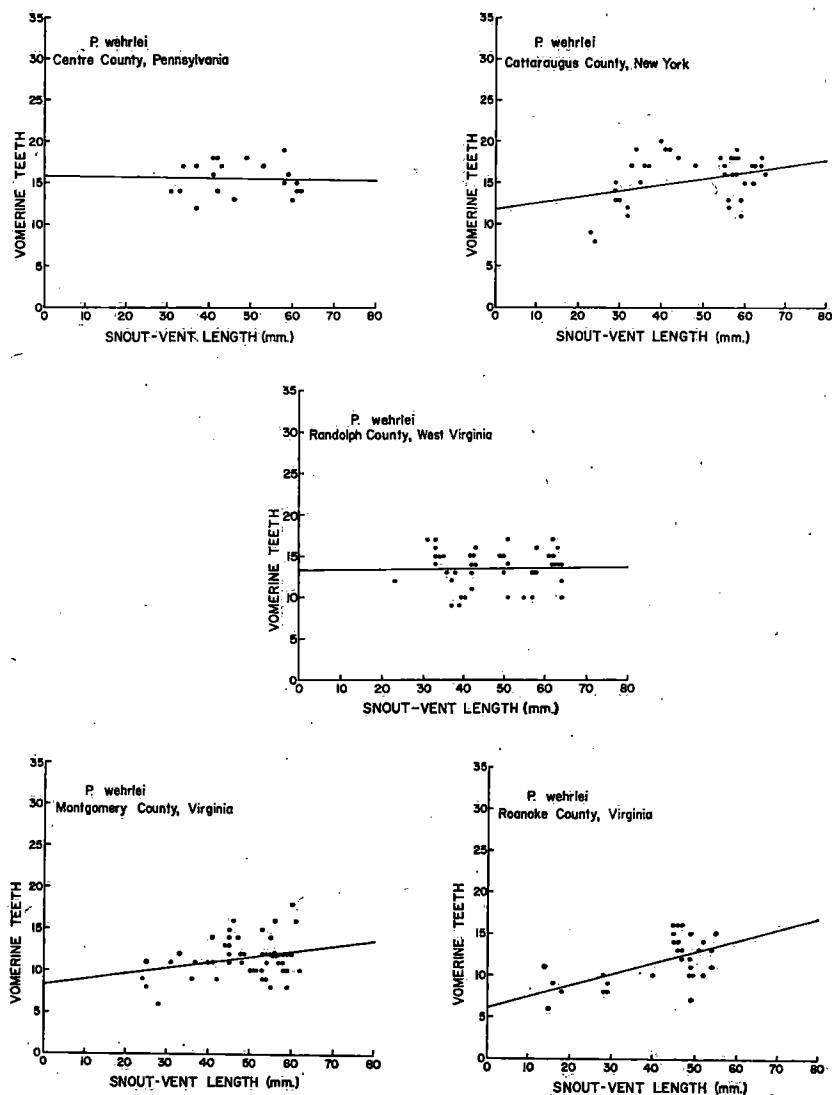


FIGURE 33. Variation in the number of vomerine teeth in 5 geographic samples of *P. wehrlei*.

Netting (1936:91) compares West Virginia *P. wehrlei* with topotypic Pennsylvania specimens. The former have white spotting on the throat and chest which the latter lack. Lateral white pigment is also more abundant in West Virginia material. Grobman (1944:287) suggests that southern *wehrlei* may grow larger than northern ones.

Two erroneous literature records of *wehrlei* are based on specimens of *glutinosus*. One (CNHM 57029) is from the Blue Ridge Province of Virginia (Grobman, 1949:136), the other (CU 4132) is from Mercer County, Pennsylvania (Lachner, 1942).

A specimen (CNHM 60010) from White Top Mountain, Virginia, typical of southern *wehrlei*, has 18 costal grooves, webbed toes, dorsal red spots, pigmented parietal peritoneum, and reduced melanophore pigmentation anteriorly on the belly. It is the southernmost record of *wehrlei* and is the only record of the sympatric occurrence of this species with *yonahlossee*. Newman (1954:13) refers a specimen (USNM 143219) from Smith Mountain Gorge, Pittsylvania County, Virginia, in the Piedmont Physiographic Province, to *P. jacksoni*. It is a typical southern *wehrlei*. Apparently this species is not plentiful in the southern part of its range.

#### YONAHLOSSEE GROUP

##### *Plethodon yonahlossee* Dunn Yonahlossee Salamander

*Plethodon glutinosus*, Brimley (1912:137-8, part).

*Plethodon yonahlossee* Dunn (1917:598-603). Dunn (1926:129-33); Bishop (1943:287-90); Grobman (1944:287); Pope (1950:79-106).

**HOLOTYPE.** AMNH 4634, collected near the Yonahlossee Road, about 1½ miles from Linville, Avery County, North Carolina, at an altitude of 4200 feet, 16 August 1916, by E. R. Dunn and W. S. Nevin.

**DIAGNOSIS.** A large species with paired dorsal red spots in the young and a dorsal chestnut-colored stripe in the adult. Iridophores are lacking in the region of the dorsal stripe, but are concentrated on the sides to form a white or light gray lateral stripe.

**DISTRIBUTION.** Northeast of the French Broad River in the Blue Ridge Province of North Carolina, Tennessee, and southeastern Virginia (fig. 34). Pope (1950:82) indicates this species has never been found east of the New River in Virginia, but more recently, Newman (1954:13) reports it from Kibler Park, Patrick County, Virginia. Possibly it may occur farther north in Floyd and Franklin Counties.

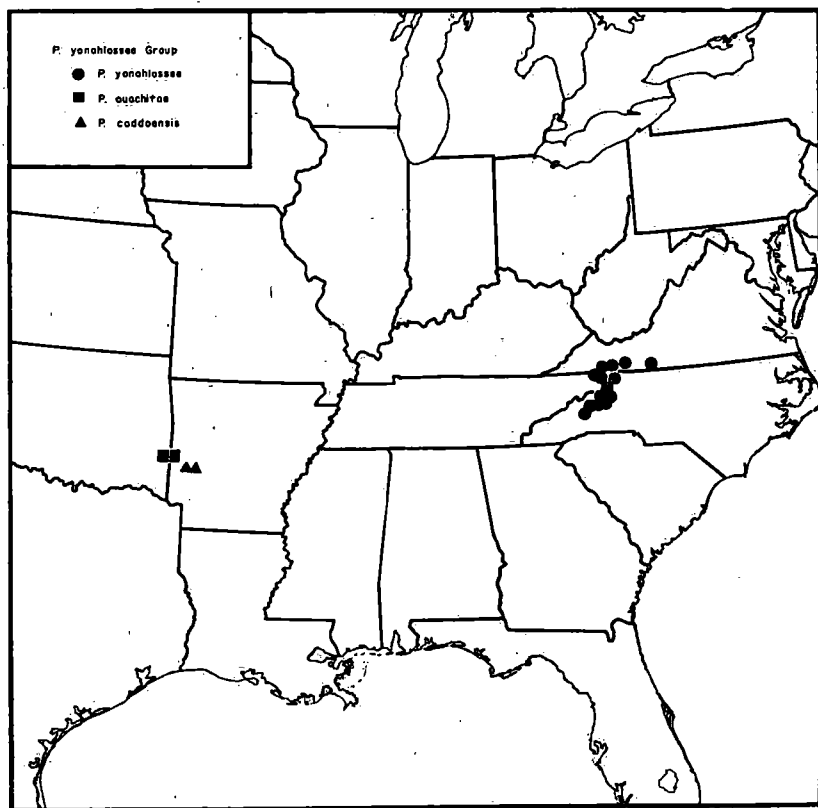


FIGURE 34. Distribution of the species of the yonahlossee group in the eastern United States.

**DESCRIPTION.** The belly is black with few to many small white spots. The throat is usually light. The dorsal chestnut-colored stripe results from a mixture of red and black pigment. The red pigment appears similar to that found in other plethodons. Dorsal melanophores are concentrated around the mucous glands in the skin. The young have paired dorsal red spots that are often visible after several years of preservation, unlike the chestnut band of the adults, owing to the melanophore-free spot that remains. When the red pigment of the adult disappears in preservative the animal appears uniformly black. Occasional specimens have reduced red pigment on the dorsum in life, and Pope (1950:97) reports one specimen that lacks red pigment completely. Lateral iridophores are so numerous that they form a light gray or white lateral stripe in most individuals.

Costal grooves usually number 16, trunk vertebrae, 17. Vomerine teeth range from 12 to 43 (Pope, 1950:103), the largest number in the genus (fig. 35). The largest specimen Pope (1950) records is a female, 85 mm. in snout-vent length. Sexual maturity is apparently reached between 55 and 65 mm. snout-vent length.

*Plethodon ouachitae* Dunn and Heinze  
Rich Mountain Salamander

*Plethodon ouachitae* Dunn and Heinze (1933:121-2). Bishop (1943:269-72); Grobman (1944:285); Pope and Pope (1951:129-52).

HOLOTYPE. USNM 92484, adult male, collected on the north side of Rich Mountain, Polk County, Arkansas, 30 May 1933, by Albert A. Heinze and Dorothy A. Boyer.

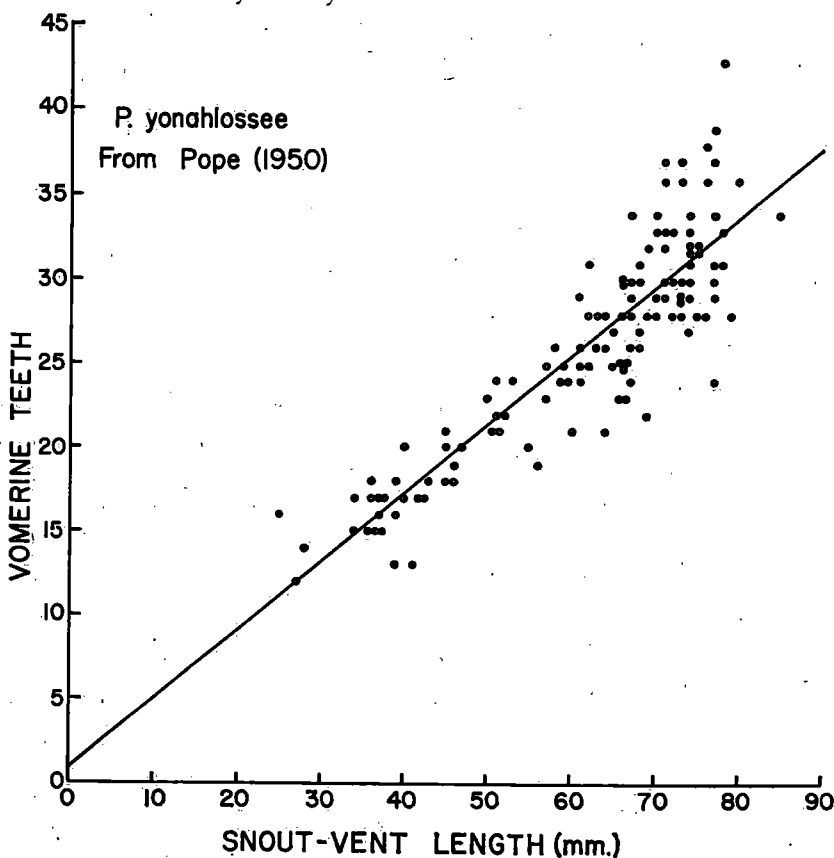


FIGURE 35. Variation in the number of vomerine teeth of *P. yonahlossee*. Data from Pope (1950).

**DIAGNOSIS.** A moderate-sized species with a dorsal chestnut-colored stripe as in *yonahlossee*, but with numerous white spots and brassy flecks on the back. The lateral stripe is often yellow, in *yonahlossee* it is usually white or light gray.

**DESCRIPTION.** Known only from Rich Mountain in Polk County, Arkansas, and LeFlore County, Oklahoma (fig. 34). Dundee (1947: 118) reports it from McCurtain County, Oklahoma, but Pope and Pope (1951:134) believe this record is based on an undescribed form, not *ouachitae*.

**DESCRIPTION.** Pope and Pope (1951) describe variation in more than a hundred individuals. Having examined only three living specimens, I give their data for the frequency of occurrence of pigmentation characters.

The belly is dark. Melanophore pigmentation on the chin ranges from heavy in a few specimens to little or none in 27 percent. Of the Popes' specimens, 93 percent have yellow or white spots on the chin and more than half have spots on the belly. Lateral white or yellow pigment is so heavy that in 85 percent it forms a continuous stripe. On the back, black pigment is concentrated around the glands of the skin, as in *yonahlossee*. Red pigment is distributed uniformly between these glands. Two kinds of iridophores—small white spots ("white speckling" of Pope and Pope), and smaller brassy flecks ("frosting")—are also present. White spotting is absent in 2 percent of their specimens and brassy flecks in 19 percent. Variation in the abundance of both types of iridophores and in the amount of red on the dorsum is considerable. In 21 percent of their specimens the back was essentially black, not chestnut. A 26-mm. juvenile showed two rows of faintly pink spots on the back after preservation, indicating that juveniles probably have dorsal red spots as do the young of several other eastern large plethodons.

Costal grooves usually number 16, trunk vertebrae, 17. Vomerine teeth range from 9 to 30 (fig. 36). The largest specimen, a female, is 67 mm. in snout-vent length. Sexual maturity is reached between 45 and 55 mm. snout-vent length.

*Plethodon caddoensis* Pope and Pope  
Caddo Mountain Salamander

*Plethodon ouachitae*, Grobman (1944:285, *part*).

*Plethodon caddoensis* Pope and Pope (1951:148).

**HOLOTYPE.** CNHM 61959, a female collected at an altitude of 1200

feet on Polk Creek Mountain, Montgomery County, Arkansas, by Sarah H. Pope, 9 May 1950.

**DIAGNOSIS.** A small species with melanophore pigmentation almost entirely absent on the chin and venter anterior to the forelegs. Dorsal spots are larger and more numerous than in *glutinosus*. Vomerine teeth are more numerous than in any other plethodon in its size range except *ouachitae*. The toes are slightly webbed at the base.

**DISTRIBUTION.** Known from the Caddo Mountains of southern Montgomery County and southeastern Polk County, Arkansas. Reported by Blair (1957) from the south side of Poteau Mountain, near Oliver, Scott County, Arkansas (fig. 34).

**DESCRIPTION.** I have examined only 2 living specimens, both from Bard Spring Recreation Area, Polk County, Arkansas. The belly is dark, but anteriorly with large melanophore-free spots occupied by white iridophores. The chin is almost completely devoid of melanophores and iridophores. Large white spots and smaller brassy flecks are scattered over the back, but the latter are most numerous in and around the white spots. One individual has a little red on the dorsum, much as in *ouachitae* and *yonahlossee*. White pigment is abundant on the sides.

Costal grooves usually number 16, trunk vertebrae, 17. Vomerine teeth range from 15 to 25 (fig. 37). The largest of 46 specimens examined is 52 mm. in snout-vent length. Sexual maturity is reached at about 40 mm. snout-vent length.

\* \* \* \* \*

Most previous workers have considered the *yonahlossee* group closely related to *P. wehrlei*, and Grobman (1944:276) suggests that *yonahlossee* and *wehrlei* may eventually be proved conspecific. I think the *yonahlossee* group is more closely related to the *glutinosus* group than either is to the *wehrlei* group. The species in the *yonahlossee* group—*yonahlossee*, *ouachitae*, and *caddoensis*—differ from the *glutinosus* group mainly in pigmentation and in having more vomerine teeth. No other differentiating characters are known, although size and some other characters vary considerably within each group.

Gaps between the ranges of the species of the *yonahlossee* group suggest that the prototype was once widely distributed in the eastern United States, and subsequent environmental changes isolated the three forms. In external appearance *yonahlossee* is similar to *ouachitae*. *P. caddoensis*, though occupying an area adjacent to *ouachitae*, differs from it conspicuously. This suggests that the two forms,

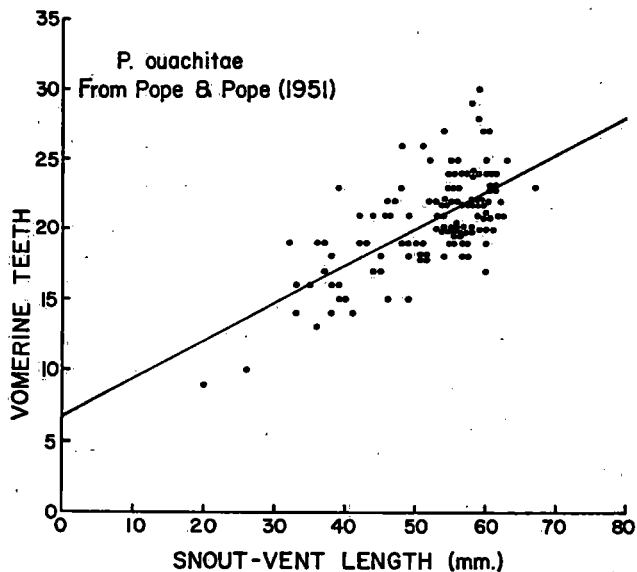


FIGURE 36. Variation in the number of vomerine teeth of *P. ouachitae*. Data from Pope and Pope (1951).

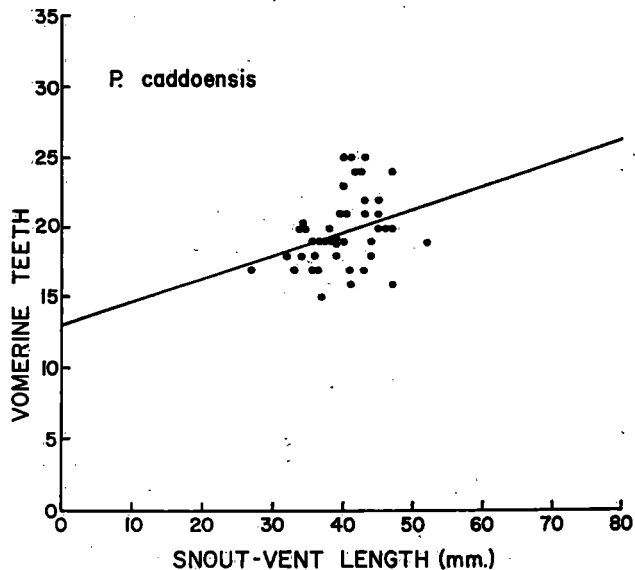


FIGURE 37. Variation in the number of vomerine teeth of *P. caddoensis*.

*ouachitae* and *caddoensis*, have been differentiating from one another for a long time. Pope and Pope (1951) suggest that two additional undescribed forms of this group occur in Oklahoma and Arkansas.

*P. yonahlossee* is most abundant at intermediate altitudes in the southern Appalachians, being rare or absent in the high altitude spruce-fir forests and below 2500 feet (Pope, 1950:81). In Arkansas and Oklahoma, *ouachitae* is known from 1700 to 2800 feet on Rich Mountain; *caddoensis* occurs from 950 to 1200 feet. Both *ouachitae* and *yonahlossee* are abundant in some places where *glutinosus* occurs. As they are able to coexist under some conditions, competition with *glutinosus* is apparently not the sole factor responsible for the absence of the yonahlossee group at low altitudes in the eastern United States. Possibly high temperatures at low elevations restrict them, but too little is known of their life history, physiology, and ecological requirements to further speculate on limiting factors. Knowledge of the three species in this group is summarized by Pope (1950) and Pope and Pope (1951). Little new information on their variation, ecology, and life history has been presented in the last 10 years.

Grobman (1944:278) discusses the relationship between *ouachitae* and *yonahlossee* and suggests the need for morphological and experimental studies to determine whether they should be considered separate species, subspecies, or undifferentiated populations. The Popes have demonstrated that these forms differ in size at maturity, and in maximum size, pigmentation, and number of vomerine teeth, although overlap in the last two characters exists. Consequently, they certainly are not undifferentiated populations of the same species. Pope and Pope (1951:149) suggest that the relationship between *caddoensis* and *ouachitae* may be subspecific. As differences in size and color pattern are greater than usually found between adjacent geographic populations of a single species of *Plethodon*, I consider them separate species.

#### GLUTINOSUS GROUP

##### *Plethodon jordani* Blatchley Jordan's Salamander

*Ambystoma jeffersonianum*, Rhoads (1895:402-3).

*Plethodon jordani* Blatchley (1901:762). Dunn (1926:145-6); Bishop (1943:261-4); Grobman (1944:294).

*Plethodon shermani* Stejneger (1906:559-62). Type locality: Wayah Bald, Macon County, North Carolina. Dunn (1926:146-8); Grobman (1944:294-6).



*Plethodon metcalfi* Brimley (1912:138-9). Type locality: Sunburst, Haywood County, North Carolina. Dunn (1926:148-51); Bishop (1943:264-6); Grobman (1944:289-92).

*Plethodon clemsonae* Brimley (1927:73-5). Type locality: Jocassee, Oconee County, South Carolina. Bishop (1941b:20), (1943:239-42); Grobman (1944:293-4).

*Plethodon glutinosus*, Bailey (1937:3-4, *part*).

*Plethodon glutinosus shermani*, Bishop (1941b:18-9), (1943:253-6).

*Plethodon shermani rabunensis* Pope and Hairston (1948:106-7). Type locality: Rabun Bald, Rabun County, Georgia. Hairston and Pope (1948:274-5).

*Plethodon shermani shermani*, Pope and Hairston (1948:106-7).

*Plethodon shermani melaventris* Pope and Hairston (1948:107). Type locality: Highlands, Macon County, North Carolina. Hairston and Pope (1948:274-5).

*Plethodon metcalfi metcalfi*, Mittleman (1948:418).

*Plethodon metcalfi clemsonae*, Mittleman (1948:418).

*Plethodon shermani clemsonae*, Hairston and Pope (1948:274-5).

*Plethodon jordani jordani*, Hairston (1950:271).

*Plethodon jordani metcalfi*, Hairston (1950:271).

*Plethodon jordani shermani*, Hairston (1950:271).

*Plethodon jordani clemsonae*, Hairston (1950:272); Schwartz (1957:94-107).

*Plethodon jordani rabunensis*, Hairston (1950:272).

*Plethodon jordani melaventris*, Hairston (1950:272).

*Plethodon jordani teyahalee* Hairston (1950:269-70). Type locality: Teyahalee Bald, Graham-Cherokee County line, North Carolina.

**HOLOTYPE.** Dunn (1926:145) states that the type specimen was originally in the collection of W. S. Blatchley, but that it has been destroyed. It was collected between 3000 and 5000 feet on the slope of Mt. Collins or Indian Pass, Sevier County, Tennessee, by L. E. Daniels.

**DIAGNOSIS.** An eastern large plethodon with 17 trunk vertebrae, no dorsal red pigment except in young specimens from the Nantahala and Great Smoky Mountains, and white spots lacking on the dorsum except in examples from the Tusquitee, Snowbird, and Cheoah Mountains, where the spots are small.

**DISTRIBUTION.** The southern Blue Ridge Province from northeastern Georgia to Mt. Rogers, Virginia. Also recorded from Tazewell, Bland, and Giles Counties in the Ridge and Valley Province of Virginia, and in the Piedmont Province from Burke County, North Carolina, and Greenville, Pickens, and Oconee Counties, South Carolina (fig. 38).

**DESCRIPTION.** This variable species was previously divided into seven geographic races, but none is recognized here. The variable characters are discussed below. Refer to the maps (fig. 40) for data on pigmentation at any given locality.

Costal grooves usually number 16, trunk vertebrae, 17. Vomerine teeth range from 6 to 30 (fig. 39). Size is geographically variable; the

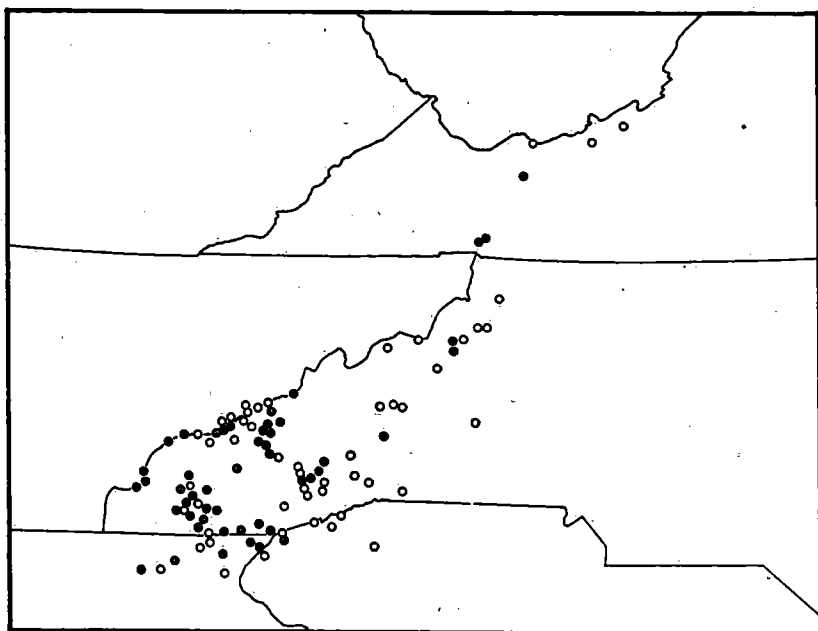


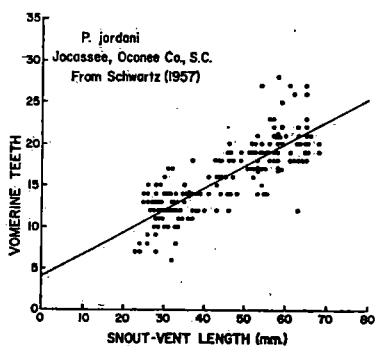
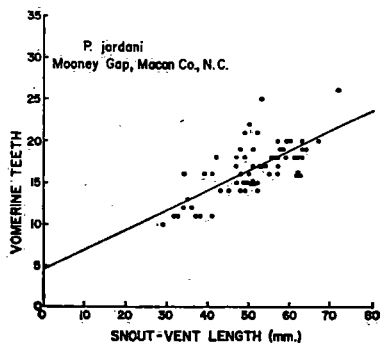
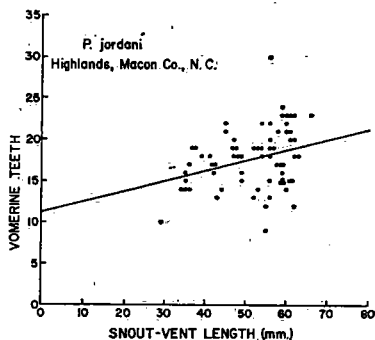
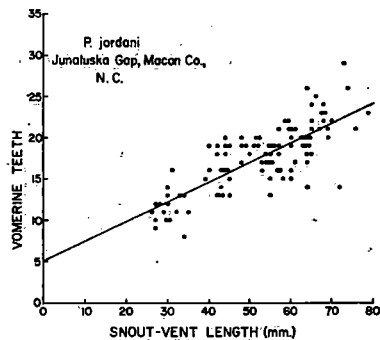
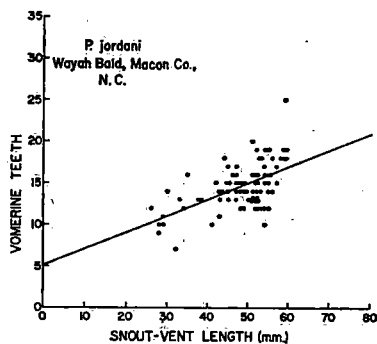
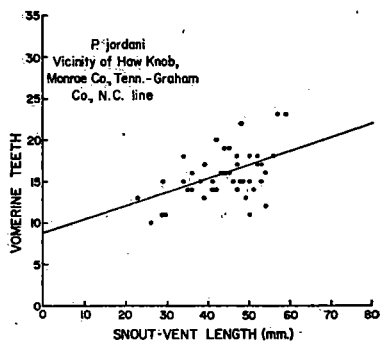
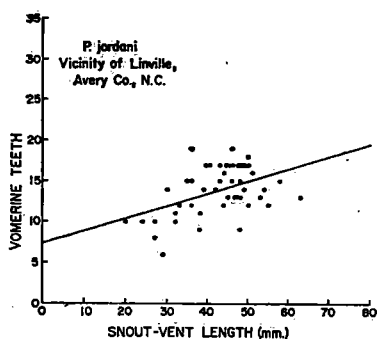
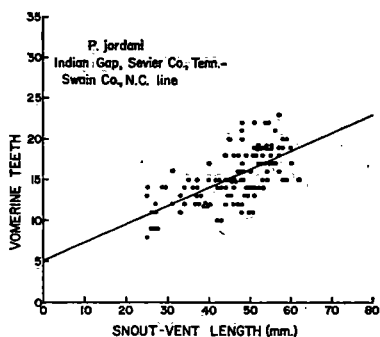
FIGURE 38. Distribution of *P. jordani* in the southern Appalachian Mountains. Living specimens were examined from localities represented by solid symbols. Hollow symbols represent localities of museum specimens and literature records.

maximum snout-vent length of the northern light-bellied populations is 66 mm. (UF 8121, from Heintooga Ridge, Swain County, North Carolina), and of the southern dark-bellied populations is 82 mm. (ChM 56.117.6, from Jack Gap, Brasstown Bald, Union-Towns County line, Georgia). Sexual maturity is reached between 40 and 60 mm. snout-vent length, and this also apparently varies geographically; maturity is reached at a smaller size in the north than in the south.

\* \* \* \* \*

In 1901, Blatchley described a red-cheeked salamander from the Great Smoky Mountains as *Plethodon jordani*. During the next three decades, three additional related forms were described by Stejneger (1906) and Brimley (1912, 1927) as separate species, although each was obviously closely related to *jordani* and inhabited an adjacent region. Both Dunn (1926:146, 151) and Grobman (1944:289) comment on the close relationship of these forms and suggest that inter-

FIGURE 39. Variation in the number of vomerine teeth in 8 geographic samples of *P. jordani*. Data for the sample from Jocassee, Oconee County, South Carolina are from Schwartz (1957).



grades between them might eventually be found. Brimley (1928:23) also recognizes their close relationship and mentions that "they hardly seem distinct enough to be full species." Studies by Hairston and Pope (1948), Pope and Hairston (1948), and Hairston (1950) added three new geographic races to the group and demonstrated that intergradation occurs between several adjacent forms. In 1950 Hairston recognized seven subspecies of *jordani*. Another supposed member of this group, *P. kentucki*, was described by Mittleman as a full species in 1951. It was later listed as a subspecies of *jordani* by Schmidt in 1953, but Clay, Case, and Cunningham (1955) show that the *kentucki* material is actually *P. glutinosus*.

Many gaps remain in our knowledge of the distribution and relationships of populations of *P. jordani*. I spent several weeks collecting in the southern Appalachian Mountains during the summer of 1955 and made a special effort to obtain this species from critical areas. These and a large number of *P. jordani* in the University of Florida Collections demonstrate the close relationship between some populations of *jordani* and *glutinosus*, and provide much information on geographic variation. This species formerly was believed restricted to the southern section of the Blue Ridge Province, but recent collecting indicates it has a more extensive range (Hoffman and Kleinpeter, 1948; Hoffman and Hubricht, 1954).

Important geographically variable characters include intensity of melanophore pigmentation of the belly, presence and distribution of red on the body, presence of dorsal brassy flecking, and presence and abundance of lateral and dorsal white spotting. I have considered the geographic variation in each of these characteristics separately for the entire species's range without regard for boundaries of previously named subspecies.

I made detailed descriptions of pigmentation in life on specimens collected in 1955, and re-examined the entire collection critically after preservation. Living specimens were examined from localities indicated by solid symbols in figure 38.

**GEOGRAPHIC VARIATION IN BELLY PIGMENTATION.** Variation in the intensity of the melanophore pigmentation on the belly is regarded by Bailey (1937), Gröbman (1944), Hairston and Pope (1948), and Hairston (1950) as important in the analysis of riation in *jordani*. They regard the subspecies *jordani*, *melaventris*, *clemsonae*, *rabunensis*, and *teyahalee* as dark-bellied races, *metcalfi* and *shermani* as light-bellied.

TABLE 10. Intensity of ventral melanophore pigmentation of freshly preserved samples of *P. jordani*, based on readings taken with the color atlas of Villalobos and Villalobos (1947). Low readings indicate dark bellies and high readings indicate light bellies. Only sexually mature individuals are included in order to minimize ontogenetic variation.

Sample	Grayness Readings														Mean
	5	6	7	8	9	10	11	12	13	14					
White Top Mt., Grayson Co., Va.					3	1	1							9.6	
Northeast of French Broad River, N.C.				1 2	5	4	4	1						9.6	
Crest of Balsam Mountains (be- tween Beech Gap and Mt. Pisgah), Haywood and Transylvania Cos., N.C.				1 5	5	7	1	1						9.3	
Max Patch Mountain, Haywood Co., N.C.					1	1	1							10.0	
Cowee Bald, Macon and Jackson Cos., N.C.					1								2	12.3	
Soco Gap and Heintooga Ridge, Swain Co., N.C.				1 1	3	3	2				1			9.7	
Chiltoskie Ridge, Swain Co., N.C.					1	1	2							9.3	
Spruce Mountain, Haywood Co., N.C.				2 2	1									7.8	
Mt. Sterling, Haywood, Co., N.C.				1 5	2	2								8.5	
Indian Gap, Sevier Co., Tenn. and Swain Co., N.C.		3	16	19 22	19	7	2	1						8.8	
Spence Field, Blount Co., Tenn.					1	1	2	1	2	1			1	11.6	
Gregory Bald, Blount Co., Tenn.				1	3	2	1	2	1					10.3	
Unicoi Mountains, Monroe Co., Tenn. and Graham Co., N.C.		1	2	5		2			1	1				8.8	
Tellico Gap, Macon Co., N.C.				1										6.0	
Wayah Bald, Macon Co., N.C.					2	1		2						9.4	
Black Gap, Macon and Clay Cos., N.C.					1	4	4	1						9.5	
Mooney Gap, Macon Co., N.C.					2	3	2	1	1					9.6	
Highlands, Macon Co., N.C.	12	25	6	3										6.0	
Rabun Bald, Rabun Co., Ga.			5	5	2									6.8	
Teyahalee Bald, Cherokee and Graham Cos., N.C.			2	2										6.5	
Junaluska Gap, Macon Co., N.C.			1	1	4									7.5	

To study the ventral pigmentation objectively, I compared the bellies of freshly preserved material with a standard color guide (Villalobos and Villalobos, 1947). As immatures of all forms are lighter-bellied than adults, variation is analyzed only in mature individuals. Table 10 summarizes the data on individual and geographic

variation in this character. Much variation exists within most populations, but with the exception of those from the Great Smoky Mountains, populations previously considered dark bellied have much darker bellies than the light-bellied races. The Great Smoky Mountain populations have an average belly pigmentation well within the range of the two light-bellied races. So do two other populations not previously studied. One of these occurs in the northern Cowee Mountains, North Carolina, a range flanked by the Nantahala and Balsam Mountains inhabited by light-bellied populations. The other occurs in the Unicoi Mountains along the North Carolina-Tennessee state line southwest of the Little Tennessee River.

The distinction between populations with light and dark bellies is not absolute, but is only an average difference detectable by examining series preserved in the same manner. Living specimens cannot be compared with freshly preserved specimens. Additional color change probably occurs, depending on type of preservative and exposure to light, after years of preservation.

Ten living specimens from Grandfather Mountain, Avery County, and 10 more from Highlands, Macon County, North Carolina, were divided into groups of 5 each and placed in 4 quart jars with moistened paper toweling. Two jars containing 5 specimens from Grandfather Mountain and Highlands, respectively, were placed in a light-proof box. The other two jars were placed outside the box and exposed to constant light for 8 days. At the end of this period the intensity of ventral pigmentation of the four groups had not changed detectably. In a similar experiment, Grobman (1950) found the light and dark belly pigmentation of different races of *Desmognathus fuscus* changed.

Any boundary between light-bellied and dark-bellied populations is an arbitrary one that can be drawn at different places depending on what intensity of ventral melanophore development is arbitrarily chosen as the point of separation. Indeed, the description of the variation in terms of "light" and "dark" is itself arbitrary, for the variation could just as easily be described in terms of three or more classes, e.g., "light," "medium," and "dark."

If populations averaging 7.5 or less are considered dark bellied and those over 7.5 light bellied (see table 10), most of the southern populations are dark bellied and the northern populations light bellied (fig. 40). Some other point of separation would yield a different distribution, but the trend toward darker belly pigmentation in the southern part of the range of *P. jordani* would still be apparent.

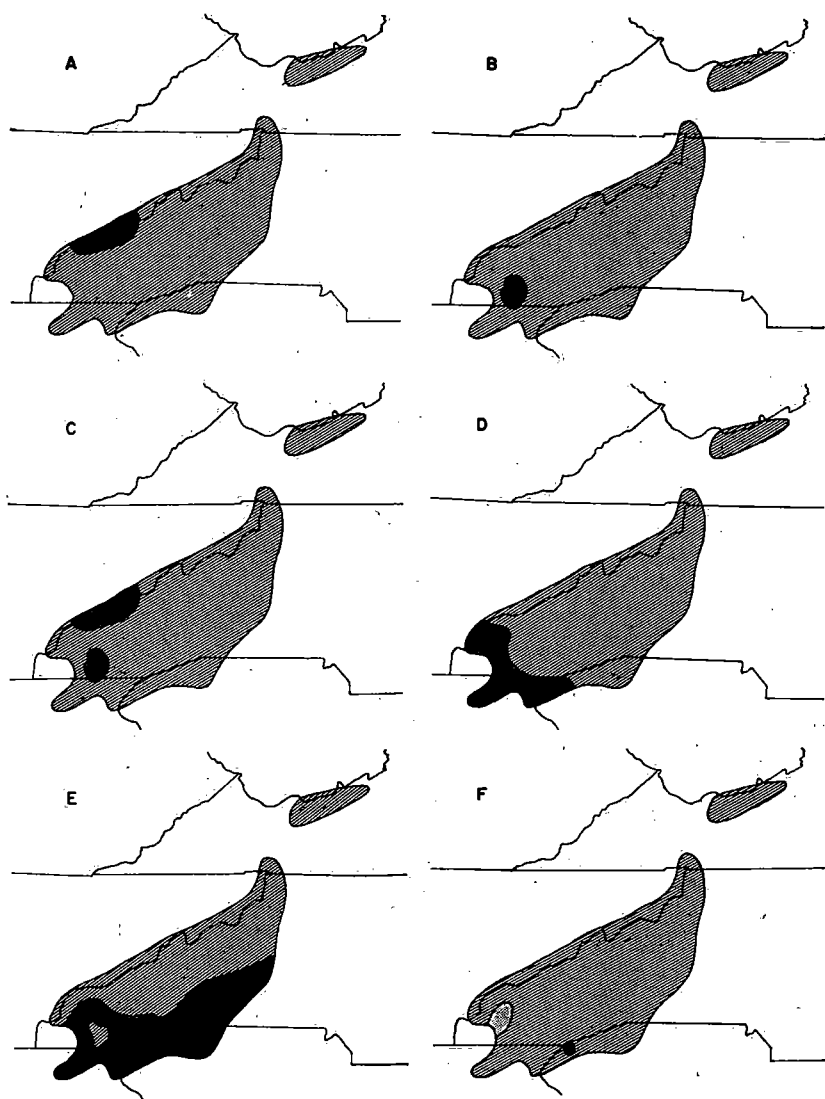


FIGURE 40. Geographic variation in *P. jordani*. Darkened areas represent regions where more than 95 percent have: (A) red cheeks, (B) red legs, (C) dorsal red spots in newly hatched young, (D) lateral white spots, (E) a dark belly, (F) small dorsal brassy flecks. Stippled area in (F) is region where *P. jordani* has small dorsal white spots.

GEOGRAPHIC VARIATION IN PRESENCE OF RED CHROMATOPHORE PIGMENT. Red pigment is present on the cheeks of all *P. jordani* in

most samples from the Great Smoky Mountains, but is absent in most samples from the remainder of the species' range. Young specimens from the Great Smoky Mountains possess paired dorsal red spots and often lack red on the cheeks (Wood, 1947a). The amount of red pigment on the cheeks of *P. jordani* from localities in the Great Smoky Mountains varies considerably, both individually and geographically. Some individuals have red not only on the cheeks but also on the gular region, shoulders, and forelimbs. Others have the red restricted to only the upper half of the cheek. The amount of red pigment is most often reduced in the extreme eastern and western parts of the Great Smoky Mountains, and in the Balsam Mountains, south of the Smokies. In a series of 14 specimens (UF 8141) from Mt. Sterling, Haywood County, North Carolina, 2 lack red cheek pigment, 6 have it greatly reduced, and 6 are similar to specimens from the central part of the Smokies. Dunn (1920:131) reports that 3 of 37 specimens from this locality lack red cheeks. In a series of 33 (UF 8125) from Gregory Bald, near the Little Tennessee River at the opposite end of the Great Smoky Mountain range, all have some red on their cheeks, but 22 (67%) have the amount of red greatly reduced.

King (1939:551) reports that only two of several hundred specimens he examined from the Great Smoky Mountains lack red cheeks. Hairston (1950:263) reports specimens with reduced red cheek pigment from Hyatt Ridge extending south from the vicinity of Mt. Guyot in the main Great Smoky Mountain chain. Material from nearby Hughes Ridge has red cheek pigment. King (1939:553) reports taking red-cheeked *P. jordani* on Hyatt Ridge only a mile from a population lacking red pigment, without any evidence of intergradation, but data now available indicate that red-cheeked populations, intermediates, and populations lacking red occur on Hyatt Ridge.

A similar situation occurs also on the next ridge east, Balsam Mountain. Ten specimens (GSMNP Pj 96 and UF 8150) from Spruce Mountain, 7 miles east of Hyatt Ridge, all have bright red cheeks. Four miles south of Spruce Mountain at Heintooga Ridge, 15 specimens (UF 8121 and 8250) lack red cheeks. At Chiltoskie Ridge, about halfway between these two localities, 6 specimens (UF 8147) are intermediate: 1 has no red, 4 have a reduced amount, and 1 has much red. The zone of intergradation between the two forms appears to be narrow on both Hyatt Ridge and in the Balsam Mountains.

The red-legged populations from the Nantahala Mountains (formerly known as *P. j. shermani*), occur from Tellico Gap south to



about the Georgia state line. More than 99 percent of specimens from this area have extensive red areas on the legs. Rarely a small amount of red is also present on the cheeks. Most red-legged *P. jordani* from the Nantahala Mountains have light bellies, but Hairston (1950:268) reports several dark-bellied series from the periphery of the range. One of these series is from Tellico Gap, in the northern Nantahala Mountains. Hairston postulates that because dark-bellied forms occur to the south and southeast (*P. j. rabunensis*), east (*P. j. melaventris*), and northwest (*P. j. teyahalee*), the dark-bellied populations on the periphery of the range of the red-legged populations may result from intergradation with these adjacent dark-bellied populations. Dark-bellied red-legged populations also occur near the Georgia-North Carolina state line.

Hairston (1950:269) describes a dark-bellied population from Teyahalee Bald in the Snowbird Mountains of Cherokee and Graham Counties, North Carolina, as a subspecies, *P. j. teyahalee*. Comparison of living topotypes (UF 8166 and 8168) from above 4000 feet on Teyahalee Bald with specimens from Tuni Gap and Junaluska Gap in the Tusquitee Mountains of Cherokee, Macon, and Clay Counties, North Carolina, reveals no consistent differences. All possess red spots on the legs, usually so small that they are barely visible. The presence of small white dorsal spots is another similarity (see below). Only one specimen of 99 from Junaluska Gap in the Tusquitee Mountains has as much red on the legs as most Nantahala Mountain populations.

A series of 8 specimens from Cheoah Bald, Graham County, North Carolina, collected along Beech Creek between 32,000 and 38,000 feet, are similar to those from Teyahalee Bald except that only two have red spots on the legs. One of these also has red pigment on the cheeks and upper and lower eyelids. Cheoah Bald is located almost equidistant from the Snowbird, Nantahala, and Great Smoky Mountains.

At high elevations in the Unicoi Mountains along the North Carolina-Tennessee line, in the vicinity of Haw Knob and Johns Knob, a light-bellied population of *P. jordani* was discovered in 1950 by Arnold B. Grobman. This population differs from that on Teyahalee Bald in having a lighter belly and a reduction in the frequency of red spots on the legs. Only 1 of 26 living specimens from the Unicoi Mountains has red pigment on its legs.

Newly hatched young from the Tusquitee, Snowbird, Unicoi, and Cheoah Mountains are not available. Wood (1947b) describes the

pigmentation of young from the Nantahala Mountains as similar to those from the Great Smoky Mountains in having dorsal red spots

GEOGRAPHIC VARIATION IN IRIDOPHORE SPOTTING ON THE DORSUM. Brimley (1927) named a population with dorsal brassy flecking from the vicinity of Jocassee, Oconee County, South Carolina, as *P. clemsonae*. The brassy flecking completely disappears in most preserved specimens. This population differs from nearby populations of *P. jordani* only in the presence of the brassy flecks. Much variation in the amount of brassy flecking exists in the Jocassee population (Schwartz, 1957). As specimens from Highlands, Macon County, North Carolina, also occasionally have this type of flecking. (Gordon, 1960:27), the Jocassee population is certainly conspecific with other *jordani* and it has been so regarded by all workers since Grobman (1944).

Dark-bellied individuals from the Tusquitee, Cheoah, and Snowbird Mountains usually have small white spots on the dorsum, about 0.15 mm. in diameter, and smaller than those of most *glutinosus*. These spots differ from those of Oconee County, South Carolina material both in size and color. Similar spots, sometimes larger in size, occur in a small percentage of *P. jordani* from northern Georgia and from the Unicoi Mountains, but are rarely found in other populations.

GEOGRAPHIC VARIATION IN AMOUNT OF LATERAL PIGMENT. All light-bellied *P. jordani* lack iridophore spotting on the sides except those in the Nantahala and Unicoi Mountains. Dark-bellied animals in the Highlands area (described as *P. j. melaventris* by Pope and Hairston, 1948), also lack this type of pigment. All other dark-bellied ones have much lateral white or yellow pigment. Light-bellied individuals in the Unicoi Mountains have similar lateral iridophore pigmentation, as do some of the red-legged light-bellied *jordani* from the Nantahala Mountains (Hairston and Pope, 1948:269). Lateral iridophores therefore occur in both light- and dark-bellied populations as well as in some that have red pigment. In the original description of *P. j. tayahalee*, Hairston (1950:269) states that the lateral color of specimens from the Snowbird Mountains differs from that of other *P. jordani*. Comparing live specimens from Teyahalee Bald with other lateral white-spotted populations reveals no significant differences in pigmentation. Sometimes the lateral pigment of large specimens is more yellowish than in small ones, but structurally the pigment appears the same.

RACIATION IN *PLETHODON JORDANI*. Figure 40 summarizes geographic variation in the pigmentation characters of *P. jordani*. Formerly 7 subspecies were recognized on the basis of this variation. A combination of characters is needed to diagnose each named race. If only a single character were used, only two races could be recognized, and in some instances the boundary between subspecies would be arbitrary (e.g. light- and dark-bellied races, size of red spots on legs). If one recognizes subspecies on the basis of nonconcordant variation of this type, then all these forms could be considered valid races. Indeed, certain populations as yet unnamed have unique combinations of characters (e.g. light-bellied, without dorsal spots, with lateral spots; red-legged, dark-bellied, without dorsal and lateral spots; red-legged, light-bellied, without dorsal spots, with lateral spots; etc.). Other characteristics of these animals vary geographically, but are more difficult to analyze. These include size, sexual dimorphism in size, altitudinal distribution, ecological occurrence in the same habitat as *glutinosus*, and others mentioned in the papers of Pope and Hairston.

Pigmentation differences among the named subspecies are often great. Rapid change in the frequency of occurrence of a character may be apparent within a few miles.

The boundary between the dark- and light-bellied populations is indicated in figure 40. It is a rather irregular line, and its somewhat arbitrary position depends on which populations are considered dark and which light bellied. The population of Cowee Bald is light bellied, although this mountain range is connected to other high altitude areas only to the south where *jordani* populations are dark bellied. Perhaps the Cowee Mountain populations were connected across the Tuckasegee River valley with the light-bellied Balsam Mountain populations during a cool period when they were able to survive at low altitudes. Perhaps they represent a parallel development.

Populations in the Great Smoky and Nantahala Mountains are obviously closely related. Both have young with similar dorsal red spots (Bailey, 1937:5-6; Wood, 1947a, 1947b). Both have fairly light bellies and red pigment in the adult. Hairston (1950:270) suggests that intergradation across the Little Tennessee River valley may have occurred during the Pleistocene. If the Nantahala populations were derived from the north, intergradation between them and adjacent dark-bellied forms is probably secondary. Change from the light-bellied red-legged form (*P. j. shermani*) to the dark-bellied form with small red spots on the legs and tiny white spots on the dorsum (*P. j. teyahalee*) is abrupt and appears to result from secondary

contact between formerly isolated populations. Contact occurs in the Nantahala River valley, which is elevated enough to support this species. It is in this valley that Bishop (1941b:18-19) found intergrades between the two forms. Bailey (1937:5) also reports intermediate material in the same area, as well as red-legged populations from Tusquitee and Weatherman Balds, west of the Nantahala River.

Hairston and Pope (1948:271) point out that material from the southern Nantahala Mountains (Mooney Gap) is intermediate between the more northern Nantahala Mountain populations and those from Georgia. Martof and Humphries (1955:246) report red-legged specimens from extreme northwestern Rabun County, Georgia.

Pope and Hairston (1948) point out that most specimens from Highlands, Macon County, North Carolina, lack lateral white spotting, while 85 percent of those from Rabun Bald, Rabun County, Georgia, have this type of iridophore spotting. These two localities are only 9 miles apart and they are not isolated by any obvious barriers. To the southwest, populations of large dark-bellied salamanders have even more lateral spotting.

Hairston (1950:267) presents evidence for intergradation between the light- and dark-bellied populations in the southern Balsam Mountains of North Carolina. He compares specimens from the northern and southern slopes of the Balsams in the vicinity of Beech Gap and finds an apparent increase in darkness of the belly from north to south. There is no apparent geographic variation in the unspotted and light-bellied populations that occur from the Balsam Mountains to the northeast into Virginia. These occur throughout the Blue Ridge Mountains at high elevations as far as White Top Mountain and Mt. Rogers, Virginia. Additional localities have also been discovered by Richard L. Hoffman at Burkes Garden (Hoffman and Kleinpeter, 1948:605), and 2 miles southeast of Bluefield, Tazewell County, Virginia (UF 8422), less than 1 mile from the West Virginia line. One specimen from near Mountain Lake, Giles County, Virginia, (AMNH 59214) may represent an artificial introduction but we have taken 4 specimens at Flattop Mountain, 4 miles west of Thassalia, Giles County, Virginia.

The average size in the northern populations is less than that in the southern populations. Hairston and Pope (1948:272) think a more marked sexual dimorphism exists in the amount of snout swelling in males in the northeastern populations. The northern populations are generally restricted to high altitudes, while the southern dark-bellied populations occur at lower elevations. Hairston (1951) presents evi-

dence that some of the southern populations occur in the same habitat as *glutinosus*, but that the northern populations usually replace *glutinosus* altitudinally. His data are based on altitudinal transects taken at a number of localities scattered through the range of *P. jordani*. In the northern part of the range, where *jordani* is light bellied, there is usually little altitudinal overlap between the two species, although considerable difference in replacement altitude may exist even on different sides of the same mountain. Hairston attributes this altitudinal replacement to competition between the species, although he presents no evidence to indicate what type of competition is involved. Two or more species of *Plethodon* are regularly found in the same habitat, but each species seems to have different ecological requirements. Thus the apparent relative abundance of two sympatric species varies from one locality to another, within habitats at one locality, and from season to season. *P. glutinosus* is rare at high elevations in the southern Appalachians, and it can easily be overlooked. I have collected it in the same habitat as the light-bellied and more abundant *jordani* at five high-altitude localities in North Carolina—Soco Gap, Swain-Haywood County line; Cove Creek Gap, Haywood County; Barnett Knob, Swain-Jackson County line; Max Patch Mountain, Haywood-Madison County line; and at Cowee Bald, Macon-Jackson County line. If only a few specimens are collected, *glutinosus* well might be missed.

It is assumed generally that *P. glutinosus* and *P. jordani* are distinct species. Bishop (1941b) thinks he had intergrades between *jordani* (this population was then called *shermani*) and *glutinosus*, but these are now considered intermediates between the Nantahala and Snowbird Mountain populations. At localities mentioned above, as well as at places where Hairston (1951) finds light-bellied *jordani* sympatric with *glutinosus*, the two forms are easily distinguished. There is marked difference in the amount of melanophore pigment on the bellies of the two species; white iridophore pigment is abundant on the sides of *glutinosus* but absent on *jordani*; dorsal white spots are present on *glutinosus* but absent on *jordani*; and adult *glutinosus* are much larger than adult *jordani*. Difficulty in distinguishing these two forms is limited largely to the southwestern part of the range of *jordani* where dark-bellied populations exist. There is overlap in the range of variation of *glutinosus* and dark-bellied *jordani* in every character that easily separates the two in the northern part of the range of *jordani*. Some North Carolina *glutinosus* even have small red spots on the legs like those present on dark-bellied *jordani* in the

Snowbird and Tusquitee Mountains. The latter intergrade with light-bellied red-legged populations of *jordani* in the Nantahala Mountains, so without doubt they are conspecific. But as these dark-bellied populations are practically indistinguishable from the "*glutinosus*" of the Balsam Mountains to the northeast, they may be conspecific with them also. If true, this is another case of a ring of populations with the terminal forms overlapping without intergradation.

It is possible that the light-throated, white-spotted, Blue Ridge and Piedmont populations of *glutinosus* from South Carolina, North Carolina, and Virginia are derived from dark-bellied *jordani*, and that these are not conspecific with *glutinosus* as presently recognized in other parts of its range. No evidence indicates that the white-spotted Blue Ridge *glutinosus* intergrade with any adjacent *glutinosus* populations. They are the most differentiated group of *glutinosus* east of the Mississippi River, if in fact they belong in that species. The relationship between *jordani* and *glutinosus* in the southern Appalachians is now under study by the writer.

*Plethodon glutinosus glutinosus* (Green)  
Slimy Salamander

*Salamandra glutinosa* Green (1818:357).

*Salamandra variolata* Gilliams (1818:460). Type locality: southern states.

Schmidt (1953:34) restricts the type locality to Charleston, South Carolina.

*Salamandra variolata* was described as inhabiting the "southern States," and Gilliams (1818) stated that the specimens on which the description was based were received from the "Florida Party."

*Salamandra cylindracea* Harlan (1825:156-7). Type locality: South Carolina, probably the vicinity of Camden. Schmidt (1953:34) also restricts the type locality of this form to the vicinity of Charleston, South Carolina, but in the original description it is stated that specimens were sent to Harlan by Dr. Blanding of Camden, South Carolina, who collected other herpetological specimens referred to in the same paper in the vicinity of Camden. Camden therefore more likely would be the type locality of *S. cylindracea* than Charleston, South Carolina.

*Plethodon glutinosus*, Tschudi (1838:58); Dunn (1926:136-44); Bishop (1941a: 219-32).

*Triton porphyriticus*, DeKay (1842:pl. 16, fig. 37).

*Plethodon glutinosum*, Gray (1850:39).

*Cylindrosoma glutinosum*, Duméril, Bibron, and Duméril (1854:80-1).

*Salamandra albopunctata* Valenciennes in Duméril, Bibron, and Duméril (1854: 81). *Nomen nudum*. Type locality: Savannah, Georgia.

*Plethodon variolosum*, Duméril, Bibron, and Duméril (1854:83).

*Salamandra elongata* Valenciennes in Duméril, Bibron, and Duméril (1854:84).

*Nomen nudum*. Type locality not designated.

*Salamandra melanoleuca* Wied (1865:130-1). Type locality: Nazareth, Pennsylvania.

*Plethodon glutinosus glutinosus*, Dunn (1920:131); Bishop (1943:250-3); Grobman (1944:278-83).

*Plethodon glutinosus grobmani* Allen and Neill (1949:112). Type locality: Half-mile Creek Swamp, about  $\frac{1}{2}$  mile northeast of Silver Springs, Marion County, Florida.

*Plethodon kentucki* Mittleman (1951:105). Type locality: Big Black Mountain, Harlan County, Kentucky.

*Plethodon glutinosus chlorobryonis* Mittleman (1951:108). Type locality: 13 miles north of New Bern, Craven County, North Carolina.

*Plethodon jordani kentucki*, Schmidt (1953:37).

**HOLOTYPE.** Dunn (1926:138) states the type is not known to exist, but that the type locality is obviously Princeton, New Jersey.

**DIAGNOSIS.** A dark-bellied, dark-chinned, eastern large plethodon with dorsal and lateral iridophore spots and no red pigment.

**DISTRIBUTION.** Southeastern Connecticut and central New York west to central and southern Illinois, south throughout all the states east of the Mississippi River except for southern Florida and the Atlantic Coastal Plain of Long Island, southern New Jersey, southern Maryland, and the Del-Mar-Va peninsula. West of the Mississippi River it occurs in east-central and southern Missouri, northwestern Arkansas, eastern Oklahoma, and eastern Texas (fig. 41).

**DESCRIPTION.** This species varies in several characters. Descriptions of *glutinosus* in the various parts of its range are given in the section on geographic variation. Most populations have large white, light gray, or yellow lateral iridophore spots, and small white or brassy dorsal iridophore spots. The dense melanophore background pigment gives the animal a dark appearance. Brassy pigment usually is distributed sparsely in the iris or may be absent. The belly is dark and in most populations the chin is also. White or yellow iridophore spots are often present on the chin, occasionally also on the belly.

Costal grooves usually number 16, trunk vertebrae, 17. Vomerine teeth range from 7 to 32 (fig. 42). Size varies geographically. The largest peninsular Florida specimen (from Eureka, Marion County), is 69 mm. in snout-vent length. The largest specimen on record (Orton, 1946), from Allegheny County, Pennsylvania, measures 88 mm. in snout-vent length. Sexual maturity is reached between 40 and 56 mm. in the southern Coastal Plain, and between 47 and 65 mm. in the northern states.

*Plethodon glutinosus albagula* Grobman

White-throated Slimy Salamander

*Plethodon glutinosus albagula* Grobman (1944:283).

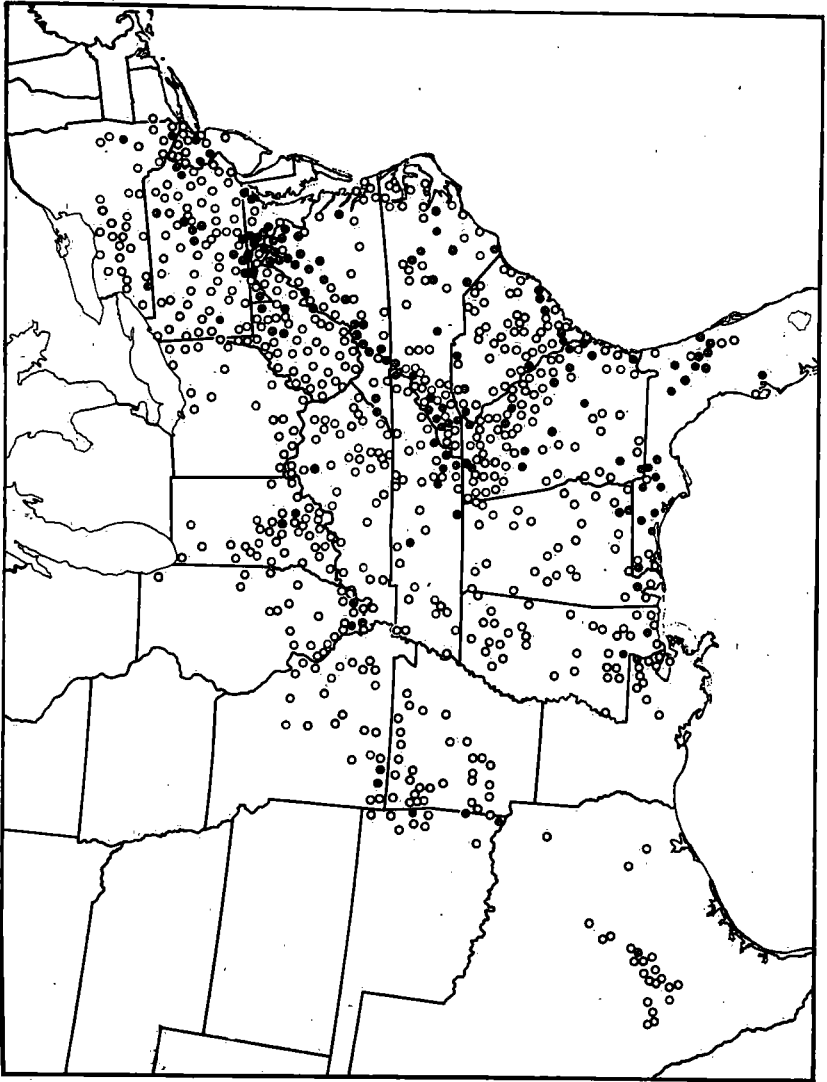


FIGURE 41. Distribution of *P. glutinosus* in the eastern United States. Living specimens were examined from localities represented by solid symbols. Hollow symbols represent localities of museum specimens and literature records.

**HOLOTYPE.** CM 9652, adult male, collected 20 miles north of San Antonio, Bexar County, Texas, 24 February 1935, by Wesley Clanton.

**DIAGNOSIS.** A subspecies of *Plethodon glutinosus* that differs from the typical race in having less melanophore pigmentation on the chin.



DISTRIBUTION. Known from Bexar, Kendall, Comal, Hays, and Travis Counties, Texas.

DESCRIPTION. Living specimens from a sink hole about 5 miles southwest of Austin, Travis County, Texas, besides having greatly reduced melanophore pigmentation on the chin, have exceptionally yellow lateral iridophore spots. These spots are often so large that adjacent spots merge to form a lateral band of yellow pigment, particularly in large specimens. The dorsal iridophore spots are small and white.

Costal grooves usually number 16, trunk vertebrae, 17. Vomerine teeth range from 8 to 26 (fig. 42). The largest specimen examined is 76 mm. in snout-vent length.

\* \* \* \* \*

The slimy salamander is the most widely distributed of the eastern large plethodons. Workers have long realized that *glutinosus* is variable throughout its range. Bishop (1943:19) thinks several salamanders, including *glutinosus*, are each "a complex of species or subspecies requiring additional study before its components can be properly delimited." Three geographic races have been named: *P. g. albagula* Grobman (1944:283), based on a series of light-chinned populations from the region of the Balcones Escarpment of Texas, *P. g. grobmani* Allen and Neill (1949:112) from southeastern Georgia and peninsular Florida, and *P. g. chlorobryonis* Mittleman (1951:108) from the Coastal Plain of North Carolina. The range of each race, as delimited by the above authors, is rather small, and the remainder of the species, including animals from every eastern physiographic province from Connecticut to Florida and Illinois to Texas is currently assigned by most workers to *P. g. glutinosus*. Geographic variation in this species is discussed by Grobman (1944); Neill (1948), Allen and Neill (1949), Thurow (MSa), Mittleman (1951), Clay, Case, and Cunningham (1955), and Humphries (1956).

Studying geographic variation in *glutinosus* is difficult because much of the variation involves pigmentation characters. As preservatives alter most of these pigments, data must be taken from living material. In addition to my own collecting, many other herpetologists have sent me live specimens from various parts of the country. This has allowed me to examine living individuals from all states in the known range of *glutinosus* except Connecticut and Ohio. Figure 41 shows the distribution of this species and the collecting sites of

living material examined. Comparison of living specimens reveals considerable local variation, but few differences remain constant among animals from different geographic regions.

GEOGRAPHIC VARIATION IN CHIN MELANOPHORE PIGMENTATION. *P. g. albagula* is diagnosed by Grobman (1944:283) on the basis of a great reduction in the melanophore pigmentation on the chin of material

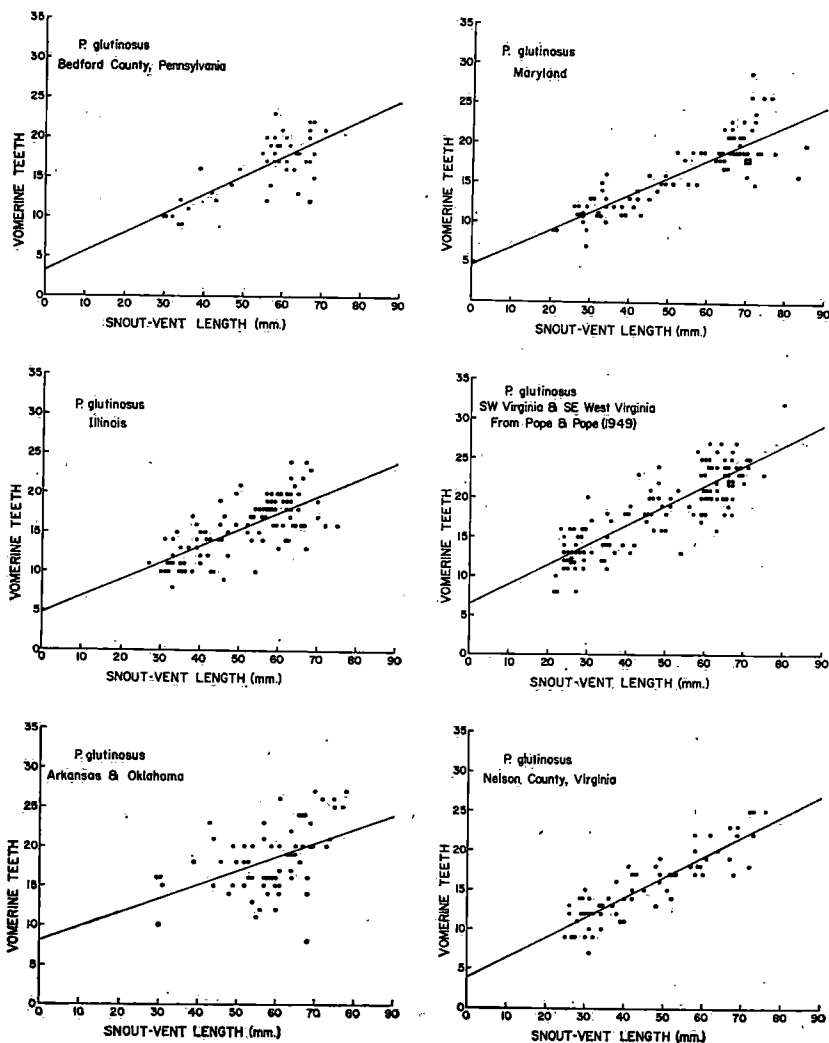
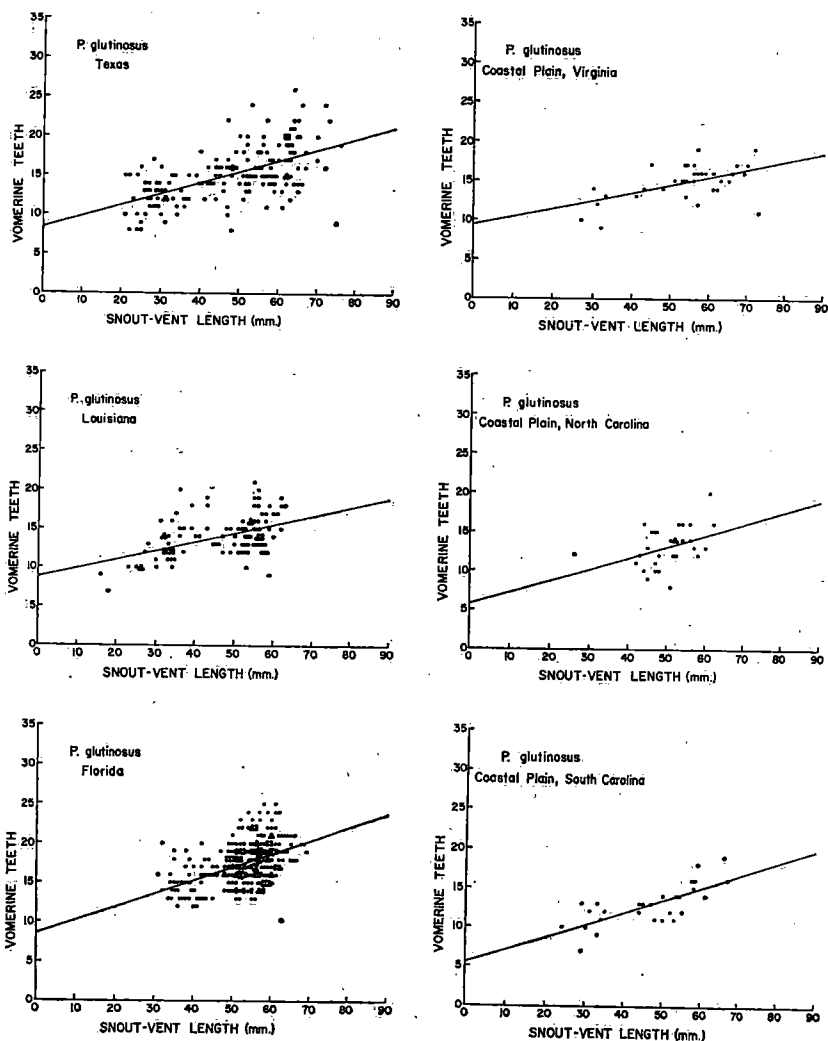


FIGURE 42. Variation in the number of vomerine

available from the Balcones Escarpment region of Texas. New material collected since 1944 indicates populations occur in Texas with chin pigmentation as dark as that in the remainder of the species' range. Figure 43 shows the distribution of the dark- and light-chinned populations of central Texas, based on preserved museum material. The only living specimens examined are 31 of the light-chinned form from 5 miles southwest of Austin, Travis County.



teeth in 12 geographic samples of *P. glutinosus*.

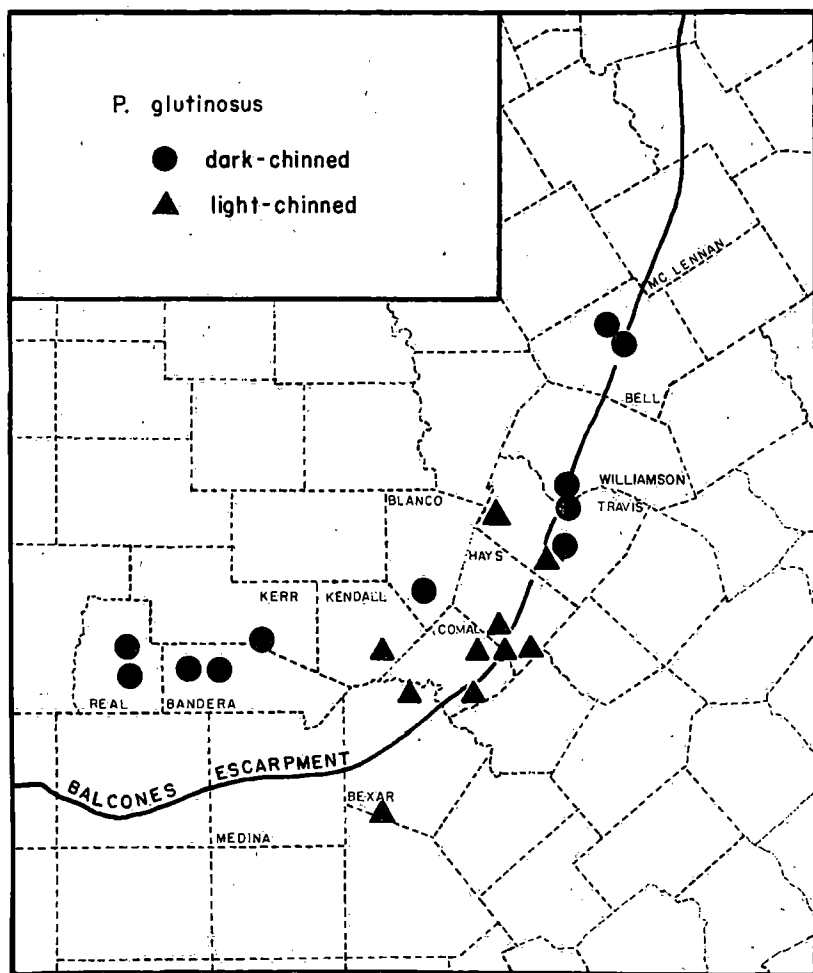


FIGURE 43. Distribution of dark- and light-chinned populations of *P. glutinosus* in central Texas.

Another area in the range of *glutinosus* where most specimens have light chins is the Piedmont and Blue Ridge Provinces of South Carolina, North Carolina, and Virginia (fig. 44).

**GEOGRAPHIC VARIATION IN NUMBER OF TRUNK SEGMENTS.** Allen and Neill (1949:112) and Mittleman (1951:111) state that in the southeastern Coastal Plain *glutinosus* has one or two fewer costal grooves than in more northern populations, which usually have 16 costal grooves (i.e. 17 trunk vertebrae). The numbers of trunk vertebrae in geographic

samples of *glutinosus*, including topotypes of the two subspecies described by Allen and Neill (*grobmani*) and Mittleman (*chlorobryonis*), are listed in table 11. Apparently these workers compared their counts with previously published counts made in a different manner, as little geographic variation in the number of trunk vertebrae occurs.

GEOGRAPHIC VARIATION IN SIZE. Allen and Neill (1949:112) and Mittleman (1951:111) note the small size of southeastern Coastal Plain *glutinosus*. Size is a difficult character to analyze in cold-blooded vertebrates unless large series are available and an accurate estimation of maximum size is possible. Average size of mature animals varies from season to season, as the average is lowered every time a group of young animals matures, and increases during the growing season. Life history data on this species in Louisiana, Illinois,

TABLE 11. Geographic variation in the number of trunk vertebrae in *Plethodon glutinosus*.

	Number of trunk vertebrae					Mean
	16	16/17	17	17/18	18	
Coastal Plain Province						
Louisiana	1	1	20		4	17.10
Mississippi	3		15			16.83
Alabama	1		7			16.88
Florida	22	2	128		4	16.88
Georgia	6	1	28	1	1	16.86
South Carolina	2	1	28		2	16.98
North Carolina	3		7	1	1	16.88
Virginia	4		27		1	16.91
Blue Ridge and Piedmont Provinces						
Georgia			14		2	17.13
South Carolina	1		19			16.95
North Carolina	1		37			16.97
Virginia	1		23	1		16.98
Other Provinces						
Texas		1	150	4	11	17.08
Oklahoma, Arkansas, and Missouri	2		40		1	16.98
Kentucky and Tennessee	3	1	52		6	17.04
Illinois		2	82	1	4	17.04
Ohio			8			17.00
Pennsylvania			8			17.00
New York			10		1	17.09
New Jersey			18			17.00
Maryland	6		59		1	16.92
Virginia (Ridge and Valley Province)	8	2	75	1	3	16.94

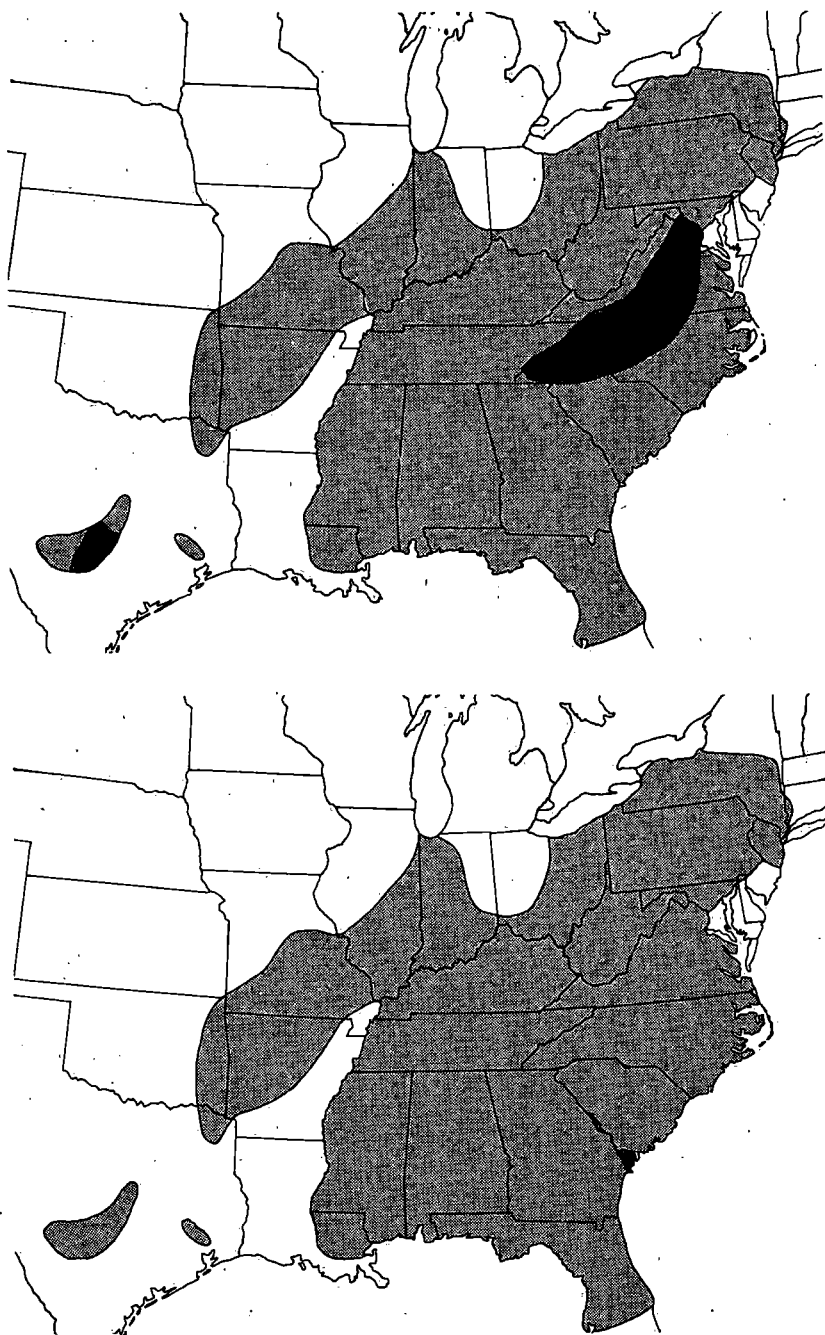
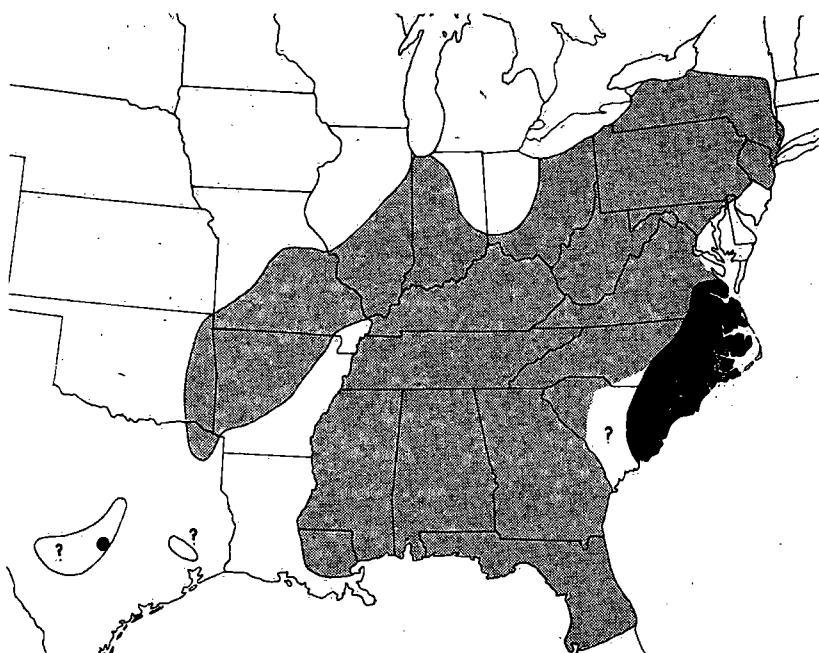
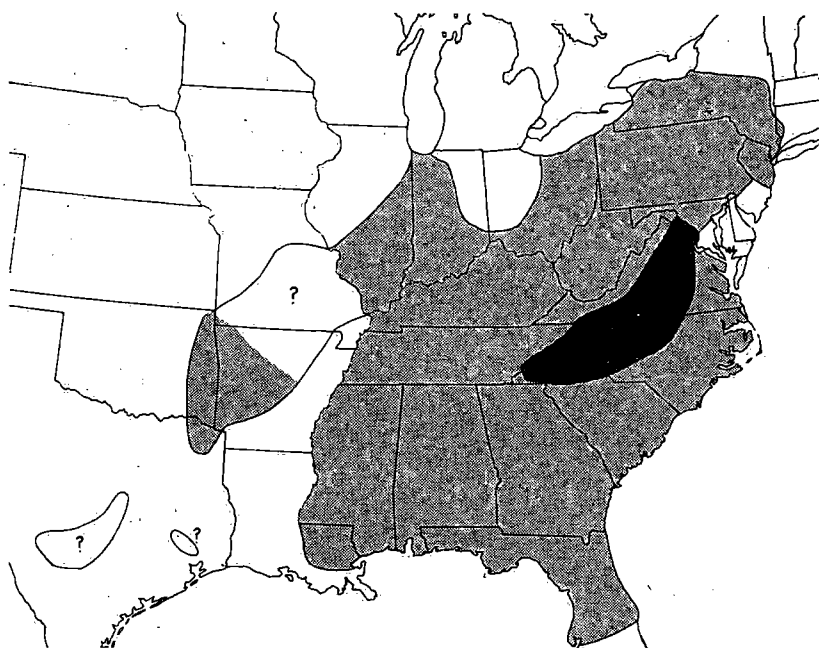


FIGURE 44. Geographic variation in *P. glutinosus*. Darkened areas represent regions where more than 95 percent of *P. glutinosus* have: (upper left) a light



chin, (upper right) white dorsal spots, (lower left) absence of iridophore spotting, (lower right) small dorsal spots.

Virginia, Maryland, and Pennsylvania are compared in a paper in press with data from Florida (Highton, 1956). Maximum size in northern populations is greater than in southern ones, but whether this change is a gradual cline or if an abrupt change occurs is not known. The largest specimen examined from northern peninsular Florida is 69 mm. in snout-vent length; more northerly individuals may grow to 88 mm.

**GEOGRAPHIC VARIATION IN NUMBER OF VOMERINE TEETH.** Mittleman (1951:109) points out that the number of vomerine teeth in the type series of *P. g. chlorobryonis* is much lower than in most other populations of *glutinosus*. He also suggests that the number of vomerine teeth in southern coastal material (*P. g. grobmani*) may be even lower. Actually the average number of vomerine teeth of *glutinosus* in Florida is larger than that in North Carolina, but most samples from the south have fewer teeth than those from northern areas. Figure 42 shows the slopes of the regression lines of all southern Coastal Plain samples are lower than northern samples. In many instances this difference is statistically significant, but considerable overlap exists in the actual number of teeth in most samples of adults. There is undoubtedly a significant difference among *glutinosus* populations in number of vomerine teeth, but this character obviously cannot be used to separate the North Carolina Coastal Plain populations as a different subspecies. Most southern samples have fewer teeth, but the variation is not concordant with the variation in other characters.

**GEOGRAPHIC VARIATION IN SIZE OF DORSAL SPOTS.** The size of dorsal spots in living or freshly preserved specimens was measured with an ocular micrometer (1 micrometer unit = 0.0685 mm.). As spot size increases with total length, the ratio between of the average size of 10 random dorsal spots on the right side of the animal to the snout-vent length was used as a basis of comparison. Individuals of different lengths in the same population usually show similar variation when compared in this manner. The data are summarized in table 12.

In the Atlantic Coastal Plain the spots apparently decrease in size from south to north. There is wide overlap between adjacent populations, and nowhere is an abrupt change from small to large spots apparent.

Average size of the dorsal spots is large throughout the range of *glutinosus*, except in Texas and in the eastern Coastal Plain. In North



TABLE 12. Geographic variation in dorsal spot size in *P. glutinosus*.

Geographic area	Ratio, $\frac{\text{Mean spot size}^*}{\text{Snout-vent length}} \times 100$							True mean (not the mean of the categories to the left)
	1.0- 4.9	5.0- 8.9	9.0- 12.9	13.0- 16.9	17.0- 20.9	21.0- 24.9	over 25.0	
Coastal Plain:								
Virginia	2	12	1	1				7.2
North Carolina	1	7	5					8.3
South Carolina		3	12	2	1			11.1
Georgia	1	2	12	5	8	3	3	15.7
Florida (peninsula)		1	7	10	16	10	2	17.9
Florida (panhandle)			1	4	3	11		20.5
Alabama				2	1	2		19.5
Mississippi			1		1			14.6
Louisiana				1				14.3
Other Provinces:								
New York	1	1		1		1		12.9
New Jersey						1	1	24.5
Pennsylvania			1	4	14	10	4	20.9
Maryland					1	2		22.6
Virginia								
Blue Ridge		3	5	7	2	2	3	16.0
Ridge and Valley					5	6	1	21.6
North Carolina								
Piedmont			7	9	1		1	15.0
Blue Ridge	1	12	18	5			1	10.4
South Carolina		1	7	14	5	1	1	15.1
Georgia		2	6	7	6	2	1	15.3
Tennessee			7	7	6	3	2	16.8
Kentucky						3	1	23.3
West Virginia			1		4	4		20.7
Illinois			1	2	1			14.8
Indiana			1	4		2		17.4
Texas		8	2					8.6

\* Measured in micrometer units, 1 unit equals 0.0685 mm.

Carolina the spots of 18 specimens from the Piedmont averages 15.0 units, those of 37 from the Blue Ridge Province 10.4. Available specimens do not support the contention that a west-to-east reduction in spot size exists in North Carolina, as the Piedmont series' spots average slightly larger than those from the mountains to the west.

GEOGRAPHIC VARIATION IN COLOR OF DORSAL SPOTS. In their description of *P. g. grobmani* Allen and Neill (1949:112) consider the "metallic golden color" of the dorsal spots of specimens from southeastern

Georgia and peninsular Florida its most conspicuous diagnostic feature. Many specimens from the range they assign to *grobmani* do have dorsal spots with numerous brassy iridophores, but this type of spotting occurs elsewhere, as in Shelby County, Tennessee (Sinclair, 1950). Living specimens from many other localities throughout the range of *glutinosus* show brassy flecking as heavy as in topotypical *grobmani*, and it is even heavier in many individuals from northern Georgia and southeastern Tennessee. However, even though some specimens are heavily flecked, the average amount of brassy flecking is usually less than in northern Florida. All living specimens examined from the Blue Ridge and Piedmont Provinces of Virginia, North Carolina, and South Carolina have white dorsal spots with reduced brassy flecking occurring, if at all, usually only on the edges of the spots.

The Potomac River is the northern limit of the white-spotted Piedmont and Blue Ridge populations. Specimens from the Maryland Piedmont and Blue Ridge Provinces have moderate to heavy brassy spotting. The white-spotted populations seem restricted to areas of crystalline rocks, for specimens from areas of sedimentary formations to the east (Coastal Plain) and west (Ridge and Valley) have brassy flecking in the dorsal spots. Two individuals from Stone County, Missouri, the only living *glutinosus* examined from that state, have white dorsal spots.

**GEOGRAPHIC VARIATION IN ABUNDANCE OF LATERAL PIGMENT:** Grobman (1944:282) discusses the north-south cline in the amount of white lateral pigment in this species. Specimens from the southeastern Coastal Plain have large lateral spots and in many adults the spots coalesce to form a band of white. Specimens from the southern Appalachians have smaller lateral spots, and farther north the spots are not much larger than those on the dorsum. Grobman states that some Texas specimens have a large amount of lateral pigment that may form a band in adults.

The pigment is much more concentrated in the center than on the edges of the lateral spots of many adult specimens from New York, New Jersey, Pennsylvania, Maryland, and West Virginia. In southern specimens with larger spots the pigment is usually more evenly distributed.

It is difficult to measure and evaluate the size of the lateral spots especially when they fuse. Though no measurements were made, examination of specimens from different areas confirms the observations of earlier workers. A lateral band seems most prevalent in

specimens from the Coastal Plain of Virginia, North Carolina, and South Carolina, and from Texas. Allen and Neill (1949:113) report that specimens from Burke, Jefferson, Washington, Glascock, and Richmond Counties, Georgia, also have much white on the sides.

**GEOGRAPHIC VARIATION IN COLOR OF LATERAL PIGMENT.** The color of the lateral spots is used as a diagnostic character in the original descriptions of both *P. g. grobmani* and *P. g. chlorobryonis*. Those of *grobmani* are described as grayish, those of *chlorobryonis* as greenish white or yellow-green. Analysis shows the lateral spots of many living specimens from Florida are gray, those of most Coastal Plain specimens of North Carolina and Texas yellow to orange. Though the lateral spot color varies greatly in other samples, it shows no geographic trends.

Yellow lateral pigment is not due to the presence of brassy iridophores, but to a difference in the color of the iridophores. Young individuals of all samples examined have white lateral spots, so presumably an ontogenetic change in the color occurs in those that have yellow pigment as adults.

**GEOGRAPHIC VARIATION IN PRESENCE OF IRIDOPHORES.** Individuals with no dorsal and lateral iridophore pigmentation occur occasionally in various parts of the species' range. In at least two areas this characteristic is present in many individuals. Neill (1948) reports a population in Jasper County, South Carolina, characterized by the absence of iridophore spotting. Iridophores are absent in some individuals from adjacent areas, but normally spotted individuals also occur (Hallowell, 1858:343; Cope, 1889:142; Schmidt, 1924).

Many individuals from another Coastal Plain locality lack spotting. On the east side of the St. Johns River, about 1 mile south of Astor, Volusia County, Florida, 14 of 30 specimens are entirely black. In Lake County on the west side of the St. Johns River at three localities within 10 miles of Astor, only 1 of 107 specimens has no spotting. Apparently the genes responsible for this condition occur with low frequency in some *glutinosus* populations, but have become fixed in the Jasper County, South Carolina, population and are present in unusually high frequency in the Volusia County, Florida, population.

Grobman (1944:281) states that preserved specimens of *glutinosus* ranging south from the Cumberland Plateau in Alabama, Georgia, Kentucky, Mississippi, South Carolina, North Carolina, and Tennessee are devoid of white pigmentation. I have examined living specimens from some of the counties listed by Grobman and many others within

the range of the supposedly unspotted form, and all have both dorsal and lateral iridophore pigmentation. The apparent difference noted in some preserved specimens is not present in life and must result from the disappearance of the spots after preservation.

*P. glutinosus* without iridophore pigmentation are not easily distinguished from dark-bellied southern *P. jordani*. Perhaps literature records of dark-bellied *jordani* (subspecies *melaventris*) from east of the French Broad River, North Carolina are based on unspotted *glutinosus*. Only one living specimen of this type has been, examined—from the Swannanoa Mountains—and it appears more like sympatric spotted *glutinosus* in size, proportions, and chin and cheek melanophore pigmentation than it does to dark-bellied *jordani* from west of the French Broad River.

**SUMMARY AND DISCUSSION OF GEOGRAPHIC VARIATION IN PLETHODON GLUTINOSUS.** Geographic variation is present in some of the characters previous workers used as a basis for naming geographic races. Certain populations in Texas have reduced melanophore pigmentation on the chin; others do not. Reduced chin pigmentation occurs in other populations of *glutinosus* in the Piedmont and Blue Ridge Provinces from Virginia to South Carolina. Southeastern Coastal Plain specimens are significantly smaller than northern material. The number of vomerine teeth is low in most samples from southern parts of the range, including Texas. Dorsal spots exhibit clinal variation in the Atlantic Coastal Plain increasing in size from north to south. Dorsal spots of other populations, except those in the Blue Ridge Province of North Carolina and those in Texas, are about the same size as in southern Coastal Plain animals. The color of the dorsal spots is extremely variable, but uniformly white in the Piedmont and Blue Ridge Provinces from Virginia to South Carolina, and uniformly brassy in the Gulf Coastal Plain from Mississippi to Florida. Lateral spots are larger and more yellow in parts of the Atlantic Coastal Plain and in Texas, and are smaller in the north.

Populations along the Balcones Escarpment in Texas now seem isolated from the remainder of the species. Living Texas specimens are the most distinctive of all *glutinosus* examined. The relationship between the dark- and light-chinned populations in Texas is not clear; no living material of the dark-chinned form was studied. It may be that the Balcones Escarpment area was invaded twice, the earlier invasion differentiating into the light-chinned form (*albagula*) and the later one remaining dark-chinned as the Arkansas and Oklahoma populations. Whether the light- and dark-chinned populations

are different species, subspecies, or ecophenotypes cannot be determined from the evidence at hand. For the present no change is recommended in the current nomenclature, and the light-chinned populations should continue to be called *P. g. albagula* until their status is clarified. Available specimens from Upshur County in north-eastern Texas and from Walker County in southeastern Texas have dark chins. These populations also may be isolated now from the main range of *glutinosus*.

Specimens from the Virginia, North Carolina, and South Carolina Coastal Plain differ from most other *glutinosus* in several ways. Few vomerine teeth, small dorsal spots, a lateral row of yellow spots, and small size serve to distinguish many of them from those of most other populations of the species. None of the characters is limited to this area, however, and all but size show a gradual clinal change from south to north in the Coastal Plain with wide overlap between adjacent populations. Difference in size is negligible from Florida to Virginia in the Coastal Plain. Most systematists do not recognize the ends of such a cline as separate subspecies. If the northern end of this cline is so designated, the name *cylindracea* Harlan (1825:156) is available; its type locality is probably Camden, South Carolina. *P. g. chlorobryonis* Mittleman, based on specimens from the North Carolina Coastal Plain would be a junior synonym, as there is wide morphological overlap between the North and South Carolina populations. If the southern end of the cline be recognized as a valid subspecies, the name *variolata* Gilliams (1818:460) is available; its type locality is probably Georgia or Florida. *P. g. grobmani* Allen and Neill (1949:112) is a junior synonym. The name *variolata* is available for all Coastal Plain *glutinosus* if, in the future, it is shown that these populations should be designated nomenclaturally. At present no known characters adequately diagnose a southern race.

Florida and Georgia samples are closer to non-Coastal Plain samples than are those of the Virginia and Carolina Coastal Plain in every character except maximum size. If wide-ranging *glutinosus* were first able to adapt itself to the Coastal Plain in Georgia or farther west, it might have migrated northeastward through coastal areas of the Carolinas and southeastern Virginia. This could explain the great morphological differences between adjacent Piedmont and Coastal Plain populations of North Carolina and Virginia, as these populations are rather distantly related. No records of *glutinosus* exist from Long Island, southern New Jersey south of Ocean County, the Coastal Plain of Maryland, the Del-Mar-Va peninsula and the northern Coastal

Plain of Virginia. The sole exception is a series from Essex County, Virginia (USNM 143088-96), that appears to be of the Piedmont form. Apparently *glutinosus* of the northeastern Piedmont rarely has been able to expand its range into the adjacent Coastal Plain, though *P. cinereus* has adapted to Coastal Plain conditions in all these areas. Because *glutinosus* of the Virginia Coastal Plain are so different from Piedmont animals, the hypothesis of a southerly origin of the former, rather than a closer relationship to the adjacent upland populations, gains support. It would be of interest to study the relationship between the two in the area of probable secondary contact along the Fall Line in Virginia and North Carolina.

In addition to the lack of iridophore spotting, Neill (1948) mentions several other differences between the unspotted *glutinosus* from Jasper County, South Carolina and other adjacent populations. I can detect no consistent differences in number of costal grooves, proportional length of tail, paravomerine teeth, melanophore pigmentation, size, head shape, or structure of the vent in males. However, while collecting specimens at the locality mentioned by Neill, 7 miles north of Tillman, Jasper County, South Carolina, I was impressed by the unusual agility of the animals in escaping the collector, and by the apparent delicacy of the skin compared with other Coastal Plain *glutinosus*. Histological examination of the skin might reveal structural differences other than the absence of white spots.

Nicholls (1950:310, 312) suggests more than one altitudinal form of *glutinosus* occurs in eastern Tennessee, but does not describe them. In western North Carolina, Blue Ridge *glutinosus* invariably have white dorsal spots. This form has been collected also at several localities in eastern Tennessee. Elsewhere in eastern Tennessee *glutinosus* with much brassy flecking occur, and they also have been taken in northern Georgia on Potato Patch Mountain, Murray-Gilmer Counties, and in Tallulah Gorge, Rabun County.

The complex relationship between *P. jordani* and *P. glutinosus*-like populations in the southern Blue Ridge Mountains was discussed earlier. These "*glutinosus*-like" *jordani* may be conspecific with white-spotted *glutinosus* from the Blue Ridge and Piedmont Provinces. The latter differ greatly from *glutinosus* from surrounding areas in having reduced melanophore pigmentation on the chin and in the color of the dorsal spots. No truly intergradient populations are known between these white-spotted *glutinosus* and adjacent populations of supposedly the same species.

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