GEOGRAPHIC VARIATION AND SPECIATION IN APPALACHIAN SALAMANDERS (*Plethodon jordani* Group) *

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Received May. 17, 1948

INTRODUCTION

The family Plethodontidae is the largest, the most flourishing, and the most highly specialized group of recent salamanders. Its early evolution seems to have taken place in the Appalachian Highlands, where a considerable percentage of the known species still live. The first plethodontids were undoubtedly mountain stream inhabitants. From this restricted habitat adaptive radiation headed each of three evolutionary lines toward terrestrialism. Two of these lines remained at least partially bound to water and are restricted to eastern North America. The third and truly successful group developed independence of water even for breeding and was then able to invade Europe and South America. Some forms have gone so far as to have become arboreal (species of *Oedipus* and *Aneides*) and to bear living young (*Hydromantes*).

Dunn (1926) and Piatt (1935), who have discussed in detail the lines of evolution summarized above, show that species of the genus *Plethodon* were probably the first to adapt themselves to environmental conditions that require no aquatic stage. It is with a group of closely allied forms of *Plethodon* that we are concerned here. By studying their type of speciation we hope to shed some light on the mode of salamander evolution in general. It should be remarked that our forms occur in the original home of the family. Their names follow in chronological order of description: *jordani, shermani, metcalfi, clemsonae, rabunensis,* and *melaventris*. Figure 1 shows the general topography of the area inhabited by these forms and Figure 11 their ranges.

We are indebted to the following for the loan of specimens: Mr. M. Graham Netting of the Carnegie Museum; Dr. Doris M. Cochran of the United States National Museum; Dr. Norman Hartweg of the Museum of Zoology, University of Michigan. Mr. Netting also kindly lent us his notes on these salamanders. Mrs. John Moyer assisted in the preparation of the illustrations. Part of the field work was done with the aid of a University of North Carolina scholarship to the Highlands Biological Laboratory.

HISTORY

The knowledge of these salamanders [1] began in the summer of 1900 when Mr. L. E. Daniels, while collecting molluscs in the Great Smoky Mountains, dropped two salamanders in a bottle of alcohol. A year later these were named *Plethodon jordani* by Blatchley. Since then, a new form has been brought to light every eight years or so and the distribution of each has been delimited, chiefly by Dunn (1926), Bailey (1937), Bishop (1943), and Grobman (1944).

There is now general agreement in regard to the ranges of *jordani* and *shermani,* forms restricted to the Great Smoky and the Nantahala Mountains, respec-

* Contribution of Northwestern University and Chicago Natural History Museum.

[1] Variously known as the *"jordani,"* the *"metcalfi,"* and the *"jordani-metcalfi"* group.

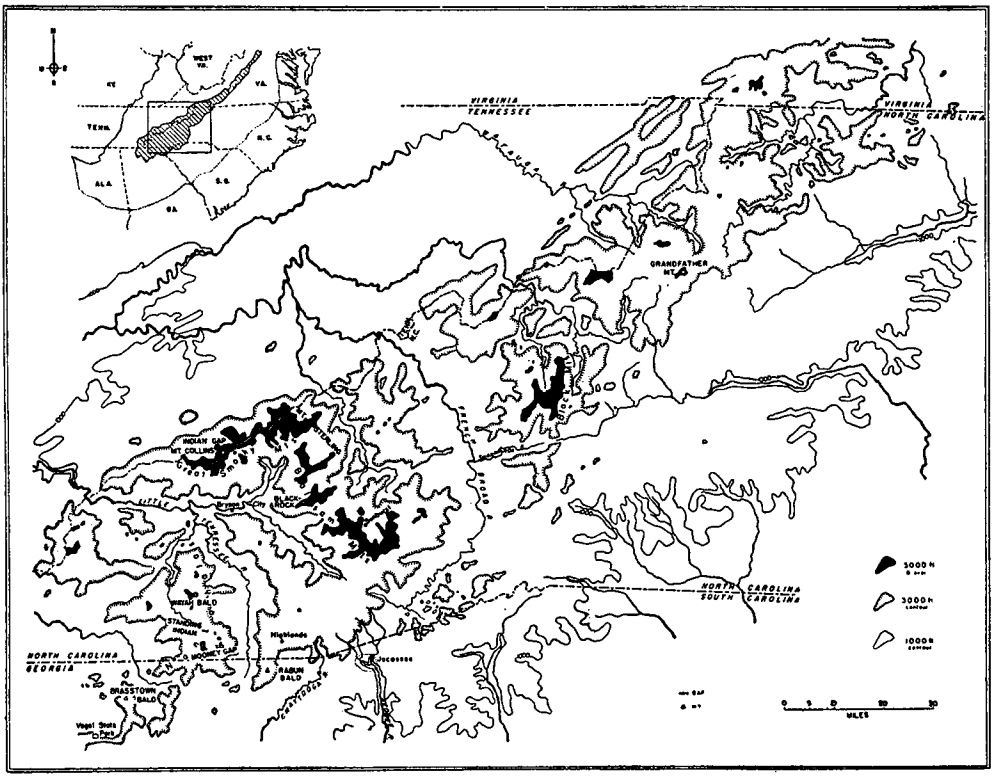

FIG. 1. Contour map of the southern Appalachian Highlands showing the places referred to in the text and the principal ranges and valleys. Corresponding area is outlined on inset map indicating Blue Ridge province (shaded) and limits of Appalachian Highlands (dotted line). Type localities are also included, as follows: SUNBURST: *P. metcalfi;* INDIAN GAP and MT. COLLINS: *P. jordani;* WAYAH BALD: *P. s. shermani;* JOCASSEE: *P. s. clemsonae;* RABUN BALD: *P. s. rabunensis;* HIGHLANDS: *P. s. melaventris;* 1.5 miles northeast of LINVILLE: *P. yonahlossee.* Map adapted from U. S. Coast and Geodetic Survey Sectional Aeronautical Charts R-8 and S-8 (Charlotte and Winston-Salem), 1936. (Linville lies southwest of Grandfather Mtn.)

tively. Two names (*rabunensis* and *melaventris*) have but recently been assigned by us, the former to the population of Rabun Bald, Georgia, the latter to the southern segment of a population long designated as *"metcalfi."* *P. clemsonae* has nearly always been applied to salamanders from Jocassee, a locality in extreme northwestern South Carolina. However, in 1944 Grobman used this name so that it included *"clemsonae"* of other workers with the blackbellied, southern segment of their *"metcalfi."* He thus disregards the dorsal and lateral markings of *clemsonae* but advisedly calls attention to the difference between the southern and northern populations of *"metcalfi."* Bailey had noticed this difference but associated it with altitude rather than with latitude.

ANALYSIS OF CHARACTERS

Our field observations and a study of ample fresh material collected by us indicate that only the analysis of the geographical distribution of the various characters, especially those of color, fully reveals the biological situation. We are therefore considering these in detail before taking up the taxonomically recognizable populations.

The definitive color characters in the

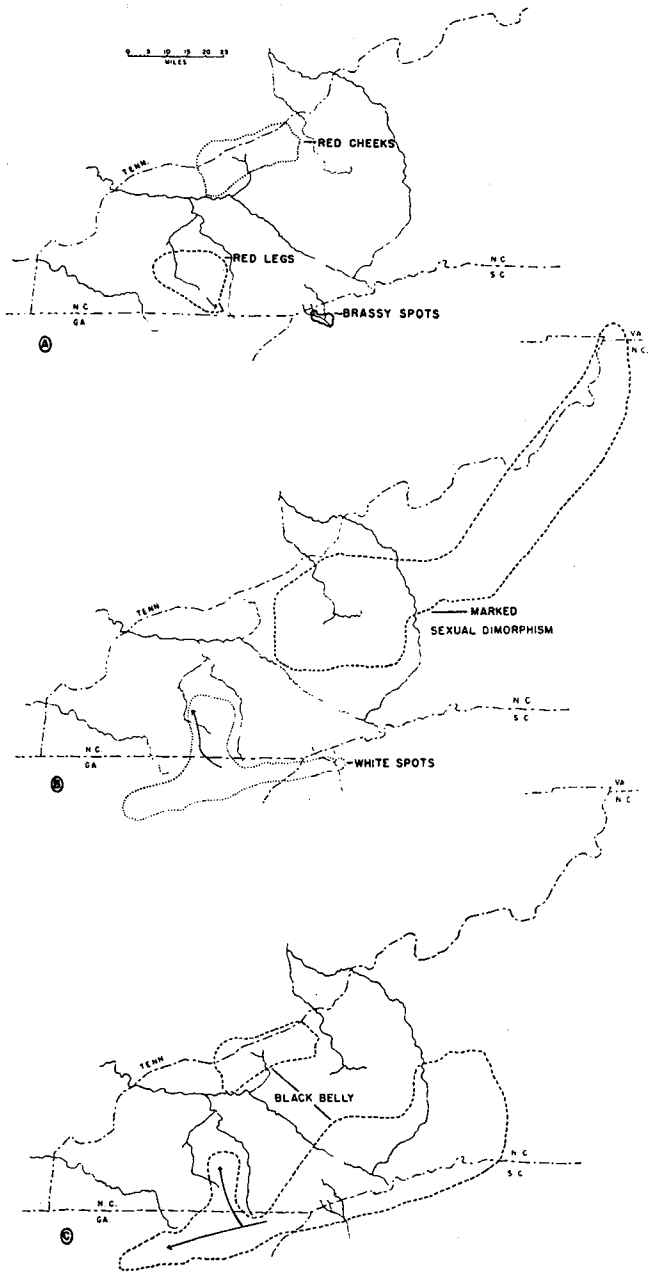

FIG. 2. Distribution of six characters among the populations of the *jordani* group. Arrows indicate *decreasing* incidence of characters. A. Distribution of red cheeks, red legs and brassy dorsal markings. B. Distribution of lateral white spots and marked sexual dimorphism. C. Distribution of black belly.

jordani group are: (1) red markings on the cheeks or legs; (2) white spots on the sides; (3) brassy flecks on the dorsal surface; (4) black ground color of the belly. Other characters are size and sexual dimorphism.

Color:

1. Red markings. Wood (1947, a and b) has indicated the close similarity of the juveniles of the two red-marked populations. All specimens less than 29 mm. in total length have red spots on the dorsum but lack red marks in the areas where they occur in adults.

Cheeks: Specimens having red cheeks are confined to the Great Smoky Mountains, from Mt. Sterling to the mountains north of Bryson City, North Carolina (fig. 2, A). With the exception of the *metcalfi* collections (see sexual dimorphism below), nearly all of the specimens from this area have red cheeks: 34 of 37, 76 of 78, and all but two of "several hundred" (Dunn, 1926; Pope, 1928; King, 1939; respectively).

Legs: Red-legged salamanders are confined to the Nantahala Mountains (fig. 2, A).[2] To the published records as summarized by Grobman[3] we add: Standing Indian Mountain, directly south of Wayah Bald and just north of the Georgia line; Mooney Gap,[4] east of Standing Indian and midway betwen it and the Little Tennessee River. The 23 specimens from Standing Indian show the same amount of red as a series of 18 topotypes from Wayah Bald. Although some individuals of the two series have the red reduced, all possess the character. The Mooney Gap specimens, on the other hand, show a marked reduction in the amount of red on the legs, and one of the twenty-four lacks the red entirely.

2. White spots. Populations having white spots (fig. 2, B) along the sides of the head and body are found along the southwestern periphery of the range of the *jordani* group, i.e., from Wayah Bald, North Carolina, to Jocassee, South Carolina, as indicated by the map. The maximum incidence of these white spots is found in the populations from Mooney Gap (21 of 24 specimens) and Rabun Bald (85 of 101 specimens). At Jocassee, to the east, the incidence is practically undiminished (14 of 17 specimens). Northwestward from Mooney Gap there is a significant decrease: 14 of 23 specimens at Standing Indian and 7 of 18 at Wayah Bald are white-spotted. Bailey's 31 specimens from Weatherman Bald and Tusquitee Bald lack white spots. These two mountains are about twelve miles west of Wayah Bald. There is thus a distinct cline from the southeastern to the northwestern Nantahala Mountains. All the remaining populations of this species group lack the lateral white spots.[5]

On the basis of the white spots and other characters, Bishop (1941) regards the red-legged population as closely (subspecifically) related to *P. glutinosus*. Grobman (1944) wisely rejects this relationship, and we present the following additional evidence.

An examination of living *Plethodons* under the highest feasible magnification (about 50 ×) shows that the white spots are divisible into two distinct types. One of these types is found in *P. yonahlossee* and *P. glutinosus* (both from the Black Mountains, Buncombe County, North Carolina). The pseudopodia of the white pigment cells (guanophores) tend to overlie the dermal glands and invade the ad-

[2] A single specimen with red spots on the legs was recorded by Dunn (1926) from Mt. Sterling in the Great Smoky Mountains.

[3] Grobman's easternmost record is apparently Franklin. Since this town is in a flat valley we conclude that the specimen actually came from the Nantahala Mountains to the west.

[4] Mooney Gap is on the southern flank of Bearpen Mountain at 4500 feet altitude. The series herein designated as from "Mooney Gap" actually includes three individuals from nearby Reynolds Gap (3700 feet) on the northeastern flank of Picken's Nose, which is adjacent to Bearpen Mountain.

[5] Breder and Breder (1923) record a single white-spotted individual from Ashe County, North Carolina, at the opposite extremity of the group range.

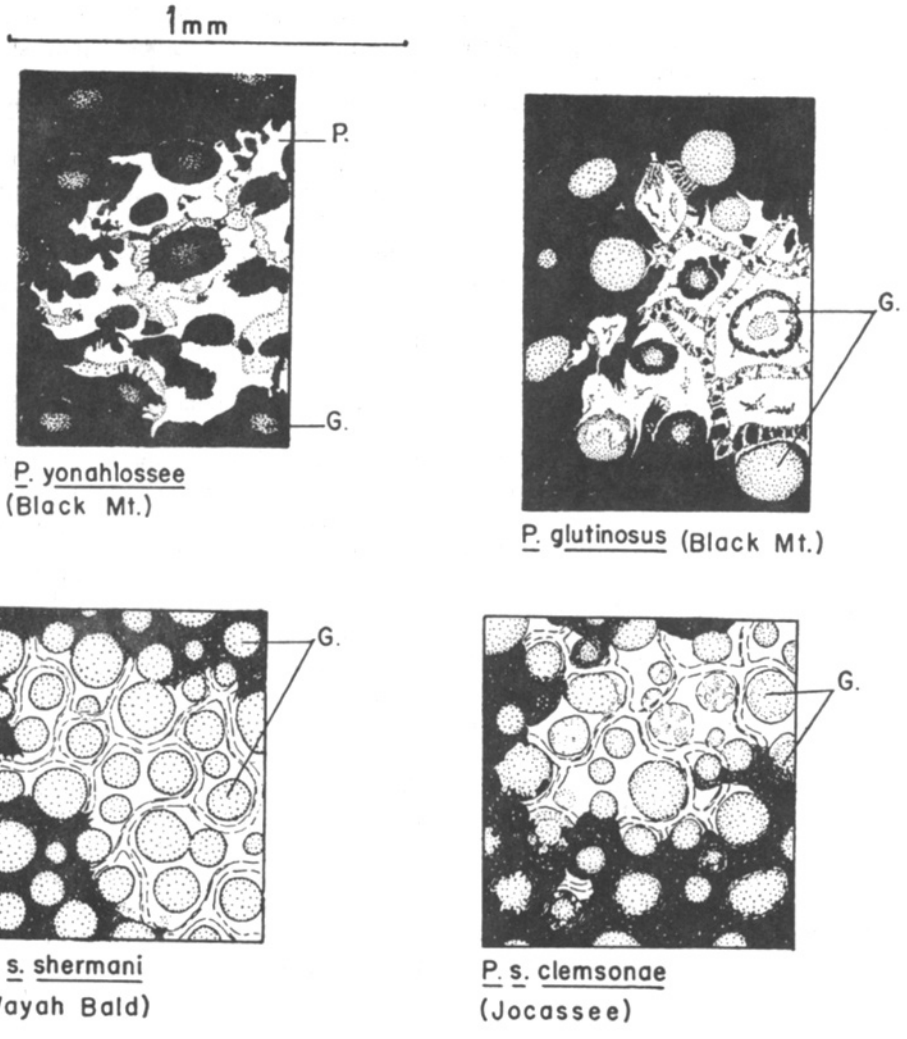

FIG. 3. Lateral white spots in *Plethodon* magnified about 50 times; G. for gland, P. for pseudopodia. Note the numerous pseudopodia formed by the guanophores of *P. yonahlossee* and *P. glutinosus* and their complete absence in *P. s. shermani* and *P. s. clemsonae*. All drawings from living specimens. *P. yonahlossee* and *P. glutinosus* from the Black Mountains, Buncombe County, North Carolina; *P. s. shermani* and *P. s. clemsonae*, topotypes.

jacent black area, as shown in figure 3. The other type of white spot was found in salamanders from Wayah Bald and Jocassee, obviously distinguishable from *glutinosus* by the presence of red legs or brassy markings. Due to the absence of the underlying black pigment and the failure of the guanophores to produce evident pseudopodia, these white spots appear as sharply delimited areas (fig. 3), though actually less conspicuous than the other type of spot.

3. Brassy markings. All of our eleven specimens from Jocassee (fig. 2, A) have conspicuous brassy specks crowded together on the dorsum. In some, these markings cover the back; in others, they are reduced to more or less discrete areas. Bishop's two specimens also had these markings but Brimley described the dorsal

markings of the type series variously as "white," "greyish" and "frosted with white." We assume that these terms apply to the markings that we call "brassy." Only this low-altitude population restricted to Jocassee exhibits this character.

4. Black belly. The black (or dark) belly is the only character with a discontinuous distribution (fig. 2, C). It is found in the Great Smoky Mountains and over a large area in the southern part of the group range. (The specimens we rate as "light" or "pale" are not entirely devoid of melanin.)

Only occasional individuals from the Nantahala Mountains have black bellies, except for the Mooney Gap series from the extreme southeast, where 7 of 24 are so colored. This series is clearly intermediate between the other Nantahala populations and the ones from Rabun Bald, where virtually all adults have black bellies.

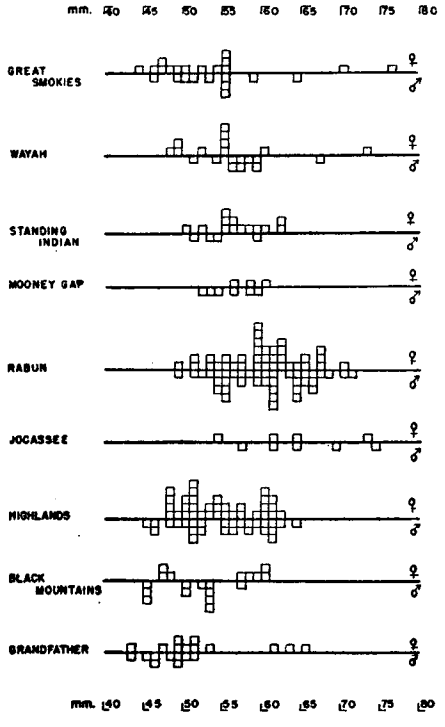

FIG. 4. Size distribution in nine populations of the *jordani* group.

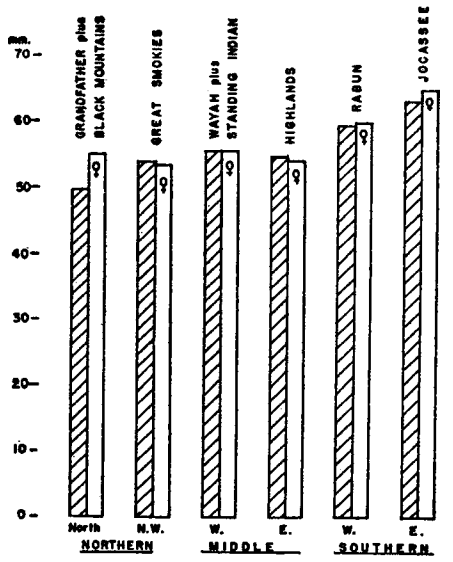

FIG. 5. Average size of the sexes of the *jordani* group, beginning at the left with the northern populations. The size gradient is more pronounced in the males than in the females.

This quantitative character is a troublesome one because its analysis calls for direct comparison of uniformly preserved material. We agree with Grobman that belly-color is darker in the southern populations; unlike him, we have no difficulty in allocating specimens from the Highlands-Brevard area to the dark-bellied population. It should be mentioned that only adults can be used in analyzing this character, because juveniles of all populations have pale bellies.

Size and sexual dimorphism:

Considerable variation in length is evident between the populations of the *jordani* group. The longest specimens come from the south (Jocassee and Rabun Bald), the shortest from the north (Grandfather Mountain). The remaining populations are made up of individuals intermediate in length (fig. 4). Thus there is more or less decrease in body size from south to north (fig. 5). This tendency is strengthened by altitude as well as by latitude, since the southernmost popu-

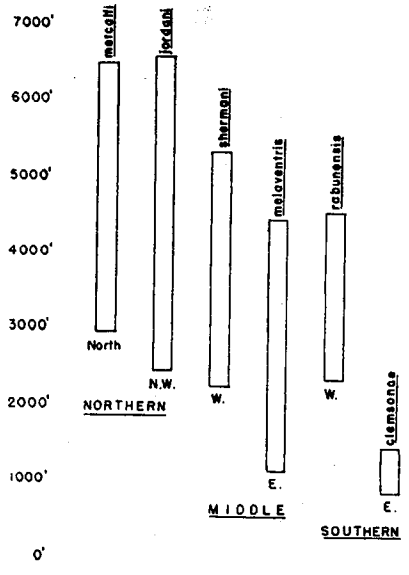

FIG. 6. Vertical distribution of the members of the *jordani* group, beginning at the left with the northern forms.

lations are also found at the lowest elevations (fig. 6).

Due to a marked dimorphism in the northeastern populations (Grandfather Mountain and the Black Mountains), the differences between samples of the populations in mean length are more pronounced if the males are compared separately. Bailey's series from Blackrock in the Balsam Mountains exhibited a similar difference between the sexes. The distribution of populations with this marked sexual dimorphism is shown on the map (fig. 2, B).

In addition to this, the bilateral swelling of the snout of the males is most pronounced in this northeastern population. This seems to be correlated with the degree of development of the mental gland.

Vomerine teeth:

The number of vomerine teeth possessed by the members of the different populations (fig. 7) approximately parallels general size as in other genera of the Plethodontidae. Specimens from Jocassee and Rabun Bald have the longest vomerine series, those from Grandfather Mountain have the shortest.

SYNTHESIS OF CHARACTERS

Besides the incidence of occurrence, the degree of development of the characters is also instructive in comparing populations. Although 96 per cent of the specimens from Mooney Gap had some red on the legs, nearly all had reduced amounts

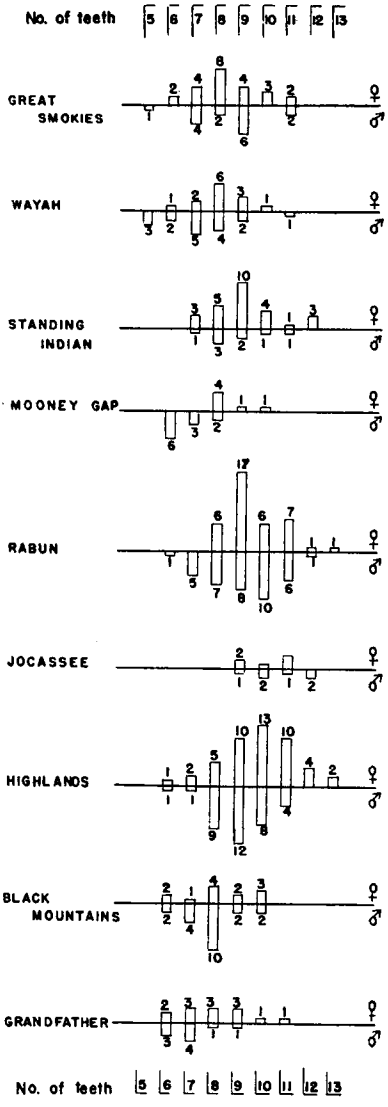

FIG. 7. Number of vomerine teeth in nine populations of the *jordani* group.

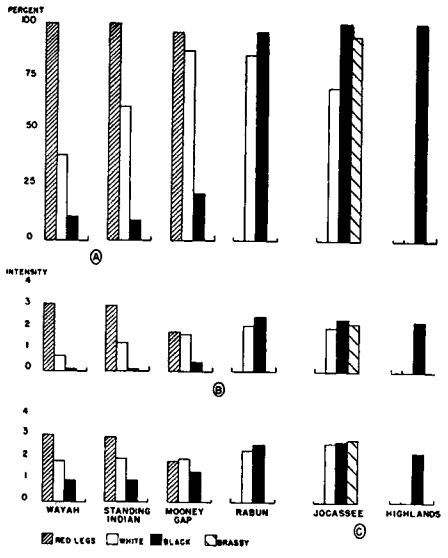

FIG. 8. Variation in six populations of *Plethodon shermani* as indicated by four color characters: red legs; lateral white spots; black belly; brassy dorsal markings. Histograms separated by spaces proportional to distance between localities. A. Incidence of occurrence. B. Average intensity based on all specimens (maximum 4, minimum 0). C. Average intensity based only on specimens possessing the characters (maximum 4, minimum 1).

as compared with the Wayah Bald and Standing Indian populations. We have represented this type of phenomenon graphically for four color characters in figure 8, B and C. In constructing these charts, an arbitrary scale was set up; the preserved specimens were separated into four groups according to the development of the character, with the lowest number standing for the weakest development.

There are two ways of representing the amount of development of a character in a population: In figure 8, B, we have averaged the intensity for all specimens collected in a locality; in figure 8, C, only the intensity of those that possess the character, since it may be maintained that negative ones should not be included. The pictures presented are the same. Preferring the former procedure, we have put the histogram of figure 8, B on the map (fig. 9).

The populations of salamanders in the northern areas are sharply separated by all characters analyzed. In contrast to this, each of the southern populations possesses at least one character in common with all neighboring ones. It would

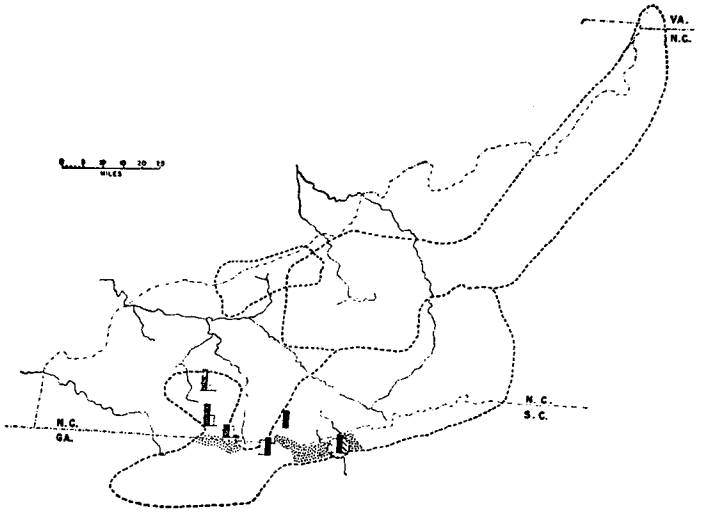

FIG. 9. Distribution of specifically distinct members of the *jordani* group (broken lines) and of the populations analyzed by the histograms of figure 8, B. Probable areas of intergradation indicated by dotting.

thus appear that gene flow has ceased between the salamanders from three areas, one extensive southern area and two northern ones (fig. 9). The two northern forms overlap geographically and vertically (King, 1939) with no evidence of intergradation, a situation that requires further study. Within the large southern area, outlined on the map, there is continuing gene flow, as evidenced by the overlapping distribution of four color characters.

Taxonomy

Considering the *jordani* group as a whole from the taxonomic standpoint, the two northern forms are properly designated as species distinct from each other and from the southern forms. The northwestern one continues to be known as *Plethodon jordani;* it is confined to the Great Smoky Mountains and has red cheeks. As shown by Grobman (1944), the name *Plethodon metcalfi* must be restricted to the northeastern form, which exhibits marked sexual dimorphism and is light bellied. Its specific distinctness from the southern form rests upon the lack of intergradation of these two characters despite the absence of an evident physiographic barrier.

As regards the southern populations, the characters analyzed in the foregoing section overlap in such a way that any taxonomic arrangement must be somewhat arbitrary. The chief difficulty lies in the distribution of white spots: Were it not for this character, there would simply be a narrow zone of intergradation between salamanders with red legs and those with black bellies. The white spots, however, reach their maximum incidence in this narrow zone around the headwaters of the Little Tennessee River. They disappear gradually to the northwest, and abruptly to the northeast (fig. 8). In considering nomenclature, it is no more proper to ignore this character than any other.

The oldest name applicable to any of these southern forms is *Plethodon shermani,* assigned by Stejneger (1906) to red-legged specimens from the Nantahala Mountains. We regard the remaining members of this southern complex as subspecies of *shermani.* The black-bellied, low-altitude population from Jocassee, most examples of which have brassy dorsal markings and white lateral spots, are designated *P. s. clemsonae* Brimley. We have recently (1948) assigned two names to the remaining southern salamanders. These are *P. s. rabunensis* from Rabun Bald, a population with black bellies and white lateral spots, and *P. s. melaventris,* the unmarked population found to the north and east of the other subspecies of *P. shermani.* Both of these have long been known as *metcalfi.*

Dunn lists *metcalfi* from Brasstown Bald, Georgia; Long Island, Alabama; between Andrews and Aquone, North Carolina. These are the three southernmost records, and actually lie beyond the range of *P. shermani.* It is interesting to note that Howell (1909) lists *P. shermani* from Brasstown Bald. Bailey however, relegates all of the Alabama and Georgia specimens to *P. glutinosus* except those from Rabun Bald, Georgia. The specimen from between Andrews and Aquone is apparently *shermani,* as Bailey and Grobman conclude. In view of the similarity of *P. s. rabunensis* to *P. glutinosus* we have examined all of the available specimens from northern Georgia. Two of these (USNM 86834–5) cannot be assigned to *glutinosus.* These two specimens from Vogel State Park, Lumpkin County, Georgia, although hard and shrunken, are definitely assignable to *P. s. rabunensis.* One has white lateral markings of the *shermani* type; the other is unmarked. The vomerine tooth counts, 10–9 and 9–8, are low for *glutinosus,* and the bellies of both, "1" on our scale, are paler than any *glutinosus,* all of which we would rate as "3" or "4." Howell's single specimen (USNM 45358) from Brasstown Bald is apparently *rabunensis* (vomerine teeth 9–8, belly "3"). It is in a worse state of preservation than the Vo-

gel specimens. Bailey's large series from Vogel State Park and adjacent Blood Mountain (UMMZ 76334–66) are definitely *glutinosus,* having black bellies, high tooth-counts, and extensive white spotting of the *glutinosus* type.

The following key will be helpful in identifying the six forms of the *jordani* group:

Red markings
  Cheeks red (Great Smoky Mountains). *P. jordani*
  Legs red (Nantahala Mountains). *P. s. shermani*
No red markings
  With other markings
    Brassy dorsal markings and white lateral spots (Jocassee).....*P. s. clemsonae*
    White lateral spots only (northeastern Georgia).....*P. s. rabunensis*
  Immaculate
    Belly black (South of Balsam Mts. and Swannanoa R.).....*P. s. melaventris*
    Belly pale (North and east of *melaventris*). *P. metcalfi*

Considerable difficulty may be encountered in separating *P. s. melaventris* from *P. metcalfi.* In this case, the provenance of the puzzling specimens should be helpful.

Evolution and Intrageneric Relationships

Primitive characters in the genus *Plethodon* are large size, long vomerine series, lack of sexual dimorphism, and a colored dorsal pattern (either spots or a stripe). Considering these characters collectively, *metcalfi* is the most specialized member of the group, and *clemsonae* is the most primitive. Of the remaining four, *rabunensis* is next to *clemsonae,* whereas *shermani, jordani* and *melaventris* cannot be arranged in sequence with certainty. *P. s. shermani* and *jordani* are primitive in the retention of dorsal markings in the juveniles, but *melaventris* has longer vomerine series. *P. jordani* is smaller than the other two, although the difference is slight and may not be significant. However, since it is a distinct species, and more like *metcalfi* in altitudinal distribution, it may be ranked next to that form in degree of specialization.

In altitudinal distribution *clemsonae* is sharply set off from the other forms as the only one confined to and occurring in the low elevation on the edge of the Piedmont plateau. The other five ascend to the tops of the humid, forested mountains on which they live and, with the exception of *melaventris,* descend to elevations between 3000 and 2300 feet. *P. s. melaventris* occurs as low as 1200 feet. We conclude that the tolerance for low altitude in *clemsonae* is further evidence of its primitiveness. This form appears to be a relict, confronted on the south by the drier and mostly deforested Piedmont country, and on the north by its close relative, the more successful *melaventris* (fig. 10). The locality inhabited by *clem-*

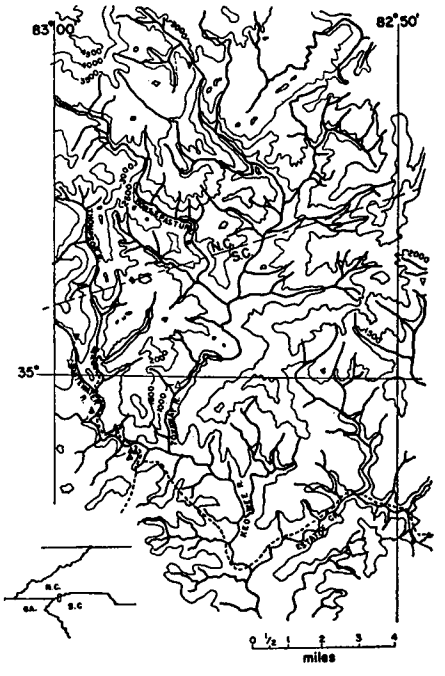

Fig. 10. Contour map of the headwaters of the Keowee River, showing collecting sites of *Plethodon shermani clemsonae* (triangles) and *P. s. melaventris* (inverted triangles). Contour interval 500 ft. Adapted from U. S. Geological Survey, Pisgah and Pickens Quadrangles. Inset map shows location of area.

sonae also harbors the relict plant *Shortia galacifolia,* which has a closely similar if not identical range (House, 1907).

There is a trend for the more specialized members of the *jordani* group to be increasingly restricted to higher elevations with increasing latitude. This is contrary to expectations, which would place the more southern forms at higher altitudes.

The key to the situation seems to lie in the relationships of this group to the other large species of *Plethodon* inhabiting the area, namely, *glutinosus* and *yonahlossee.* Superficially, resemblance of the *jordani* group, especially *rabunensis,* is more to *glutinosus* than to *yonahlossee,* but this may be due to parallel evolution. The group is closer to *glutinosus* in the smaller number of vomerine teeth, but is more like *yonahlossee* in retention of the dorsal color pattern and general body proportions. As far as tooth-counts are concerned, the loss of vomerine teeth occurs independently in many plethodont genera, and *P. wehrlei,* admittedly close to *yonahlossee,* has few vomerine teeth.

Of some importance are the geographical and ecological relations. *P. glutinosus,* although partially separated altitudinally from certain members of the *jordani* group, overlaps all of them geographically. *P. yonahlossee,* on the other hand, is separated geographically from all of the *jordani* group except *metcalfi,* the most specialized member (fig. 11).

Without raising the question of whether geographic variation is the universal method of speciation (Mayr, 1942, 1947), such variation evidently occurs within the *jordani* group. There is no reason to doubt that the original separation was achieved in this manner. The region has been ideally suited to this type of speciation since the close of the Paleozoic.

If the present distribution, geographical and vertical, is of any value in determining phylogenetic relationships, *yonahlossee* rather than *glutinosus* appears to be the ancestor of the *jordani* group, a conclusion not unwarranted on morphological grounds. This theory postulates:

(1) Speciation by geographic isolation into *yonahlossee* (northern) and the ancestor of the *jordani* group (southern).

(2) Speciation (evidently still geographic) of the *jordani* group.

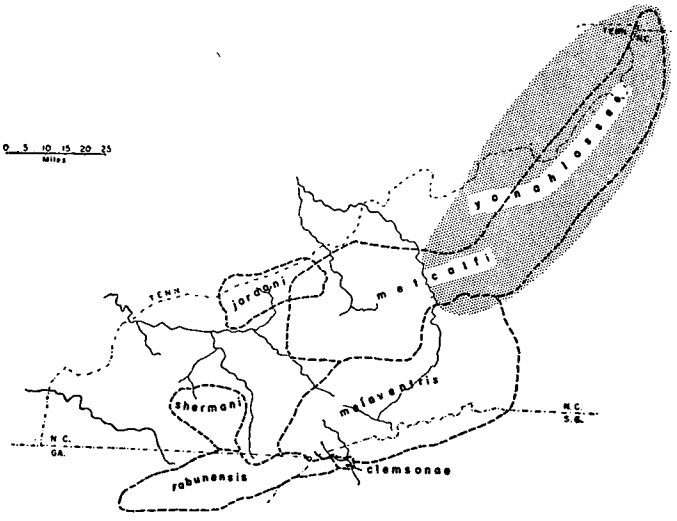

FIG. 11. Distribution of the members of the *jordani* group (broken lines) and of *P. yonahlossee* (shaded). *P. glutinosus* is widely distributed in the eastern United States.

(3) Invasion of the range of *yonahlossee* by *metcalfi*, the most specialized and presumably the most ecologically divergent, and consequently the least competitive, member of the *jordani* group.

It may be argued that *glutinosus* is the ancestor of the *jordani* group and that the present situation is the result of a re-invasion by *glutinosus*. The difficulty here lies in the fact that the overlap by *glutinosus* is most complete in the case of the primitive, low-altitude members of the *jordani* group and least complete in the case of the high-altitude *metcalfi*. This species would presumably be the most divergent ecologically, and would therefore offer the least amount of competitive resistance to such re-invasion.

The ecological argument for *yonahlossee* ancestry is based on the assumption that in the varying requirements of the *jordani* group, *metcalfi* is furthest from the original. We realize that theoretically the reverse may be true, but there is no supporting evidence. Morphological and ecological changes are generally correlated, especially in the Plethodontidae (cf. *Desmognathus*).

Although Bishop (1941) has stated that the group is derived from *glutinosus*, and others have implied the same, Bailey (1937) doubts that such is the case.

Divergence Within the Group

In considering speciation within the *jordani* group, rivers and mountain ranges are both a help and a hindrance, since it is not always clear which have been the isolating factors. Following the original separation from *yonahlossee* by the French Broad valley, the first isolation was that of *metcalfi* in the northeast. The evidence for this is the greater specialization of this form, as well as its present range on both sides of the French Broad River. We advance the thesis that the territory now occupied to the northeast of this river represents an extension of the original range. *P. metcalfi* has been able to extend its range because it occupied the favored northeastern position, this being the only direction in which any member of the group could find suitable ecological conditions. To the south, west and northwest, the mountains end abruptly, limiting the remaining members of the *jordani* group about to their original positions.

Following the separation of *metcalfi*, the second step was the isolation of *jordani*; this is borne out by its obviously close alliance to *shermani*, as seen especially in the juveniles of the two forms. The isolation of *jordani* from *shermani* apparently was accomplished by the deepening of the valley of the Little Tennessee River (Bailey, 1937). It is interesting to note that *metcalfi* has been able to invade the eastern end of the range of *jordani*, although there must be considerable competition between the two species.

The remaining members are still connected, although tenuously so, especially around the headwaters of the Little Tennessee River. It is likely that the area east of the French Broad and south of the Swannanoa Rivers, now occupied by *melaventris*, represents an extension of the range of this form, as the area is largely lacking in territory suitable to *metcalfi* with its preference for high altitudes.

Summary

Geographic variation in the *Plethodon jordani* group was studied by analyzing a number of characters in large samples from nine critical localities. Three allopatric forms between which gene flow has apparently ceased were distinguished on the basis of this analysis; one of these is polytypic, the other two monotypic.

The characters analyzed overlap in such a way in the polytypic form that the situation cannot be accurately represented by nomenclature. This necessitates a somewhat arbitrary taxonomic assignment of names to the various populations.

Speculations are made on phylogeny and relationships. These speculations are based on the morphology and on the present distribution, not only of the *jordani* group but of certain more primitive spe-

cies of *Plethodon* as well. The conclusion is that speciation has resulted from geographic isolation, a process that is evidently continuing.

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