THE DISTRIBUTION OF LEUROGNATHUS
A Southern Appalachian Genus of Salamanders

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INTRODUCTION

The speciation of the southern Appalachian Plethodontidae presents many interesting zoogeographic problems. This speciation is evidently correlated with long isolation on these ancient, deeply eroded highlands. Nowhere else are the results of salamander evolution so plentiful. The over-all picture is extremely complex and can hardly be understood until the component parts have been studied individually and intensively. The genus Leurognathus, with its two forms, is one of these parts well suited for intensive investigation because of its relative simplicity. Moreover, its range is confined to the region and its derivation from Desmognathus certain.

It is but recently that sufficient locality records of this rare genus have warranted a comprehensive study. Discoveries of the last few years convince us that the approximate total distribution is now known.

DISTRIBUTION

The first specimen of the genus Leurognathus was collected on Roan Mountain, Carter County, Tennessee, by Rhoads in 1895, but was listed as Desmognathus nigra (= D. quadramaculatus). Rhoads should not be severely censured for this mistake because similar ones are still being made. These mistakes emphasize the striking superficial similarity between species of the two genera. Only the most experienced and painstaking workers can recognize Leurognathus without difficulty.
This genus was not described until 1899, when Moore erected it on the basis of three specimens collected by him in Avery County, North Carolina, on the southern flank of Grandfather Mountain, at an altitude of 3,500 feet.* No further material was reported until 1917. In that year Dunn collected a larva at Pineola, Avery County, which led to recognition of Rhoads' Roan Mountain specimen, and one from Blowing Rock, Watauga County, overlooked by Moore himself. These facts were brought out in two papers by Dunn and one by Fowler and Dunn, all published in 1917. The range of the genus was greatly extended by the next specimen collected. This was reported by Dunn in 1924 from Jones Cove, Haywood County, North Carolina.

With the exception of five topotypes collected by Bishop and reported by him in 1924 and a series of 28 from the region of the type locality (Boone Fork, Watauga County) collected and reported in 1924 by Pope, no further material was found until 1927. The monotypic status of the genus was changed in 1928 by Pope, who described the series he collected in 1927 at and near Davis Gap, Haywood County, North Carolina, as *Leurognathus marmorata intermedia.* Later in the same year Bishop reported a salamander from Frying Pan Mountain, also in Haywood County, as *L. marmorata*. This individual has subsequently (Bishop, 1943) been referred to *intermedia*; Dunn's Haywood County *marmorata* long ago met the same fate (Pope, 1928).

Only a few distributional records of the genus remain to be enumerated. In 1937 Bailey extended the range of *marmorata* to the following North Carolina localities: Montreat, Buncombe County; Ramsaytown, Yancey County; two localities near Linville Falls, one in McDowell County and one in Burke County. King in 1944 reported *intermedia* from these three places in the Great Smoky Mountains: Abrams Creek and Cades Cove, Blount County, Tennessee, and Smokemont, Swain County, North Carolina. He believed these to be the first Tennessee records of the genus, evidently because of the confusion resulting from the straddling of the North Carolina-Tennessee line by Roan Mountain, where Rhoads obtained the first specimen.

In giving the generic range in his handbook (1943) Bishop includes Caldwell, Henderson, and Haywood counties, North Carolina, in the distribution of *marmorata* but adds no further details. We learn from him (letter of June 10, 1947) that the Caldwell County series in the United States National Museum was taken 9½ miles
Fig. 28. Map of North Carolina and adjacent areas, showing distribution of species of *Leurognathus*. Circles = *marmorata*; triangles = *intermedia*. Solid symbols indicate literature records, open ones new records. The circle with a cross indicates a sight record. The French Broad River (solid line) separates the two species. The broken line outlines the Blue Ridge Physiographic Province. White Top Mountain, Virginia, is indicated by X; Copperhill, Tennessee, by Y.
southwest of Blowing Rock; the Henderson County record is based on a larva (78 mm. long) from Stony Mountain, which lies about three miles northwest of Hendersonville and reaches an altitude of 2,843 feet. His listing of *marmorata* from Haywood County actually refers to an old record of *intermedia* from there.

Recent field work by both of us and examination of series of "*Desmognathus*" in the Chicago Academy of Sciences\(^1\) and Chicago Natural History Museum have brought to light important new material. In the summer of 1946 the range of *intermedia* was extended to extreme northeastern Georgia, when Whitney Pope secured a large specimen near Mountain City, Rabun County. Another was caught on Standing Indian, a mountain about twenty miles to the northwest but in North Carolina. These are now C.N.H.M. 47771 and 47772, respectively. Examination of the Museum series referred to above revealed seventeen Great Smoky Mountains specimens of *intermedia* masquerading as species of *Desmognathus*; all came from the immediate vicinity of Greenbrier Cove, Sevier County, Tennessee. Hairston collected *marmorata* at Duncan Cove Creek in western McDowell County, North Carolina, near the Yancey County boundary.

All of the locality records enumerated above are shown on the spot map. A study of the map reveals two facts about the two salamander populations hitherto designated as *L. m. marmorata* and *L. m. intermedia*: they are discrete and both are confined to the mountains. The only physical separation of the two populations is the valley of the French Broad River. Although this river, which in our area flows at relatively high elevations (about 2,000 to 1,200 feet), would not seem to be a serious barrier to a mountain stream salamander, the fact remains that it does divide them. Furthermore, *Leurognathus* is not the only plethodontid genus in which this phenomenon occurs: *Pseudotriton ruber nitidus* and *P. r. schenckii* are separated by the same valley. It is also interesting to note that the range of *Plethodon yonahlossee* ends with this valley.

The range of *Leurognathus* is confined to the southern part of the Blue Ridge Province. In contrast to this correlation with physiography, we find no watershed correlation, both forms being found in Atlantic and Gulf drainages.

We feel that the records on our map approximately delimit the total range of the genus because (1) to the northeast, extensive collecting by various experienced herpetologists at White Top Moun-

\(^1\) We are indebted to Director Howard K. Gloyd for his generous cooperation.
tain, Virginia, has failed to reveal specimens; (2) to the southwest, in the region of Copperhill, Tennessee, the vegetation has been destroyed; (3) elsewhere the natural habitat of the salamanders is eliminated with the abrupt change in physiography. Further collecting in Transylvania, Henderson, Buncombe, and Madison counties (all outlined on the map) will test the validity of the French Broad Valley as a natural boundary separating the two forms.

ECOLOGY

Little is known of the ecology of *Leurognathus*. This ignorance stems partly from the comparative rarity of both forms, and partly from the fact that most collectors have been interested only in distribution. All observers are agreed that the genus is purely aquatic; no specimen has ever been taken elsewhere than in mountain streams, not even along the banks under rocks such as form typical hiding places for several species of *Desmognathus*. *Leurognathus marmorata* has been recorded solely from the larger streams, whereas *intermedia* was first collected from a bare trickle (Dunn, 1924), and
later observers have tended to confirm a preference for the smaller streams. Although this is an inconsequential difference in itself, possibly there is a correlation with other more basic ecological separations; different types of food is one worthy of investigation.

Furthermore, *intermedia* would seem to be the more tolerant of variations in altitude, both high and low (see fig. 29); until now, *marmorata* has been reported only from altitudes between 3,000 and 4,000 feet, whereas *intermedia* has been found from 1,700 (King, 1944) to 5,400 feet (Bishop, 1928). The upward distribution of *marmorata* may well be limited by the small creeks at higher elevations, a factor that would not affect *intermedia*. However, it is difficult to account for its absence from apparently acceptable streams at lower elevations than those reported. The single low-altitude record (1,900 feet) of *marmorata* given herein might be a specimen washed down in the severe flood that occurred four months earlier. An important limiting factor could be the preference of herpetologists for the higher elevations, particularly on Grandfather Mountain, where the road is placed conveniently at 4,000 feet, and high-altitude desiderata, such as *Plethodon welleri*, tempt the collector to ascend the mountain rather than to go down its more precipitous slope below. Perhaps a more thorough search along the foot of the Blue Ridge escarpment would bring more low-altitude specimens to light, just as similar collecting on the west face of the Smokies has recently revealed the presence of *intermedia*.

The breeding habits of *L. marmorata* are much like those of *Desmognathus quadramaculatus* (Pope, 1924), and *L. intermedia* probably will prove to have similar ones.

**TAXONOMY**

The nineteen specimens of *intermedia* that inspired this paper have been discussed in a preceding section. Their characters are listed in the table. All fall within the recorded size range. Six of the nineteen have vomerine teeth, and this character is not correlated with sex; both sexes thus show a lower incidence than in the type series, a difference that is not significant. The dorsal pattern proves to be surprisingly diagnostic, 74 per cent showing the two rows of light spots. Those without spots are immaculate brown above. No indication of the zigzag design of *marmorata* is evident.

In the twenty years since the description of *intermedia* no intergrades have been reported. For this reason we are raising this form to specific rank. Those who do not regard intergradation as an
CHARACTERS OF *Leurognathus intermedia*

C.N.H.M. 47771 from Mountain City, Georgia; C.N.H.M. 47772 from Standing Indian Mountain, North Carolina; others from Greenbrier, Tennessee.

The costal grooves include one in the axilla and two in the groin; the intercostal spaces are counted between the tips of the adpressed toes.

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>Sex</th>
<th>Total length (in mm.)</th>
<th>Snout to vent length (in mm.)</th>
<th>Vomerine teeth</th>
<th>Costal grooves</th>
<th>Inter-costal spaces</th>
<th>Rows dorsal white spots</th>
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<td>95</td>
<td>50</td>
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<td>47</td>
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<td>14</td>
<td>3 1/2</td>
<td>2</td>
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essential criterion of subspecific status will no doubt continue to regard *intermedia* as a subspecies, a position to which we do not seriously object.

**DISCUSSION**

*Desmognathus quadramaculatus*, obviously the closest living relative of *Leurognathus*, has been assumed to be its direct ancestor by Dunn, Noble, and others. Ecologically, *Leurognathus* is a completely aquatic extrapolation of *D. quadramaculatus*. This fact is borne out by morphological characters: flattened skull, lack of vomerine teeth, more lateral location of the internal nares. We interpret the flattened head as an adaptation to bottom-crawling habits. The relative position of the two species of *Leurognathus* is clear: *intermedia*, with vomerine teeth and a simple pattern, is an early step, whereas *marmorata* is the end product. The wider vertical range of *intermedia* bears this out, indicating greater tolerance of a less specialized species. The larger size of *marmorata* is not a valid contradiction of this explanation, as size may have been secondarily acquired in correlation with a preference for larger streams.
REFERENCES

BAILEY, J. R.

BISHOP, S. C.

DUNN, E. R.

FOWLER, H. W. and DUNN, E. R.

KING, WILLIS

MOORE, J. P.

POPE, C. H.

RHOADS, S. N.