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THREE NEW SUBSPECIES OF *LEUROGNATHUS*  
*MARMORATA* FROM THE SOUTHERN  
APPALACHIAN MOUNTAINS

BY BERNARD MARTOF

SALAMANDERS of the genus *Leurognathus* have long been an enigma to most collectors. Actually, they have been regarded as somewhat of a rarity. This status is clearly indicated by even a brief survey of the literature. Encouraged by some good luck in collecting, I am now making a study of the biology of these salamanders. Surprisingly enough, I have found them to be abundant in most parts of their previously known range and in adjacent areas as well.

Knowledge of the genus *Leurognathus* dates from 1899 when Moore described *L. marmorata*. The next information was added by Pope (1928), who described *intermedia* as a subspecies of *marmorata*. Later, Pope and Hairston (1947) recognized *intermedia* as a full species. In the recent checklist, however, Schmidt (1953) relegated *intermedia* and *marmorata* to subspecific status, a classification that is followed in this report.

I am grateful to Robert Hellams, Jesse C. Nicholls, Jr., Donald C. Scott, Ralph Warner, and my sons Stephen and Andrew for their assistance in collecting specimens; to Robert L. Humphries and Donald C. Scott for the photographs and to Hugh Riley for preparing the map contained herein; to the University of Georgia Wildlife Conservation Fund and Graduate School for making possible much of the travel and for furnishing equipment necessary for this study; and to Charles F. Walker for useful suggestions concerning the style of presentation of this report.

An examination of 1,028 specimens collected in the last year has indicated that the populations of *Leurognathus* are composed of five subspecies, clearly separated geographically and morphologically.

The populations of *Leurognathus* occurring in the headwaters of the Chattahoochee and Tallulah rivers of northeastern Georgia and in the

southeastern extremity of Clay County, North Carolina, differ markedly from those of the two described forms, *intermedia* and *marmorata*. For this subspecies I propose the name

*Leurognathus marmorata aureata*, new subspecies

HOLOTYPE.—Adult male, UMMZ 111566; Jarrard's Creek, 0.2 of a mile below its crossing of U.S. Route 19, about 9 air miles north-northeast of Dahlonega, Lumpkin County, Georgia; 1,550 feet elevation; September 11, 1954; Stephen and Andrew Martof.

PARATOPOTYPES.—UMMZ 111567; 20 specimens, 10 of each sex; data as for holotype.

DIAGNOSIS.—Adults with no vomerine teeth; venter light medially; five to six large light dorsal spots on each side between verticals of limb insertions, these spots usually with bright yellow centers; dark reticulations on limbs and on dorsal surface of head; snout usually darker than body; soles of feet dark; ventrolateral row of light spots inconspicuous or absent; tail relatively long.

DESCRIPTION OF HOLOTYPE.—Adult male, total length 127 mm.; snout-vent length 68 mm. Body somewhat flattened, maximum dorsoventral diameter of trunk 9.8 mm., lateral diameter 13.4 mm. Fourteen costal grooves, counting separately two which run together in the groin. Maximum head width 11.5 mm., width of head at angle of jaws 10.6 mm., length of head 18.0 mm. Eyes prominent but small, oval-shaped, 3.7 mm. and 2.8 mm. in their greater and smaller diameters, interorbital distance 2.9 mm. Perpendicular distance, tip of snout to anterior margin of eye 5.1 mm. No vomerine teeth. Forelimbs 15.5 mm. from axilla to tip of longest digit; digits in order of increasing length 1-4-2-3. Hind limbs more robust, 19.6 mm. from groin to tip of longest digit; digits in order of increasing length 1-5-2-4-3. No webbing between digits. Tail at base somewhat flattened dorsoventrally, gradually becoming laterally compressed towards tip, which is rounded in profile; a prominent dorsal keel distally.

COLOR IN LIFE.—General dorsal color Light Brownish Olive (all capitalized color names from Ridgway, 1912) with irregularly shaped Blackish Brown patches separating dorsolateral light areas. Each light area with a round Light Orange-Yellow spot. These spots, 14 per side, extend from just posterior to the head along the back and onto the distal third of the tail, where the two rows converge. Spots on the tail somewhat brighter than those farther anterior. Dark dorsal pigment forming a reticulated pattern over the head and legs and the lateral

surfaces of the body. Tips of snout and tail darker than rest of dorsum. A light (Honey Yellow) marking extends from the eye over the anterior part of the brownish (Isabella Color) cheek to the angle of the jaws. Venter primarily Deep Neutral Gray with a large whitish central area between the forelimbs extending about two-thirds the distance to the vent. Edge of lower jaw strongly mottled brown (*Sepia*). Ventrolateral surfaces of tail suffused with yellowish (Empire Yellow) pigment. Soles of feet conspicuously Blackish Plumbeous; tips of the digits black.

VARIATION.—In total length the paratypes range from 97 to 131 mm., average 111.6 mm.; snout-vent measurement from 51 to 68 mm., average 59.2 mm. These specimens are the adults included in a series of 139 individuals taken on the same day. To date, the longest specimen which I have collected is a male with a snout-vent length of 74 mm. and a total length of 143 mm. It was taken at the type locality on May 8, 1954. All members of the type series possess 14 costal grooves on each side, counting 1 in the axilla and 2 in the groin.

In general, the paratypes show the same coloration as the type. The major differences are primarily in the intensity of the pigments rather than in pattern. About one-fourth are lighter (more golden) than the type, and about as many are somewhat darker in general body color. However, in the 475 specimens of this subspecies that have been collected, there are some interesting color variants. Perhaps the most striking are two specimens that, when living, were bright yellow with irregular-shaped large blotches of dark brown scattered over the entire body. Four other specimens are intermediate between the two individuals described above and those with the usual pigmentation. Another type of color variant has been observed in about 3 per cent of the specimens collected. In these the dorsum is heavily reticulated with dark pigment with no trace of light areas or yellowish spots. In about 28 per cent of the specimens the dorsal spots fuse over the base of the tail forming a zigzag marking. In about 20 per cent of the animals the reticulations on the head are obscured by dark pigment making the snout brownish black in color. In adults there is much variation in the extent of the ventral coloration. In some specimens dark pigment is almost completely absent; in others most of the venter is dark but not as intensely pigmented as most specimens of *marmorata* or as all specimens of *intermedia*. Specimens from the eastern part of the range (Tallah-Coleman rivers) are somewhat larger and more darkly pigmented dorsally.

The name *aureata* (*L. aureatus*, "adorned with gold") refers to the distinctive dorsal markings.

COLLECTION RECORDS:—In addition to the type locality, I have collected this subspecies at the following places:

*Georgia, Habersham Co.*, 5 air mi. NW Clarksville, Soque R., 1,575 ft. *White Co.*, Unicoi State Park, Smith Cr., trib. of Chattahoochee R., about 2,000 ft.; 1 air mi. S Nacoochee, trib. of Duke's Cr., Chattahoochee R. drainage, 1,350 ft.; 6 air mi. N Helen, Spoilcane Cr., trib. of Chattahoochee R., 2,500 ft. *Lumpkin Co.*, 6.5 air mi. NE Dahlonge, Frogtown Community, trib. of Chestatee R., 1,450 ft.; 2 air mi. S Neal's Gap, Frogtown Cr., trib. of Chestatee R., 2,200 ft.; Cedar Mt., Jarrard's Cr., 2 mi. above crossing of U.S. Route 19, trib. of Chestatee R., 2,000 ft. *Rabun Co.*, 6 air mi. NW Lake Burton Dam, Wildcat Cr., trib. of Tallulah R., 2,600 ft.; 2.5 air mi. NW Tiger, Timpson Cr., trib. of Tallulah R., 1,950 ft.; 4.5 air mi. N Persimmon Community, Bear Gap, trib. of Coleman R., 3,600 ft.; 3 air mi. N Persimmon Community, Coleman Camp, Coleman R., 2,680 ft.; 3.5 air mi. N-NE Persimmon Community, Persimmon Cr., trib. of Tallulah R., 2,100 ft. *Towns Co.*, 2 air mi. S Tate City Community, Tallulah R. at junction with Line Cr., 2,280 ft.

*North Carolina, Clay Co.*, 1 mi. S Standing Indian, Chimney Rock Branch, trib. of Tallulah R., 3,050 ft.

The populations of *Leurognathus* occurring in the headwaters of the Chattooga River are distinct from *intermedia*, *marmorata*, and the above-described *aureata*. For this subspecies I propose the name

***Leurognathus marmorata roborata*, new subspecies**

HOLOTYPE.—Adult male, UMMZ 111568; Reed Creek, along Burrell Ford Road, 0.5 of a mile from its junction with Glade School Road, about 3.5 miles northwest of Pine Mountain Community, Rabun County, Georgia; 2,350 feet elevation; September 18, 1954; the Bernard Martof family.

PARATOPOTYPES.—UMMZ 111569; 20 males and 6 females; data as for holotype.

DIAGNOSIS.—Adults, with no vomerine teeth. Venter darker than in *aureata* but not as dark as in other subspecies; a light area medially. Body large and robust; head very long, relatively wide at angle of jaws. Dark heavily mottled dorsal pattern with a dorsolateral row of small bright yellow spots on each side.

DESCRIPTION OF HOLOTYPE.—Adult male, total length 131 mm.; snout-vent length 74 mm. Body stout, maximum dorsoventral diameter 11.4 mm., lateral diameter 15.1 mm. Costal grooves 14, counting separately two which run together in the groin. Maximum head width 13.6 mm., width of head at angle of jaws 12.2 mm., length of head 19.8 mm. Greater and smaller diameters of eye, 4.5 mm. and 3.6 mm.; interorbital distance 3.1 mm. Perpendicular distance, tip of snout to anterior margin of eye 5.7 mm. No vomerine teeth. Forelimbs 16.3 mm. from axilla

to tip of longest digit; digits in order of increasing length 1-4-2-3. Hind limb 20.4 mm., digits 1-5-2-4-3. No webbing between digits. Tail with prominent dorsal keel (notched as a result of use).

**COLOR IN LIFE.**—General dorsal color uniform Dark Olive with many small light spots and flecks. The larger of these spots located dorso-laterally, with those at the base of the tail the largest. Five such dorso-lateral spots on each side of trunk between the fore- and hind limbs, all with a small Citron Yellow center becoming Buffy Olive toward the outer edge. Light dorsal flecks also Buffy Olive. Snout darker than other parts of dorsum. Sides of the body Dark Olive, becoming Light Grayish Olive ventrally. Venter pigmented Deep Neutral Gray with an irregular-shaped central whitish area between the fore- and hind limbs. Darkest part of venter around the vent, the lightest in the throat region. A light marking from eye to angle of jaws. Cheek and edge of lower jaw dark olive brown, the latter with light flecks. Soles of feet dark brown, tips of digits black.

**VARIATION.**—The type series is composed of the adults in a collection of 66 specimens taken on the same day. In total length they range from 96 to 133 mm., average 121.3 mm.; in snout-vent measurement from 54 to 76 mm., average 67.9 mm. The largest *roborata* I collected was taken in King Creek, Oconee County, South Carolina, on August 1, 1954. It is a male with a snout-vent measurement of 76 mm., but in total length it measures only 134 mm. because of a partly regenerated tail. All specimens have 14 costal grooves.

Twenty-one of the 26 paratypes have dorsal patterns and coloration which closely approximate those of the holotype. The dorsal markings of three of the specimens are so dark that the usual mottled pattern is largely obscured. In two others the dorsal markings are typical except for the absence of the yellow spots. All others have five or six spots between the fore- and hind limbs, average 5.1. In position the dorso-lateral spots are opposite each other on most specimens, especially over the posterior half of the trunk. On the anterior third they tend to alternate. None shows the light areas around the dorsolateral spots which are characteristic of *aureata*. In all specimens the snout is the darkest part of the dorsum. In all paratypes the dark lateral coloration extends onto the venter; nevertheless, there is much variation in its extent and intensity. The usual pattern is that of the holotype—an irregularly shaped, light, central area between the fore- and hind limbs. In one specimen, only a trace of this light area is present.

The name *roborata*, derived from the Latin word *roboratus* meaning "strengthened" or "made strong," refers to the stout, robust body.

COLLECTION RECORDS.—In addition to the type locality, this subspecies has been collected at the following places:

*South Carolina, Oconee Co.*, 4 air mi. N Oconee State Park, King's Cr., trib. of Chattooga R., 2,350 ft.; 0.2 mi. S North Carolina on S. C. Route 107, East Fork Chattooga R., 2,740 ft.

*North Carolina, Jackson Co.*, 5.5 air mi. S-SE Cashiers, Mulkey Gap, East Fork Chattooga R., 3,050 ft.; 6 air mi. S-SE Cashiers, Scotsman Cr., trib. of Chattooga R., 2,650 ft.

*Georgia, Rabun Co.*, 6 air mi. E-SE Clayton, Licklog Cr., trib. of Chattooga R., 1,400 ft.; 2 air mi. SE Clayton, Chechero Cr., trib. of Chattooga R., 1,550 ft.

The *Leurognathus* from western North Carolina and adjacent Tennessee are easily distinguished from the subspecies which have been described for this species. For these salamanders I propose the name

*Leurognathus marmorata melania*, new subspecies

HOLOTYPE.—Adult male; UMMZ 111564; Otter Creek, tributary of the Nantahala River, 0.5 of a mile west of Tellico Gap, Macon County, North Carolina; 3,600 ft. elevation; September 4, 1954; the Bernard Martof family.

PARATOPOTYPES.—UMMZ 111565; 9 males, 11 females; data as for holotype.

DIAGNOSIS.—Vomerine teeth present in all females and all but the largest males. Venter darker and more uniformly pigmented than in other races. Coloration very dark. Dorsum of adults usually uniformly pigmented, devoid of pattern. Dorsal pattern of subadults and of those few adults in which it is perceptible (about 5 per cent) suggestive of that of *intermedia*, but dorsolateral markings darker and greatly reduced in size, about one-fourth the diameter of those of *intermedia*, and usually absent from head and neck. Tip of tail pointed.

DESCRIPTION OF HOLOTYPE.—Adult male, total length 120 mm.; snout-vent length 68 mm. Maximum dorsoventral diameter of trunk 8.7 mm., lateral diameter 11.2 mm. Fourteen costal grooves on each side, counting separately two which run together in the groin. Maximum head width, just anterior to gular folds, 10.9 mm.; width of head at angle of jaws 9.8 mm.; length of head 16.5 mm. Eyes oval-shaped, 3.4 and 2.6 mm. in the greater and smaller diameters. Interorbital distance 2.4 mm. Perpendicular distance, tip of snout to anterior margin of eyes 4.2 mm. Vomerine teeth, 1 on each side. Forelimbs 13.0 mm. from axilla to tip of longest digit; length of hind limb 17.1 mm. Digits same relative length as in other subspecies. No webs between digits. Tail with fin moderately well developed, tip more pointed than in other *Leurognathus*.

**COLOR IN LIFE.**—General dorsal color dark brownish black with no distinct pattern evident as in other subspecies. Dorsum (under close examination) grayish black mottled with dark grayish brown. The head, especially the snout, slightly lighter than the rest of the dorsum. Venter almost uniform grayish black, the lightest parts being the soles of the feet; the throat is the lightest part of the body, the base of the tail the darkest. A row of light dots at level of limb insertion from near the axilla to the groin. Vent conspicuous, white, with scattered black melanophores in its posterior half. Sides of the body dark, intermediate in coloration between the venter and dorsum. Soles of feet and tips of the digits grayish brown.

**VARIATION.**—The type series has an average total length of 117.8 mm., range 107 to 133 mm., average snout-vent measurement 65.4 mm., range 57 to 73 mm. The longest specimen in my collections is a male which has a total length of 142 mm. and a snout-vent measurement of 75 mm. It was taken near the head of Choga Creek, Macon County, North Carolina. All paratypes possess 14 costal grooves. All females have vomerine teeth, as many as three per side. Only 6 of the 12 males have these structures. In general, vomerine teeth are lacking in the males above 70 mm. in snout-vent measurement; however, one 62 mm. male has none. Furthermore, the males with vomerine teeth have fewer teeth than do the females; average for these males is 1.8 teeth, as opposed to 3.3 for females.

All paratypes possess the same general coloration as the type specimen. A slight variation is evident dorsally in four of the smaller paratypes. They are somewhat more brownish than the others and one has a dorsal pattern of light markings. Ventrally, the paratypes are more variable. In contrast to the uniform coloration of the holotype, about half of the specimens have white flecks scattered over the venter. These flecks are most abundant over the throat region. Most subadults have dorsolateral rows of small dots suggesting the pattern of *intermedia*. In some adults this pattern can still be seen, especially in specimens from the vicinity of Birdtown, Swain County, North Carolina. In general, those specimens showing a dorsal pattern are not as melanistic as others, i.e., they have a lighter brownish body color.

*Melania*, from a Greek word meaning "blackness," refers to the dark coloration.

**COLLECTION RECORDS.**—In addition to the type locality this race has been collected in the following places:

*North Carolina, Graham Co.*, about 5 air mi. E-NE Andrews at Dry Cove Branch, trib. of Tulula Cr. of the Cheoah R. drainage, about .3 mi. above where it crosses U.S. Route 129 near base of Snowbird Mts., 2,800 ft. *Macon Co.*, 1.3 mi. NE Topton

on U.S. Route 19, Rowlin Branch, trib. of the Nantahala R., 2,300 ft.; 8 air mi. E-SE Andrews, head of Choga Cr., trib. of Nantahala R., about 4,000 ft. *Macon-Swain Co. line*, Bradley Cr., trib. of Nantahala R., above crossing of U.S. Route 19, 2,000 ft. *Swain Co.*, about 13 air mi. NE Andrews, DeHart Branch of Wesser Cr. of Nantahala R. system, about 2,800 ft.; Cherokee Indian Reservation, about 0.5 mi. N Birdtown, Adams Cr., trib. of Oconaluftee R., 2,400 ft. *Clay Co.*, 0.1 mi. E Glade Gap on N. C. Route 64, Glade Branch, trib. of Buck Cr. of Nantahala R. system, 3,600 ft.; 2 mi. E-NE Deep Gap, Buck Cr., 3,750 ft.

*Tennessee, Sevier Co.*, 5 mi. E Pittman Center, trib. of Webb Cr. of Little Pigeon R. system, 1,680 ft.

#### COMPARISONS AND RELATIONSHIPS

Because I collected large numbers of *Leurognathus* from all parts of its known range, I did not examine the relatively few specimens available in other collections. Accordingly, it was possible to make comparisons (Table I) of these newly described subspecies with recently collected topotypes of both *intermedia* and *marmorata*.

The longest specimen taken is an *aureata*. It is 143 mm. in total length. The longest *roborata* is 139 mm., *melania* 142 mm., *intermedia* 131 mm., and *marmorata* 133 mm. It should be noted, however, that Bishop (1943) reported a *marmorata* with a total length of 145 mm. In contrast to the total length, the maximum snout-vent measurements, ranging only from 75 to 77 mm. for all the subspecies, are very similar. Generally, the snout-vent measurement is a more reliable indication of size than is the total length because the tail may be in various stages of regeneration. On the other hand, a comparison of average sizes of adult specimens indicates that *aureata*, with an average total length of 111.6 mm. and an average snout-vent measurement of 59.2 mm., is smaller than the other races and that *roborata*, having average measurements of 121.3 and 67.9 mm., is the largest of the subspecies. As a rule, the larger specimens of all subspecies are males, an indication that sexual dimorphism in body size exists in this genus.

The incidence of vomerine teeth among the subspecies of *Leurognathus* is of special interest. They are absent in all the adult *aureata* and *roborata* examined. All but one specimen of *marmorata* lack vomerine teeth, the exception (a female) has but a single tooth. These subspecies are in sharp contrast to *intermedia* and *melania* wherein all females have vomerine teeth, the average total number being 3.3. Among the larger males of the last two subspecies mentioned, vomerine teeth are generally absent. Thus, this preliminary survey of vomerine teeth suggests that *intermedia* and *melania* are closely related; so, too, are *aureata* and *roborata*. Furthermore, *aureata* and *roborata* are more closely related to *marmorata* than are *intermedia* and *melania*.



Moreover, relationships among the subspecies are indicated by their dorsal markings. The number of light areas, spots, or dots on each side of the body between the fore- and hind limbs provides a quantitative indication of these relationships. *Intermedia* is the most obviously spotted member of the group. It has, on the average, 7.8 spots per side. In the few specimens of *melania* whose spots could be counted (mainly subadults) an average of 7.5 per side was noted. In general, the spots on one side of *intermedia* and *melania* are opposite those of the other side. In contrast, *aureata* with an average of 5.2 spots per side and *roborata* with 5.1 light dots on each side are again in a group by themselves. *Marmorata* has 6.3 light areas per side and once more is intermediate between the two groups mentioned above. As a rule, the dorsal markings of *aureata*, *roborata*, and *marmorata* are alternate in position; however, in many individuals the markings on one side are opposite those of the other side. In addition to having fewer dorsal markings, *aureata* and *marmorata* have proportionately larger markings than *intermedia* has. The markings of *roborata* are largely obscured by dark pigments and those of *melania* are usually completely obscured.

Ventrally *aureata*, *roborata*, and *marmorata* have similar patterns but generally *aureata* is the lightest, *marmorata* the darkest. Ventral pigmentation is similar in *intermedia* and *melania*; however, there is a tendency for *intermedia* to be more heavily flecked with light markings and for *melania* to be uniformly dark. Thus, the vomerine teeth and body markings, but not the average measurements of body size, suggest that *aureata* and *roborata* are more closely related to *marmorata* than are *intermedia* and *melania*.

An analysis of the ratios of the head width at the angle of the jaws to the snout-vent measurement for the various subspecies (Table I) serves to illustrate the relatively large head width of *roborata*. The ratios obtained for the other subspecies are too similar to be of value in ascertaining intraspecific relationships.

#### DISTRIBUTIONS

The distributions of the subspecies of *Leurognathus* are shown in Map 1, on which collection localities are plotted. *Marmorata*, the most eastern subspecies, is not shown; however, I have taken it in Yancey, Caldwell, Avery, and Watauga counties, North Carolina. A complete list of locality records is presented by Pope and Hairston (1947). In summary, *marmorata* occurs east of the French Broad River; its range is not in juxtaposition to those of the other subspecies.

TABLE I

A Comparison of the Subspecies of Leurognathus marmorata

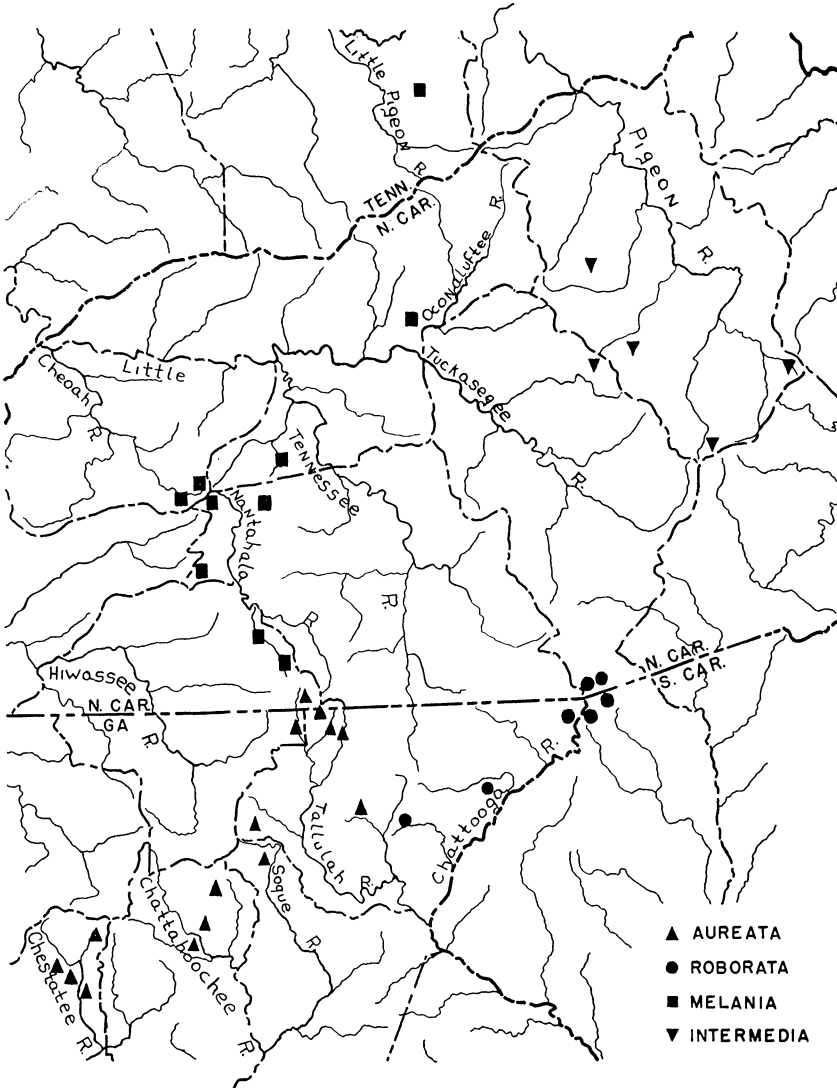
All measurements are in millimeters; those in parentheses apply to all specimens collected, others to topotypes only.

L = length; S-V = snout-vent length; T = tail length; HW = head width.

Subspecies	Total Number Collected	Number of Topotypes	Maximum Total L	Average Total L	Maximum S-V	Average S-V	Average T/S-V	*Average HW/S-V	Vomerine Teeth
<u>intermedia</u>	179	25	131	117.5	75	64.0	.805	.151	All ♀♀ Many ♂♂
<u>melania</u>	195	21	133 (142)	117.8	72 (77)	65.4	.810	.154	All ♀♀ Many ♂♂
<u>marmorata</u>	22	20	133	115.6	75	61.6	.866	.157	Few ♀♀ No ♂♂
<u>aureata</u>	474	21	127 (143)	111.6	68 (76)	59.2	.904	.155	None
<u>roborata</u>	158	27	134 (139)	121.3	75 (76)	67.9	.803	.162	None

\* Adjusted to compensate for uneven representation of sexes.

I have taken *melania* in the Nantahala, Cheoah, Oconaluftee, and Little Pigeon River drainages. The specimens reported by King (1944) from the Abrams Creek-Cades Cove area, Blount County, Tennessee, and from Smokemont, Swain County, North Carolina, in all probability are *melania*. It is of considerable interest that specimens of *melania* have not been found in the Hiwassee River drainage nor in the Little



MAP 1. The geographic distribution of four subspecies of *Leurognathus marmorata*.

Tennessee River drainage above its junction with the Tuckasegee River. On several occasions I have searched for them in these drainages but as yet with no success. On the basis of its relatively wide distribution and its primitive anatomical features (Dunn, 1926), e.g., the presence of vomerine teeth and the great similarity in coloration to that of *Desmognathus quadramaculatus, melania* appears to be the most primitive member of the *Leurognathus* group.

*Aureata* occurs in the following drainages: the Soque-Chestatee-Chattahoochee River system and the Coleman-Tallulah River system. Numerous attempts to locate this subspecies in the adjacent Hiwassee, Etowah, and Little Tennessee River drainages have likewise been unsuccessful. *Roborata* has the smallest range of all the subspecies. It is restricted to certain headwater streams of the Chattooga River system.

The distribution of *intermedia* is confined chiefly to the Pigeon River drainage, Haywood County, North Carolina. It does occur, however, in the adjacent Tuckasegee drainage. On September 21, 1954, Ralph Warner and I collected 46 specimens in the headwaters of Scott Creek near Balsam, Jackson County. These animals closely approximate those from the Pigeon River system. Meanwhile specimens from near Birdtown, Swain County, tend to approximate *intermedia* but are best classified as *melania*. It is anticipated that intergrades between *intermedia* and *melania* may occur in the eastern part of the Great Smoky Mountain National Park. This expectation is based on the close anatomical similarity of these two subspecies and on the tendency toward intergradation exhibited by the Birdtown specimens. On the other hand, an analysis of specimens from the headwaters of the Nantahala and the Tallulah rivers does not reveal any indication of recent gene flow between *melania* and *aureata*.

Thus the distributions of the various subspecies are closely correlated with drainage systems. Furthermore, field observations indicate that *Leurognathus* is aquatic. Accordingly, one would anticipate that the ridges between the various drainage systems are effective barriers to dispersal and, in general, the evidence presented here supports such a conclusion. There are, however, some noteworthy exceptions: (1) *melania* occurs on both sides of the Great Smoky Mountains; (2) *aureata* occurs in both the Atlantic and Gulf drainages; (3) *intermedia* occurs in the drainages of the Pigeon and Tuckasegee rivers; (4) *marmorata* occurs in both the Atlantic and Tennessee River drainages. In general, stream captures may have accounted for the distributional patterns of the subspecies of *Leurognathus*. Fenneman (1938) mentioned several pertinent examples of stream piracy which have occurred in

the southern Appalachians. Nevertheless, the absence of *Leurognathus* from several of the adjacent drainages where apparently favorable habitat exists is, as yet, not satisfactorily explained on the basis of the data at hand.

KEY TO THE SUBSPECIES OF *Leurognathus marmorata*

- 1 Vomerine teeth present in females, usually absent in large males; dorsolateral light markings, if present, opposite those of other side, 7 or more rounded spots per side between fore- and hind limbs; venter uniformly dark, sometimes with small light flecks ..... 2
- Vomerine teeth absent in all males and usually in all females; dorsolateral light markings usually alternate in position, 5-6 per side between fore- and hind limbs; venter usually with a large, light colored, central area ..... 3
- 2 Dorsal pattern spotted; general body color brownish ..... *intermedia*  
Dorsal pattern without light markings; general body color blackish .... *melania*
- 3 Light dorsal markings on body form a broad, conspicuous, zigzag pattern .... 4  
Light dorsal markings on body are small spots, usually no broad zigzag pattern is evident; body large, stocky, dark ..... *roborata*
- 4 Dorsal color lighter, more yellowish; dorsal light markings usually with bright yellow centers; dorsal part of head and limbs reticulated; snout tends to be darker than rest of body; eyes relatively small ..... *aureata*  
Dorsal color darker, more grayish; dorsal light markings lack light colored centers; dorsal part of head and limbs not reticulated; snout usually not darker than rest of body; eyes larger, more prominent ..... *marmorata*

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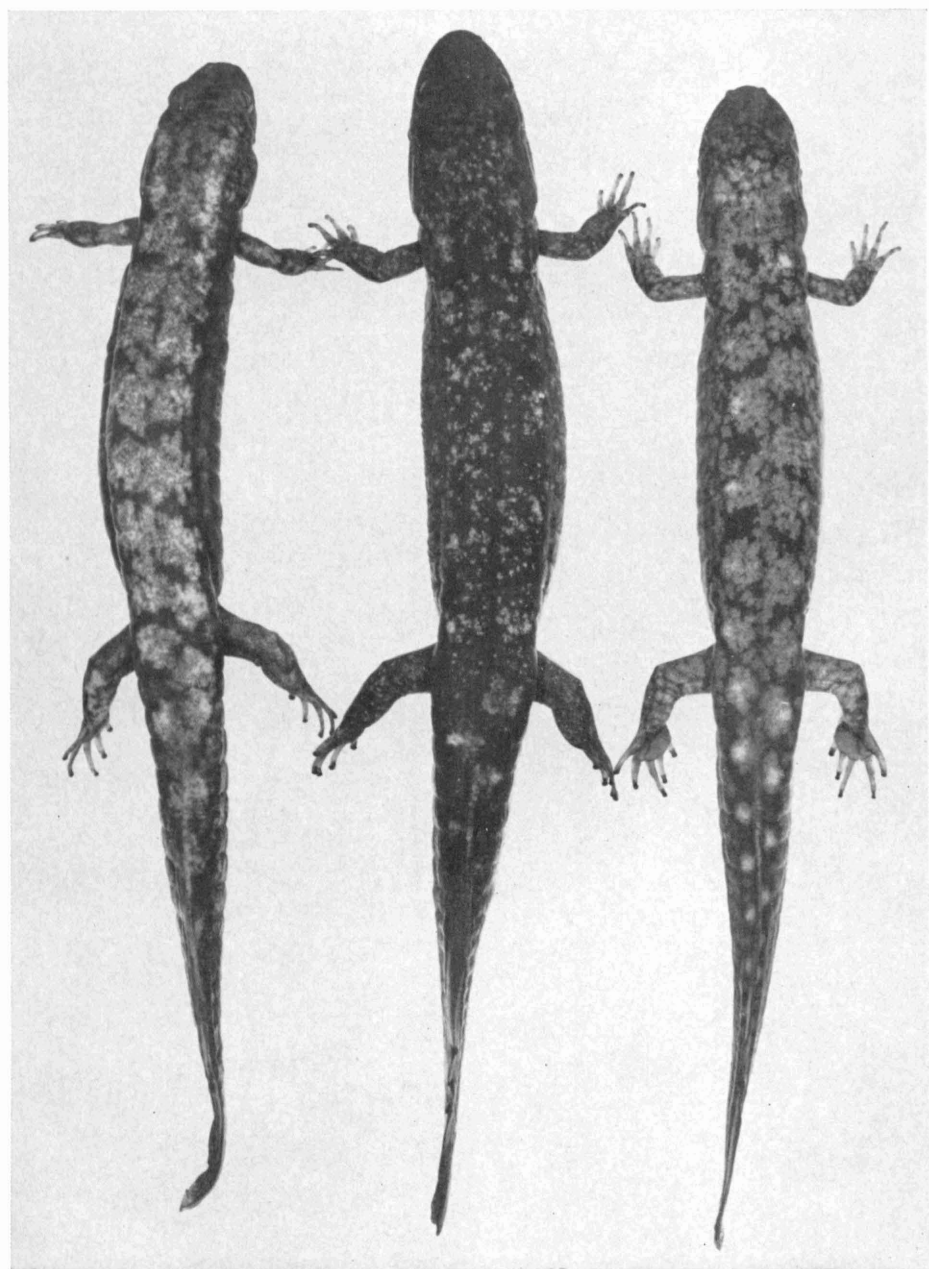
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PLATE I

Dorsal view of a topotypic specimen of *marmorata* (left) and of the type specimens of *robolata* (center) and *aureata* (right).

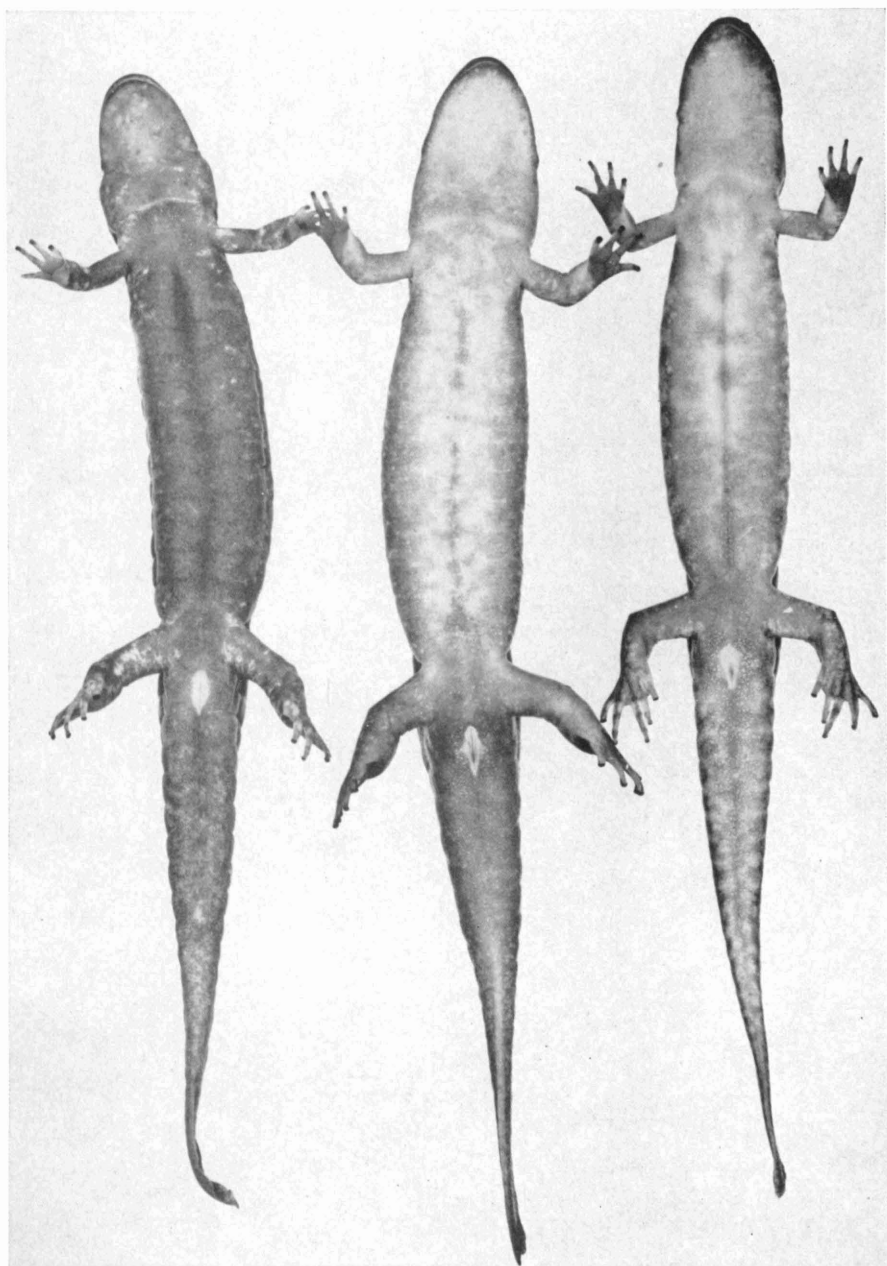


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PLATE II

Ventral view of a topotypic specimen of *marmorata* (left) and of the type specimens of *roborata* (center) and *aureata* (right).



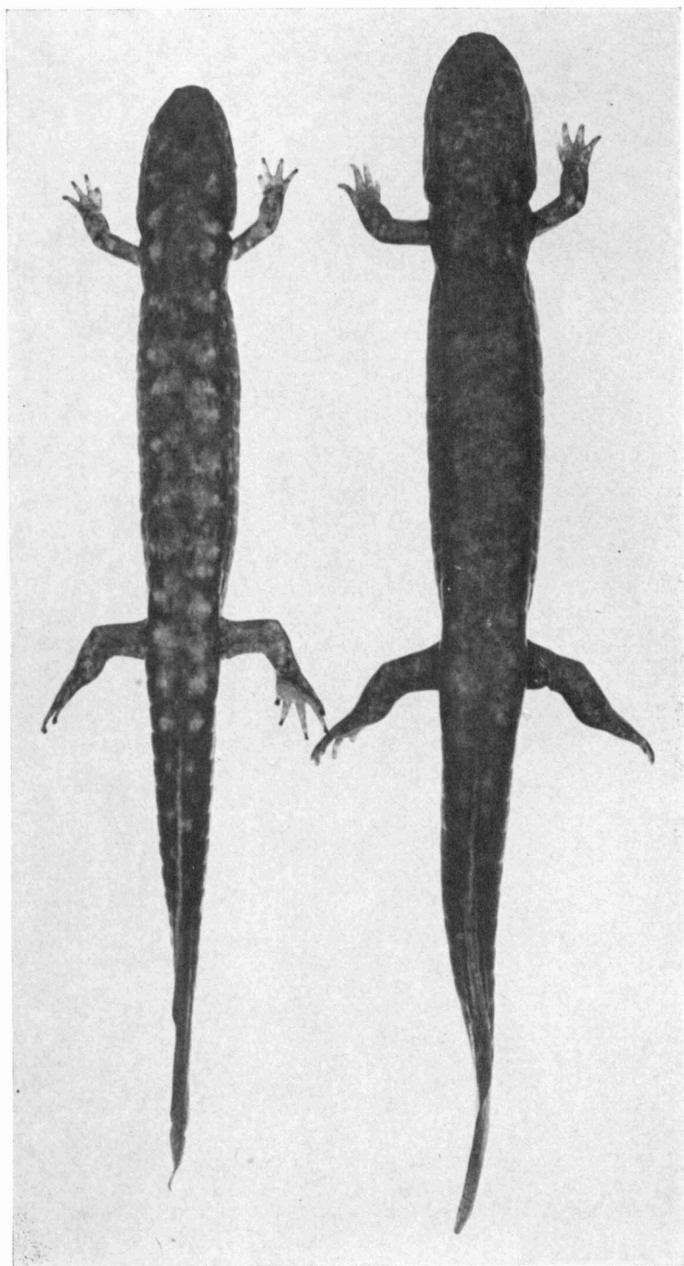


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PLATE III

Dorsal view of a topotypic specimen of *intermedia* (left) and of the type specimen of *melania* (right).

PLATE III



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PLATE IV

Ventral view of a topotypic specimen of *intermedia* (left) and of the type specimen of *melania* (right).

PLATE IV

