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A NEW SPECIES OF *DESMOGNATHUS* (AMPHIBIA:
CAUDATA: PLETHODONTIDAE) FROM THE SOUTHERN
APPALACHIAN MOUNTAINS

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In a recent study of electrophoretic variation among salamanders of the *Desmognathus fuscus* complex, Tilley and Schwerdtfeger (1981) showed that populations occurring in the Unicoi, Great Smoky, and Great Balsam Mtns. of the southwestern Blue Ridge Physiographic Province were distinct from populations in surrounding lowlands of the Ridge and Valley and Piedmont. We demonstrated that high and low elevation populations separated by only 6 km in the Citico Cr. drainage of the Unicoi Mtns. were fixed for alternative electromorphs at three of the 18 protein loci that were surveyed. The low elevation Unicoi Mtn. populations were more similar to those in the Ridge and Valley, Piedmont, and northern Appalachians than to high elevation populations in the same watershed, while the high elevation Unicoi Mtn. populations most closely resembled those in the Great Smoky and Great Balsam Mtns., 63 and 131 km distant. We concluded that high elevation populations of the Unicoi, Great Smoky, and Great Balsam Mtns. collectively warranted recognition as a separate species endemic to the southern Appalachians. I now formally describe this new form, document its morphological distinctness, and present the available information on its distribution, ecology, and genetic interactions with its close relative, *Desmognathus fuscus*.

METHODS.—Morphological measurements (Table 1) were made either with calipers to the nearest mm or with an ocular micrometer to

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TABLE 1
MORPHOLOGICAL MEASUREMENTS USED IN
THE DISCRIMINANT ANALYSES.

SVL measured to the nearest mm, all other characters to the nearest 0.1 mm.

Character	Explanation
SVL	Snout-vent length. Tip of snout to posterior margin of the vent.
AXW	Axillary width. Trunk width at the axilla.
PELW	Pelvic width. Trunk width above the hindlimb insertions.
HDL	Head length. Tip of snout to the posterior margin of gular fold.
HDHM	Head height at the jaw musculature.
HDHJA	Head height at the angle of the jaw.
HDWM	Head width at the jaw musculature.
HDWJA	Head width at the angle of the jaw.
IOW	Interorbital width. Distance between the orbits.
INW	Internarial width. Distance between the nares.
OND	Orbitonarial distance. Distance from orbit to nares on the animal's right side.
TWB	Tail width at base. Measured at the first caudal fold posterior to the vent.
TW5CF	Tail width at the fifth caudal fold posterior to the vent.
THB	Tail height at base. Measured at the first caudal fold posterior to the vent.
TH5CF	Tail height at the fifth caudal fold posterior to the vent.
VOMT	Number of vomerine teeth.
TOE1A-TOE4A	Lengths of the toes on the right forelimb, measured from web to tip along the medial margin of each toe.
TOE1P-TOE5P	Lengths of the toes on the right hindlimb, measured as on the forelimb.
FLL	Length of the right forelimb. Measured from the axilla to the tip of the longest toe.
HLL	Length of the right hindlimb. Measured from the groin to the tip of the longest toe.

the nearest 0.1 mm. The electrophoretic procedures were identical to those described in Tilley, et al (1978) and Tilley and Schwerdtfeger (1981). Discriminant analyses were performed using program 7M of the BMDP statistical package (Brown, 1977) adapted for use on the *Digital VAX 11/77* system at the Smith College Academic Computing Center. Museum collections are cited as follows: AMNH, American Museum of Natural History, N.Y.; NCSM, North Carolina State Museum, Raleigh; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, United States National Museum (National Museum of Natural History), Washington; UTKVZC, University of Tennessee at Knoxville Vertebrate Zoology Collection.

Desmognathus santeetlah n. sp.

HOLOTYPE.—USNM 214218, an adult female 37 mm SVL (snout to posterior end of vent), collected in a seepage area at ca. 1219 m (4000') in the headwaters of the N. Fork of Citico Cr. below Cherry Log Gap, Unicoi Mtns., Monroe Co., TN; S.G. Tilley and R.L. Jones; 26 June 1979.

PARATOPOTYPES.—USNM 214219-45, same data as the holotype.

PARATYPES.—UMMZ 169042-59, along the Heintooga-Round Bottom Rd. 0.8 km (0.5 mi) S of the trail to Spruce Mtn., Great Smoky Mtns. National Park, Swain Co., NC; S.G. Tilley and M.L. Tilley, 6 August 1968. USNM 214246-62, headwaters of streams draining the NW slopes of Rough Butt Bald, 1585-1646 m (5200-5400'), Great Balsam Mtns., Jackson Co., NC; S.G. Tilley, J.W. Tilley, P.M. Schwerdtfeger, S. Haskell, and D.C. Wiernasz; 30 May 1978.

ETYMOLOGY.—“Santeetlah” is a prominent geographic name in the vicinity of the type locality. It may or may not be derived from a Cherokee Indian word meaning “blue water” (Powell, 1968).

DIAGNOSIS.—A *Desmognathus* most similar in general morphology to *Desmognathus fuscus*, smaller and slightly more gracile in body form than either *D. fuscus* or *D. monticola*, but larger and more robust than *D. ochrophaeus* or *D. imitator*. In the vicinity of the type locality transformation occurs by 15 mm SVL and sexual maturity at 30-35 mm; males reach 55 mm and females 45 mm SVL. In the same area, *D. fuscus* mature at 35-40 mm, males reaching 60 mm and females 55 mm. *D. monticola* are even larger, most individuals in the size range of adult *D. santeetlah* being sexually immature. When complete, the tail is normally weakly keeled or trigonal distally. It is less keeled than in *D. monticola*, more keeled than in *D. ochrophaeus* or *D. imitator*, and identical to *D. fuscus*. Adult male *D. santeetlah* have less sinuate jaw margins and slightly more rounded snouts than *D. ochrophaeus* or *D. imitator*. The toe tips lack the cornfield friction pads described in *D. monticola* by Caldwell Trauth (1979).

D. santeetlah normally lack the distinct dorsolateral melanophore stripes and dorsal bands of parapatric *D. fuscus*, and the large crescent-shaped dorsal melanophore patches of *D. monticola* (illustrated by Conant, 1975, plate 41). Large individuals are often uniformly greenish-brown dorsally and laterally with no discernable dorsal patterns. The ventrolateral and ventral surfaces are often washed with yellow pigment and contain patches of melanophores and iridophores which impart a “salt and pepper” effect. Iridophore patches are scattered uniformly over the entire bodies of some specimens. Distinct

rows of "porthole"-like iridophore patches are usually present ventrolaterally. The yellowish ventral and ventrolateral coloration and presence of ventrolateral rows of iridophore patches distinguishes the species from *D. ochrophaeus* and *D. imitator*, which have gray rather than yellowish venters and typically lack ventrolateral "portholes." *D. monticola* are unpigmented ventrally.

Biochemically, *D. santeetlah* and *D. fuscus* are fixed for alternative electromorphs at three protein loci: *Isocitrate dehydrogenase-2 (Idh-2)*, *Indophenol oxidase (Ipo)*, and a muscle protein (*Pt-3*) (Tilley and Schwerdtfeger, 1981). In each case *D. santeetlah* has the slower electromorph.

DESCRIPTION OF THE HOLOTYPE.—A mature female (Fig 1A) with spent ovaries containing numerous small ovarian follicles, the largest ca. 0.4 mm in diameter. Oviducts enlarged and convoluted.

Measurements after preservation: snout-vent length, 37 mm; head length, 9.0 mm; head width at the jaw musculature, 6.0 mm; head width at the jaw angle, 5.5 mm; width at the axilla, 5.5 mm; width at the pelvis 4.5 mm; tail length, 28 mm, the last 7 mm regenerated; tail width at base, 3.5 mm; tail height at base, 4.0 mm; tail width at the fifth caudal fold, 2.9 mm; tail height at the fifth caudal fold, 3.5 mm. A distinct keel on the tail beginning at the fifth caudal fold and reaching 0.5 mm in height. Right forelimb length (insertion to tip of longest toe), 6.4 mm. Toe lengths on the right forelimb (medial to lateral), 0.5 mm, 0.9 mm, 1.3 mm, and 0.7 mm. Right hindlimb length (insertion to tip of longest toe), 9.6 mm. Toe lengths on the right hindlimb, 0.4, 1.3, 1.9, 1.9, and 1.2 mm. 16 costal grooves, counting additional grooves in the axilla and groin. Three costal folds between adpressed limbs. Six vomerine teeth on the left and six on the right. Teeth on the posterior half of the dentary of the piercing type, described for *D. monticola* by Caldwell and Trauth (1979).

Coloration in life: A series of rounded, sparsely pigmented spots ca. 1 mm in diameter extended from ca. 1 mm posterior to the axilla to the first caudal fold posterior to the vent. These "larval spots" all occurred in pairs, with the members of each pair opposite one another. Five of the larval spots were anterior and three were posterior to the groin on the left, while five were anterior and two posterior to the groin on the right. They contained reddish pigment with a diffuse patch of melanophores and a few iridophores lateral to each. The small melanophore patches lateral to the larval spots were not connected between adjacent spots on the same side of the dorsum, and dorsolateral stripes and a dorsal band were thus not evident. Isolated iridophores were scattered uniformly over the dorsum. The background coloration of the dorsum was greenish-brown except for the reddish coloration within the larval

spots. Iridophores were scattered over the lateral surfaces of the trunk, 5-8 cells per costal fold. Each costal fold had a large iridophore encircling a ventrolateral dermal pore, at about the level of the limb insertions. This produced a distinct ventrolateral row of light "porthole-like" spots. Melanophores were sparser ventral to these iridophore patches, exposing a distinctly yellow ventrolateral and ventral background coloration. The venter was covered with a patchy, somewhat reticulate pattern of melanophores and a fairly dense, uniform distribution of iridophores. The density of iridophores and melanophores decreased abruptly ventral to the limb insertions, exposing a distinctly yellow background pigmentation. A concentration of iridophores occurred ventral to the heart.

The dorsal surface of the head displayed diffuse melanophore patches between and posterior to the orbits and in a V-shaped fold above the temporal musculature. Scattered iridophores were also present. The background coloration of the temporal area and eyelids was greenish-brown as on the dorsum. The area above the cranium posterior to the orbits and anterior to the temporal area was brownish and slightly less greenish than more posterior areas. The sides of the head bore distinct rows of regularly spaced iridophores above and below the mouth, with cells scattered on the lateral aspects of the temporal musculature. A yellow line extended from the posterior corner of each orbit to the jaw angles. These lines were defined by rows of melanophores dorsally, thick patches of melanophores ventrally, and on the right side of the animal by a patch of bright orange pigment at the angle of the jaw. The gular area was pigmented with patches of melanophores alternating with depigmented areas. The melanophores within these patches were more sparsely distributed than in similar patches on the venter. Iridophores were scattered over the gular area but these too were more sparsely distributed than on the venter. The background color of the gular area was distinctly yellowish.

An orange dorsal stripe 0.5 mm wide and outlined by melanophores extended from the second to about the 16th caudal fold. The remaining regenerated 7 mm of the tail was almost black. Iridophores were concentrated in the larval spots and in the dorsal stripe of the tail. The background coloration of the tail lateral to the dorsal stripe was similar to that of the dorsum. The pigmentation of the lateral caudal surfaces was similar to that of the sides of the trunk, with a row of enlarged iridophores extending caudally on each side from the dorsal aspects of the hindlimb insertions. These rows lay midway from the dorsum to venter of the tail and higher on the body than the iridophore rows down the sides of the trunk. Iridophores were scattered over the

ventral surface of the tail except in the unpigmented area along the midventral axis.

The forelimbs contained melanophore patches on the dorsal surfaces of the toes and joints. Ventrally, the joint areas and feet were unpigmented, with the other ventral limb areas having scattered melanophores and a few iridophores on distinctly yellow backgrounds.

VARIATION AND COMPARISONS WITH *DESMOGNATHUS FUSCUS*.—*D. santeetlah* and *D. fuscus* are most readily distinguished by their color patterns (Fig. 1). While there is much intraspecific variation and occasional specimens defy identification, the dorsal patterns of southern parapatric *D. fuscus* are usually much brighter and bolder than those of *D. santeetlah*. The dorsolateral melanophore stripes of southern

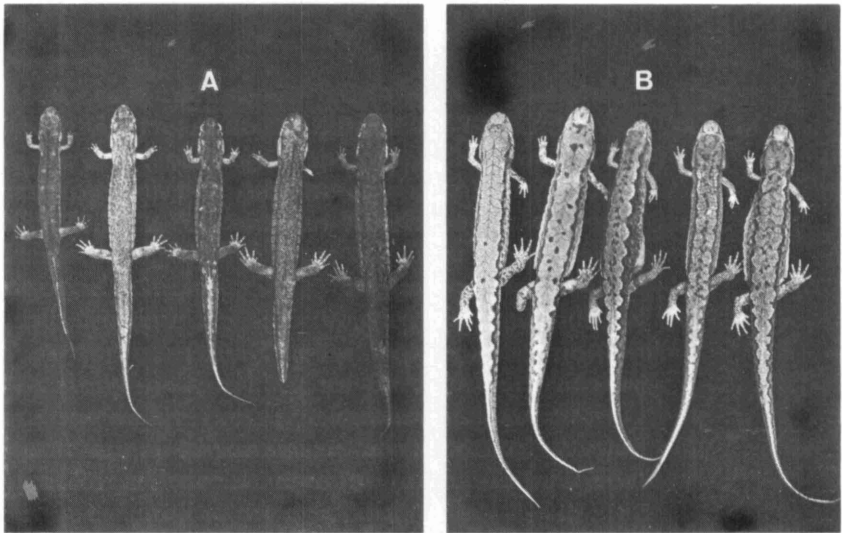


Fig. 1. A: Specimens of *Desmognathus santeetlah* from the type series. From left to right: USNM 214218 (holotype), USNM 214219-22. B: Specimens of *Desmognathus fuscus* from tributaries of Citico Cr., in the Unicoi Mtns. near the type locality of *D. santeetlah*. From left to right: UTKVZC 519, 522, 3193, 604, and 3208. Both series of specimens shown to same scale. Measurements of the type specimen are given in the text.

D. fuscus are normally bold and continuous and are frequently wavy or zigzagged. Except in the oldest, darkest specimens, these stripes typically enclose bright, broad dorsal bands which often contain yellow or crimson pigment. By comparison, the dorsal colorations of *D. santeetlah* are typically much more somber. The dorsolateral stripes are usually thinner and are often interrupted or absent altogether. Dorsal bands are thus less evident, and when present often contain a band of dull red or rusty pigment. Larval spots are often still evident in adults and reddish dorsal pigment is often concentrated in or restricted to these

otherwise sparsely pigmented areas. There are fewer larval spots anterior to the groin than in *D. fuscus*. Transformed and larval *D. fuscus* have more spots between the axilla and groin and also frequently have an "extra" pair anterior to the axilla which *D. santeetlah* nearly always lack. Larval spot counts were compared statistically for the series of Unicoi Mtn. *D. santeetlah* and *D. fuscus* cited in Fig. 2. The differences in numbers of larval spots anterior to the groin (mode = 10 for *D. santeetlah*, 12 for *D. fuscus*) and between groin and axilla (modes = 10 and 12) are highly significant (Mann-Whitney U tests, $P < 0.001$). Southern *D. fuscus* frequently display ventrolateral patterns of vermiform melanophore patches alternating with unpigmented areas. In contrast *D. santeetlah* is more uniformly speckled with melanophores and iridophores ventrolaterally and ventrally. Melanophore densities usually decrease at the level of a pronounced ventrolateral row of iridophore patches, exposing background colorations of yellow chromatophores which impart distinctly yellow hues to the ventral and ventrolateral surfaces. Many *D. santeetlah* virtually lack dorsal patterns, and are uniformly greenish-brown dorsally and yellow ventrolaterally and ventrally.

Figure 2 shows body size distributions for mature male and mature female *D. santeetlah* and *D. fuscus*, with males grouped by testis lobe number (see Tilley, 1977 for the method of counting testis lobes). The SVL distributions of the two species differ significantly for adult females and for 1, 1.5, and 2-2.5 lobed males (2-tailed Mann-Whitney U tests, $P < 0.005$), with *D. santeetlah* being smaller in each case.

D. santeetlah and *D. fuscus* differ slightly in body proportions. When corrected for SVL, *D. santeetlah* has a relatively narrower trunk and shorter toes (Figs. 3-4). The results of stepwise discriminant analyses (Brown, 1977) comparing *D. santeetlah* with Unicoi Mtn. and Massachusetts *D. fuscus* are shown in Figure 5, the morphological characters employed in Table 1, and the discriminant function coefficients and classification functions in Table 2. The specimens used are the same as for the larval spot analysis, plus the series of northern *D. fuscus* from Franklin Co., MA cited in Figure 5. The figures show the results of the discriminant analyses for sexually mature males and females, first using specimens with complete data for all the characters and then for the larger samples of specimens complete for the characters selected by the initial discriminant analyses.

The analyses indicate that restricted sets of morphological characters can be used to reliably separate individuals of the two species. For the characters employed here, *D. santeetlah*, southern *D. fuscus*, and northern *D. fuscus* seem to be more distinct with respect to female than

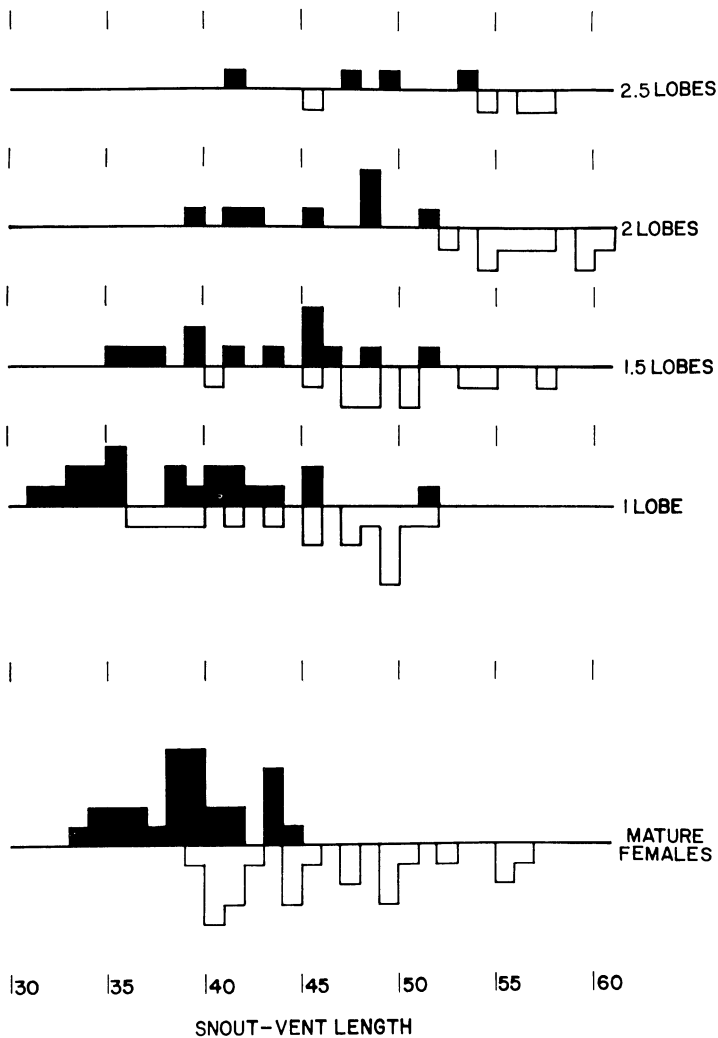


Fig. 2. Snout-vent length distributions of adult Unicoi Mtn. *Desmognathus santeetlah* (filled squares) and *D. fuscus* (empty squares) from the Unicoi Mtns. Males are classified by testis lobe categories to permit comparisons between individuals of roughly similar ages. The *D. santeetlah* are from USNM series 214395-408 and 214410-74, W of Stratton Gap at 1195 and 1134 m (3920 and 3720), Monroe Co., TN. The *D. fuscus* are from UTKVZC series 156, 161-62, 504-14, 518-22, 560-64, 598-606, 620-26, 628-33, 3187-94, 3195-97, 3200-02, 3204, 3207-14, and 3221, from tributaries of Citico Cr., Monroe Co., TN. Measurements in mm.

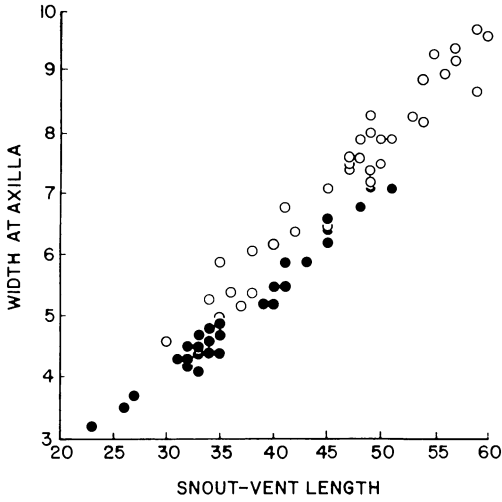


Fig. 3. Trunk width at the axilla vs. snout-vent length in male *D. santeetlah* (filled circles) and *D. fuscus* (empty circles) from the series described in Fig. 2. Measurements in mm.

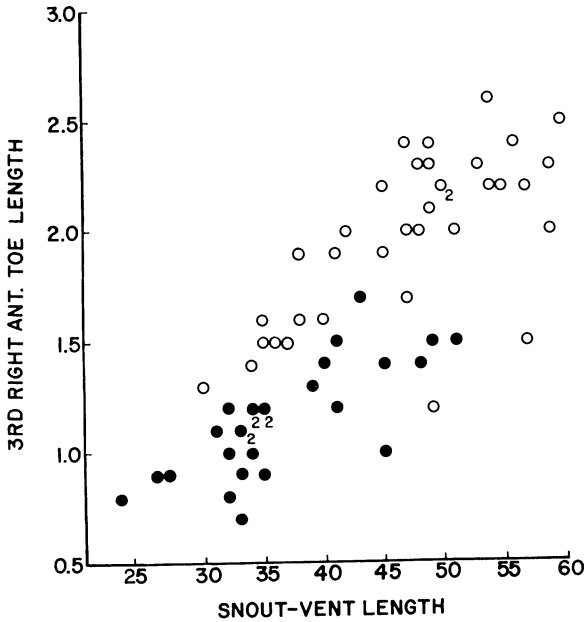


Fig. 4. Length of the third toe on the right forelimb vs. snout-vent length in male *D. santeetlah* (filled circles) and *D. fuscus* (empty circles) from the series described in Fig. 2. Measurements in mm.

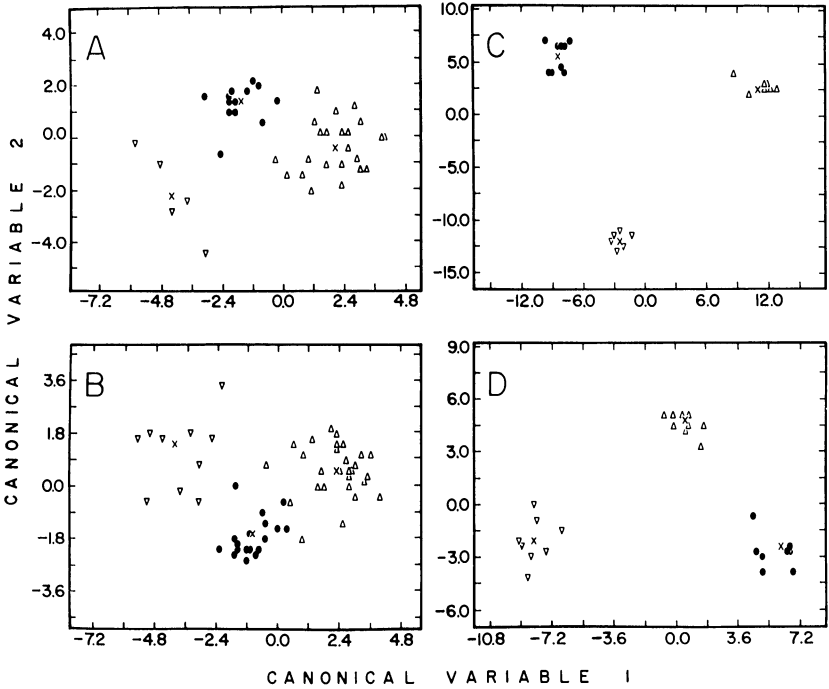


Fig. 5. Discriminant analyses based on the morphological measurements of Tables 1 and 2, for *D. santeetlah* (filled circles, the series described in Fig. 2), Unicoi Mtn. *D. fuscus* (upright triangles, the series described in Fig. 2), and Massachusetts *D. fuscus* (inverted triangles, USNM 214814-67, Hawley, Franklin Co.). A: mature males with measurements for all the characters in Table 1. B: mature males with measurements for all the characters used to generate the discriminant functions in 5A. C: mature females with measurements for all the characters in Table 1. D: mature females with measurements for all the characters used to generate the discriminant functions in 5C. See Table 2 for discriminant function coefficients. X's denote centroids of clusters.

to male morphology (Fig. 5C and D vs. A and B). This may simply reflect the fact that greater postreproductive growth in males increases male body size variances and thus overlap in body sizes between the two species. Interestingly, in three of the four plots the centroids of the clusters representing Unicoi Mtn. *D. santeetlah* and *D. fuscus* lie nearer to one another than either does to the centroid for northern *D. fuscus*. In the exceptional case (Fig. 5C), the centroids are virtually equidistant. The morphological data thus parallel electrophoretic evidence (Tilley and Schwerdtfeger, 1981) in suggesting that *D. santeetlah* is more similar to southern than to northern *D. fuscus*.

TABLE 2

DISCRIMINANT FUNCTION COEFFICIENTS AND CLASSIFICATION FUNCTIONS USED TO SEPARATE *DESMOGNATHUS SANTEETLAH* FROM NORTHERN AND SOUTHERN *DESMOGNATHUS FUSCUS* (FIG. 5).

To employ the classification functions, sum the products of the morphological measurements indicated and their corresponding coefficients, and compare the sums for the columns corresponding to southern *fuscus*, northern *fuscus*, and *santeetlah*. The largest sum corresponds to the form to which the specimen should be referred.

Character	Coef. for can. var. I	Coef. for can. var. II	Classification functions		
			s. <i>fuscus</i>	n. <i>fuscus</i>	<i>santeetlah</i>
Sexually mature males complete for all characters in Table 1 (Fig. 5A).					
SVL	-0.752	-0.119	-1.791	3.270	0.834
AXW	1.273	-1.955	-4.989	-9.632	-13.012
HDL	1.614	0.378	16.362	5.273	10.927
HDHM	1.376	2.065	1.936	-10.694	0.193
TOE4A	3.158	0.252	7.049	-13.763	-4.394
Constant	-2.352	3.332	-45.702	-46.636	-31.631
Sexually mature males complete for SVL, AXW, HDL, HDHM, and TOE4A (Fig. 5B)					
SVL	-0.664	0.006	-2.147	2.037	-0.017
AXW	1.924	1.534	0.394	-10.331	-9.249
HDL	1.532	0.320	16.852	7.504	11.194
HDHM	0.626	-1.676	-0.040	-5.485	1.695
Constant	-2.282	-5.348	-51.105	-48.172	-31.073
Sexually mature females complete for all characters in Table 1 (Fig. 5C).					
SVL	-0.930	-0.964	-5.746	21.147	9.776
PELW	4.469	5.899	-24.868	-172.667	-95.857
HDL	5.480	2.918	118.381	0.545	19.086
HDHJA	5.000	0.396	136.179	61.963	39.154
HDWJA	-5.497	1.229	-181.322	-124.190	-69.929
IOW	-4.559	-16.830	358.655	668.300	400.384
VOMT	-0.364	0.973	19.266	38.546	23.649
TOE2A	6.439	-10.931	512.749	585.278	355.313
TOE4P	5.978	-2.566	326.443	282.373	201.803
Constant	-25.202	34.677	-1297.335	-1469.710	-687.773
Sexually mature females complete for SVL, PELW, HDL, HDHJA, HDWJA, IOW, VOMT, TOE2A, and TOE4P (Fig. 5D).					
SVL	-0.379	-0.676	-0.362	7.475	2.362
PELW	3.607	2.858	-58.396	-108.991	-58.591
HDL	1.043	3.307	46.844	15.560	28.941
IOW	-10.352	-3.921	230.977	347.434	200.733
VOMT	-0.671	-0.028	22.454	28.484	18.871
TOE2A	-8.736	0.945	262.450	332.166	206.320
TOE4P	-3.613	2.835	178.290	190.707	137.490
Constant	33.290	-17.553	-818.286	-1015.207	-515.120

Tooth morphology has been used to differentiate closely related species of *Desmognathus* (Means, 1974; Caldwell and Trauth, 1979), but does not appear useful in distinguishing *D. santeetlah* from parapatric *D. fuscus*. Caldwell and Trauth found that *D. fuscus* from the Cumberland Plateau of Kentucky and Tennessee had blunt rather than piercing teeth on the posterior half of the dentary. Means (1974) made the same observation for New York *D. fuscus* and this tooth morphology also characterizes samples from Massachusetts to southwestern Virginia (populations 1-10 in Tilley and Schwerdtfeger, 1981) that I have examined. In *D. santeetlah* and southern *D. fuscus* (populations 11-13 in Tilley and Schwerdtfeger, 1981) the teeth on the posterior half of the dentary are primarily of the pointed, piercing type characteristic of *D. monticola* (Caldwell and Trauth, 1979), southern *D. fuscus* (Means, 1974 and my observations on populations 14-16 in Tilley and Schwerdtfeger, 1981), *D. ochrophaeus*, and *D. imitator*. While not a diagnostic character, tooth morphology does provide another respect in which *D. santeetlah* are more similar to southern than to northern *D. fuscus*.

Hatchling *D. santeetlah* and *D. fuscus* are illustrated in Figure 6. As indicated by the figure, hatchlings of the two species differ rather substantially in body size. The mean SVL's and standard deviations for three *D. santeetlah* broods from the Deep Cr. drainage in the Great Smokies (AMNH 106641, 106644, and 106647) are 8.40 (0.342), 8.60 (0.269), and 9.12 (0.139) mm. Means and standard deviations for three *D. fuscus* broods from the Unicoi Mtns. (UTKVZC uncatalogued) are 11.77 (0.433), 10.79 (0.488), and 8.68 (0.212) mm. The *D. santeetlah* broods had hatched but were still clustered with brooding females when collected. The Unicoi Mtn. *D. fuscus* clutches hatched in the laboratory of Mr. R.L. Jones at the University of Tennessee. The first and third were preserved at hatching and the second 22 days after. Figures 6 and 7 also indicate that hatchlings of the two species differ in the expansion of the branchial region of the head, relative to head length. When corrected for their smaller body sizes and thus shorter heads *D. santeetlah* hatchlings still have narrower branchial regions than either northern or southern *D. fuscus*. Least squares regressions for the *D. santeetlah* and Unicoi Mtn. *D. fuscus* hatchlings, treating head width and length as dependent and independent variables, respectively, differ significantly in elevation ($F = 72.0$, $DF = 1,81$, $P \ll 0.001$), but not in slope ($P \gg 0.05$). The length of the larval period in *D. santeetlah* is unknown, but the apparent tissue reduction in the branchial area makes hatchling *D. santeetlah* appear distinctly less "larviform" than hatchling *D. fuscus*. Careful comparisons of the larval

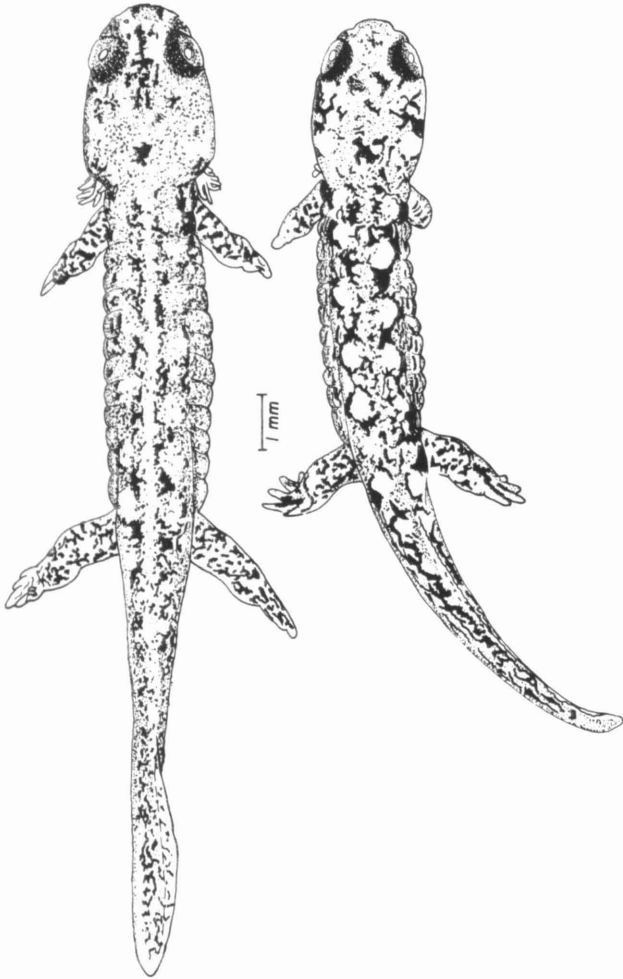


Fig. 6. Hatchling *Desmognathus fuscus* (left, Ashfield, Franklin Co. MA) and *D. santeetlah* (right, Great Smoky Mtns.).

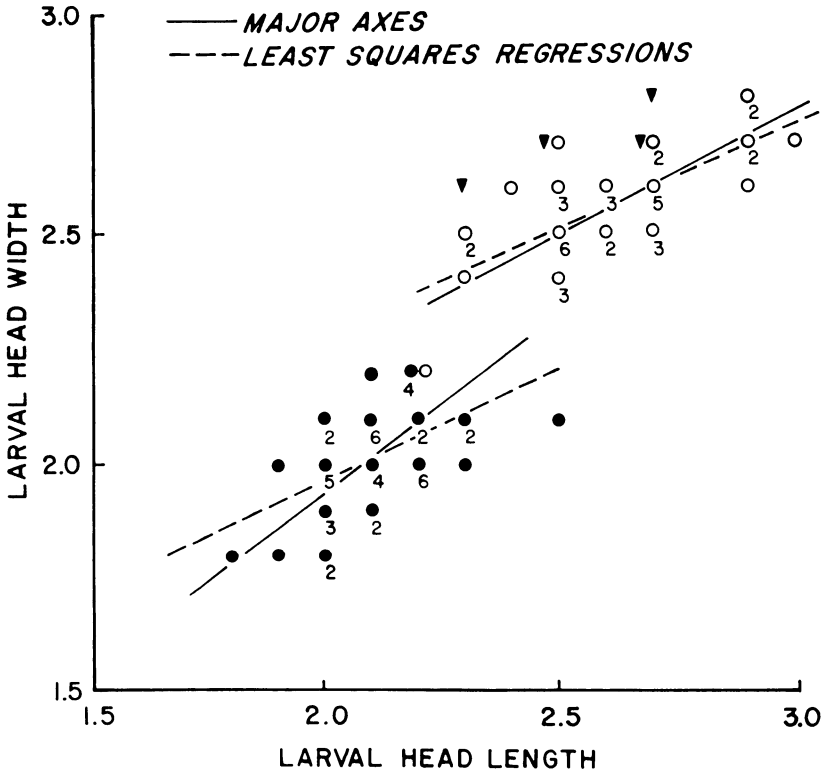


Fig. 7. Head width (across branchial region at widest point) vs. head length (tip of snout to gular fold) for hatching *Desmognathus santeetlah* (filled circles, AMNH 106641, 106644, and 106647), Unicoi Mtn. *D. fuscus* (empty circles, UTKVZC uncatalogued), and Massachusetts *D. fuscus* (filled triangles, USNM 214868). Measurements in mm.

periods of the two species under controlled conditions might prove rewarding.

Three early workers, Dunn (1926), Weller (1931), and King (1939), all recorded *Desmognathus f. fuscus* from the Great Smokies. Their comments leave little doubt that they were dealing with populations now referable to *D. santeetlah*, and Weller and King seem to have appreciated the distinctness of these animals from "typical" *D. fuscus*. Dunn encountered salamanders on Mt. Sterling which he identified as *D. f. fuscus* rather than *D. f. carolinensis* (now *ochrophaeus* and *imitator*). Weller "provisionally" referred specimens that he collected at Indian Gap to *D. f. fuscus*, noting that they differed from other *fuscus* that he had seen in having bright yellow venters. King felt that in the Smokies

D. f. fuscus and *D. f. carolinensis* could be readily separated on the basis of tail shape. He stated that the "most typical" *D. f. fuscus* occurred at low elevations, and that high elevation specimens were "commonly very light in color. . . with yellow in the ventral areas and yellow or grayish brown fairly fine mottling on the dorsal areas." After reviewing the comments of these authors and examining specimens of *Desmognathus* from the Great Smokies, Huheey (1966) concluded that *D. fuscus*, if it occurred at all in those mountains, was an inhabitant of stream valleys at low elevations, and that the reports of high elevation populations were based on misidentifications. He seems to have overlooked the presence of *fuscus*-like, yellowish salamanders at high elevations, or identified such specimens as *D. monticola* or *D. ochrophaeus*.

ECOLOGY.—*D. santeetlah* is a salamander of stream headwaters and seepage areas, where groundwater percolates to the surface through beds of muck, mossy rocks, touch-me-not (*Impatiens*), and nettles (*Laportea canadensis*). Such habitats often occur in the heads of mountain coves above 900 m, but support *D. santeetlah* as low as 677 m (2220') along Deep Cr., Swain Co., NC, in the Great Smokies (AMNH A106628). The highest known locality for the species is ca. 1805 m (5920') on Mt. LeConte, Sevier Co., TN, in the Great Smokies (UMMZ 169008-09). An apparently suitable site at ca. 1920 m (6300') yielded only *D. imitator*. On Waterrock Knob, Haywood-Jackson Cos., NC, in the Great Balsam Mtns. a seepage area at 1829 m (6000') apparently contains only *D. ochrophaeus*, while *D. santeetlah* occurs at 1737 m (5700') on the same mountain. On Rough Butt Bald, Haywood-Jackson Cos., in the Great Balsams a seepage area at 1676 m (5500') contains only *D. ochrophaeus*, but *D. santeetlah* occurs directly below at ca. 1615 m (5300'). Evidently factors other than apparent habitat quality exclude *D. santeetlah* from the very highest elevations of the Great Smokies and Great Balsams. In the Unicois it occurs in the highest springheads, such as at 1585 m (5200') on Bob Bald.

When present at a locality, *D. santeetlah* is often the most abundant desmognathine. Individuals can be encountered most readily by turning rocks in a few millimeters of water at the margins of seepages, or by raking gravel and cobble beds through which water percolates. In the well-known aquatic to terrestrial ranking of Appalachian *Desmognathus* species (Hairston, 1949 and 1981; Organ, 1961; Tilley, 1968), *D. santeetlah* and *D. fuscus* share a position between *D. monticola*, an inhabitant of larger streams, and the *D. ochrophaeus*-*D. imitator* complex, which occupies forest floor as well as seepage habitats.

During the summer, female *D. santeetlah* brood their eggs under moss on logs and rocks in seepages, the same sites used by brooding

female *D. ochrophaeus* in the southern Appalachians (Tilley, 1973). In the Great Smoky Mtns., where *D. santeetlah*, *D. ochrophaeus*, and *D. imitator* all occur, I have encountered only *D. santeetlah* females brooding eggs in these situations (Tilley, et al, 1978), but have found brooding female *D. santeetlah* and *D. ochrophaeus* sharing sites at Rough Butt in Great Balsams. Brooding site competition between these species deserves investigation.

D. santeetlah and *D. fuscus* have not yet been found in sympatry, but populations of each occur within a few kilometers of one another in the Unicoi Mtns. (see below). In the Unicois, the two species seem to exploit similar habitats but *D. santeetlah* occurs at higher elevations. The ecological factors responsible for these evidently parapatric distributions are obscure. The similar habitat requirements of the two species suggest that competitive displacement may play a role.

While similar in habitat, *D. santeetlah* and *D. fuscus* differ in behavior. *D. fuscus* run immediately upon being uncovered, and often escape the collector by vigorously burrowing in muck and gravel. In contrast, *D. santeetlah* often remain motionless when uncovered and are easier to catch when they flee.

GEOGRAPHIC DISTRIBUTION.—Populations here referred to *D. santeetlah* are restricted to the Great Smoky, Great Balsam, and Unicoi Mtns. of the southwestern Blue Ridge Physiographic Province (Fig. 8).

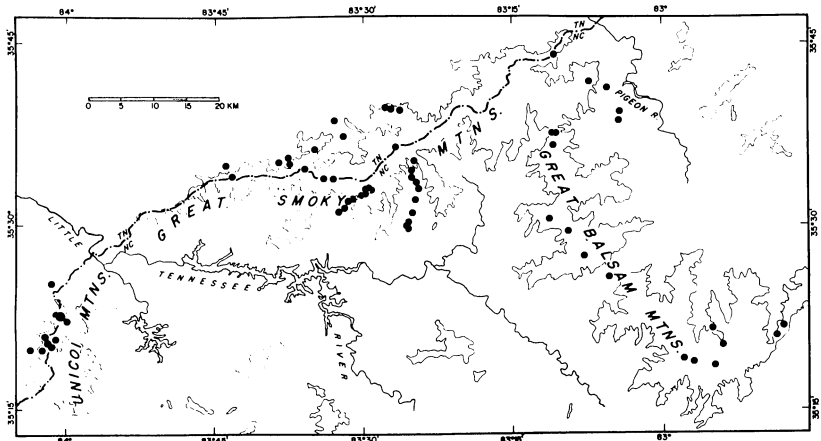


Fig. 8. Known localities for *Desmognathus santeetlah*. The large dot in the Unicoi Mtns. is the type locality. The 1219 m (4000') contour is indicated.

A series of specimens from Max Patch Mtn. on the TN-NC line northeast of the Great Smokies (UMMZ 81060) strongly resembles *D. santeetlah*, but I have not seen living specimens from that or any other locality northeast of the Pigeon R., despite efforts to locate populations. Other populations of the *D. fuscus* complex in the southern Appalachians that we have analyzed electrophoretically are referable to *D. fuscus* (Tilley and Schwerdtfeger, 1981).

In the Unicoi Mtns. the known *D. santeetlah* localities are all located along the main ridgecrest (the NC-TN state line, Fig. 9). The south-

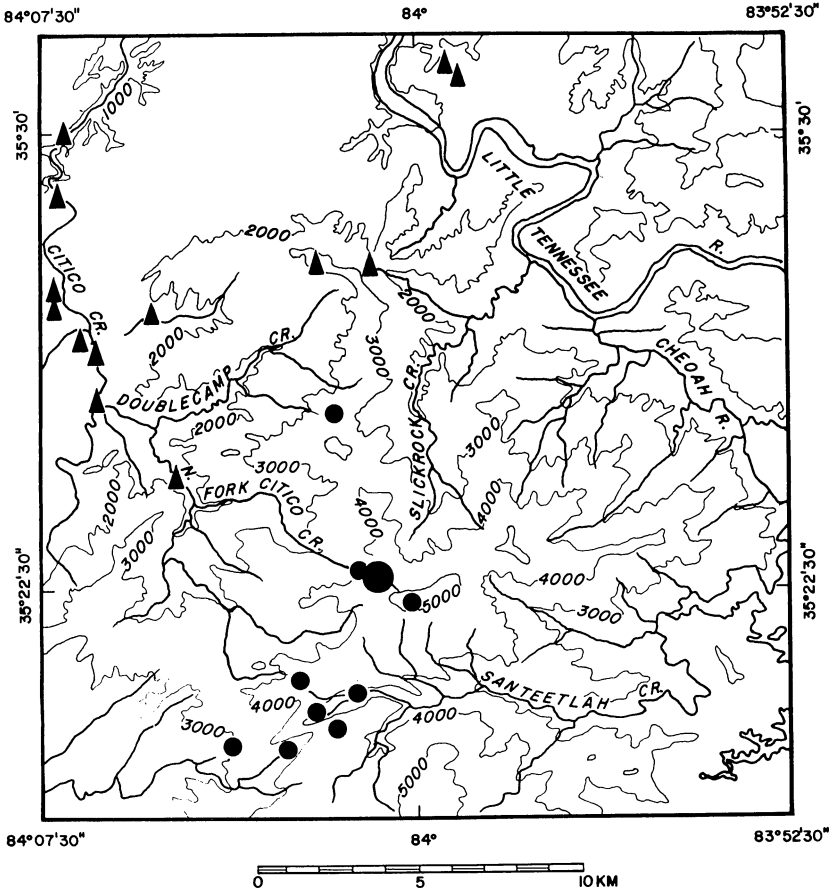


Fig. 9. Known localities for *Desmognathus santeetlah* (circles) and *D. fuscus* (triangles) in the Unicoi Mtns., Monroe Co., TN and Graham Co., NC. The large dot is the type locality. Elevations are in feet.

ernmost known locality in that mountain range is at ca. 1158 m (3800') on a tributary of Roaring Branch below Whigg Meadow, Monroe Co., TN (UTKVZC 4498-505). The northernmost locality is Big Stack Gap (1000 m, 3280') on the Unicoi crest, Monroe Co., TN (UTKVZC 4477-93). *D. fuscus* occurs at low elevations in the Citico Cr. drainage west of the Unicoi crest, and in the headwaters of Little Slickrock Cr. at the northern end of the range. In the valley of the North Fork of Citico Cr., *D. fuscus* occurs at the old warden station site at 512 m (1680', UTKVZC 620-26, 628-33), while *D. santeetlah* occurs in the headwaters below Cherry Log Gap (the type locality), 6 km ESE at 1158 m (3800'). We have failed to locate populations of either species at intermediate elevations in that drainage, where the steep slopes and stream gradients provide little appropriate habitat. Likewise, we have failed to find either form in stream headwaters along the Unicoi crest between a *D. fuscus* locality at ca. 792 m (2600') on the NE slope of Little Fodderstack Mtn. (UTKVZC 4475) and the *D. santeetlah* locality 4 km S at Big Stack Gap. The occurrence of populations of the two species within fewer than ca. 4 km of each other in the Unicois has thus not been documented.

D. santeetlah appears to be distributed throughout the Great Smoky Mtns. The southwesternmost known locality in that range is at 1402 m (4600') below Spence Field, Blount Co., TN (USNM 214475-92), although additional collecting will undoubtedly extend the known range southwestward along the main ridgcrest toward the Little Tennessee R. The northeasternmost Great Smokies locality is at 1097 m (3600') in the headwaters of Correll Branch below Mt. Sterling Gap, 3.5 km W of the Pigeon R. (USNM 214541-46). The ecological and biogeographic relationships between *D. santeetlah* and *D. fuscus* in the Great Smokies require further study. There is evidence of hybridization between the two forms at the northeastern end of these mountains, as will be discussed below.

From the main ridgcrest of the Great Smokies, *D. santeetlah* is distributed southeastward along the Great Balsam Mtns. then northeastward along the Pisgah Ledge at least as far as Pigeon Gap, Haywood-Transylvania Co., NC (USNM 214622-25). This distribution may be essentially continuous, since a population is known at ca. 926 m (3040') 1.5 km WSW of Balsam Gap, Jackson Co., NC, the lowest point along the Great Balsam and Pisgah ridgcrests (NCSM 19882).

HYBRIDIZATION WITH *D. FUSCUS*.—Electrophoretic studies of populations of *fuscus*-like salamanders in the northeastern end of the Great Smokies indicate that hybridization may occur, or have occurred, between *D. fuscus* and *D. santeetlah*. In populations along Cosby Cr. there is considerable heterozygosity at two of the loci (*Pt-3* and *Ipo*) that are

TABLE 3
 GENOTYPE AND ELECTROMORPH FREQUENCIES ALONG COSBY CR.,
 GREAT SMOKY MTNS. F, S = *fuscus* and *santeetlah* electromorphs.
 H(o), H(e) = observed and expected heterozygote frequencies.

	518 m	686 m	732 m	1432 m
	FF FS SS	FF FS SS	FF FS SS	FF FS SS
<i>Pt-3</i>	5 7 8	2 16 11	1 10 13	0 0 39
Freq. of F	0.425	0.345	0.250	0.0
Freq. of S	0.575	0.655	0.750	1.0
H(o)/H(e)	7/9.8	16/13.1	10/9.0	---
<i>Ipo</i>	3 9 7	2 6 7	1 5 12	0 3 24
Freq. of F	0.395	0.333	0.194	0.056
Freq. of S	0.605	0.777	0.806	0.944
H(o)/H(e)	9/9.1	6/7.8	5/5.6	3/2.8

fixed for alternative electromorphs in Unicoi Mtn. populations of the two species (Table 3, Fig. 10). At the third diagnostic locus (*Idh-2*) the mobilities of the two electromorphs are too similar to permit reliable detection of heterozygotes. These populations occur at 518, 686, 732, and 1432 m (1700', 2300', 2700', and 4700') above sea level. Individuals of the highest population (USNM 214556-98), near Cosby Knob on the main ridgcrest of the Great Smokies, appear to be typical *D. santeetlah* with dull, greenish or yellowish colorations and indistinct dorsal bands. This population is fixed for the *santeetlah* electromorph at the *Pt-3* locus, but three heterozygotes for the *fuscus* and *santeetlah* electromorphs were detected at the *Ipo* locus in a sample of 27 individuals. This population thus appears to be essentially pure *D. santeetlah*, but there is evidence of genetic influence from *D. fuscus*. Individuals from the three low elevation Cosby Cr. populations (USNM 214732-813) are much more *fuscus*-like in often having bright color patterns with distinct, brightly colored dorsal bands, but the largest adults are smaller than those of Unicoi Mtn. *D. fuscus*. The three populations are polymorphic at both diagnostic loci for *fuscus* and *santeetlah* variants, and exhibit all possible combinations of genotypes at the two loci. Heterozygotes occur at each locus in very near their Hardy-Weinberg equilibrium frequencies (Table 3), indicating that mating is random with respect to genotype. At each locus the *santeetlah* electromorph is more common in each population and increases with elevation and proximity to the *D. santeetlah* population on Cosby Knob. Furthermore, in each population the frequencies of the *santeetlah* electromorphs at the two loci are virtually identical (Table 3, Fig. 10). These frequencies change abruptly over the approximately 2.3 km that separate the 732

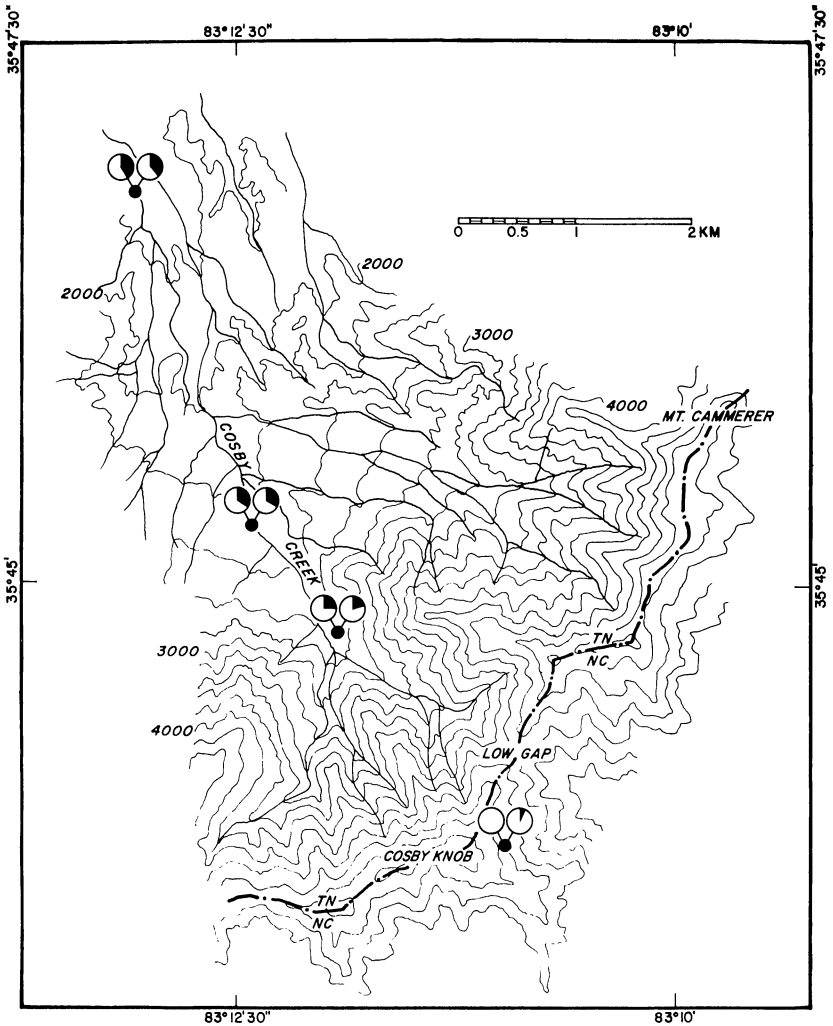


Fig. 10. Variation in allele frequencies among *Desmognathus fuscus*-complex populations along Cosby Cr., Great Smoky Mtns., showing evidence of hybridization between *D. fuscus* and *D. santeetlah*. The shaded portions of the circles are proportional to the frequencies of the *fuscus* electromorphs at *Pt-3* (left circles) and *Ipo* (right circles). Elevations are in feet.

and 1432 m populations, and we have been unable to locate populations in the steep terrain between the two sites. As in the Unicois, habitats for *fuscus*-complex salamanders seem to occur in either the very head-waters of streams at high elevations or in mucky seepages along larger, lower-gradient streams at low elevations. The steep, dry

hillsides and rushing brooks in between provide few ecological opportunities for these salamanders.

The electrophoretic evidence strongly suggests that low elevation *fuscus*-complex populations along Cosby Cr. in the Great Smokies are products of hybridization between *D. fuscus* and *D. santeetlah*. No other hypothesis seems to explain the polymorphisms for otherwise species-specific electromorphs at two loci, the apparent cline in electromorph frequencies with elevation, and the similarity between the frequencies of *santeetlah* (or *fuscus*) electromorphs at the two loci in each population. The northern extent of this presumptive zone of hybridization is not known, but must lie somewhere in the Ridge and Valley Physiographic Province northwest of the Great Smokies. Populations along the main ridgecrest of the Great Smokies above Cosby Cr. seem to be virtually pure *D. santeetlah*, and the hybridization zone thus appears to terminate rather abruptly between 700 and 1400 m on the northwestern escarpment of the Great Smokies. Whatever its history or extent, this hybridization has evidently not been sufficient to compromise the distinctness of *D. santeetlah* at high elevations in the Great Smokies, and there is no evidence of gene exchange between parapatric populations of the two forms in the Unicois. The two species are as divergent electrophoretically and more dissimilar morphologically than *D. ochrophaeus* and *D. imitator*, which occur sympatrically without hybridizing. While *D. santeetlah* and *D. fuscus* do seem to be a case of evolutionary intermediacy, maintaining their genetic integrities in some areas while hybridizing in others, their overall distinctness warrants regarding them as taxonomic species.

SUMMARY

Desmognathus santeetlah, a new species of dusky salamander, is described from the Unicoi, Great Smoky, and Great Balsam Mtn. ranges of the southern Blue Ridge Physiographic Province. *D. santeetlah* is most closely related to *D. fuscus*, with which it occurs parapatrically in the Unicoi Mtns. In that mountain range *D. santeetlah* occupies seepages in the heads of coves while *D. fuscus* occurs in seepages along streams at lower elevations. Neither form appears to occupy the high-gradient streams of intermediate elevations.

D. santeetlah and *D. fuscus* differ in color pattern, body size, and body proportions, and are fixed for alternative electromorphs at three loci. Evidence from morphometrics, mandibular tooth structures, and isozyme patterns suggests that *D. santeetlah* is more closely related to

southern than to northern *D. fuscus*.

D. santeetlah and *D. fuscus* appear to hybridize, or to have hybridized, in the Cosby Cr. drainage on the northwestern margin of the Great Smokies. Nevertheless, the distinctiveness of the two forms, and their co-occurrence without evidence of hybridization in the Unicois, justifies treating them as full species.

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