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THE STATUS OF *Desmognathus brimleyorum* STEJNEGER
AND AN ANALYSIS OF THE GENUS *Desmognathus*
(AMPHIBIA: URODELA) IN FLORIDA

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UNIVERSITY OF FLORIDA

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D. BRUCE MEANS¹

SYNOPSIS: This is a systematic study of three externally similar species of plethodontid salamanders (genus *Desmognathus*) previously considered to occur sympatrically in northern Florida (*D. auriculatus*, *D. brimleyorum*, and *D. fuscus*). Larval morphology, color pattern, relative size, and tail morphology were reinvestigated. The morphology of teeth, jaw profile, premaxillary fontanelle, and prearticular spine were studied in detail for the first time, and color changes due to ontogenetic melanization and to metachrosis were also evaluated. All the above characteristics were found to be taxonomically significant. In addition, the microhabitat selection and ecological associates of *D. auriculatus* and *D. fuscus* were different, indicating ecological isolation of the two species in the area of sympatric contact in northern Florida. *Desmognathus brimleyorum* Stejneger is a species endemic to the Ouachita Mountains of Arkansas and Oklahoma. The name *D. fuscus carri* Neill is a synonym of *D. auriculatus* Holbrook. Populations referred to *D. fuscus* in this study compared morphologically more closely with *D. ochrophaeus* from the southern Appalachians than with populations from near the type locality of *D. fuscus* Rafinesque.

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INTRODUCTION

The plethodontid salamander genus *Desmognathus* Baird, 1849, has a long and complicated taxonomic history (for partial reviews, see Dunn 1917, Folkerts 1968, Hinderstein 1969). Over 30 species and subspecies were described between 1820 and 1958. Of these at least six species (*D. aeneus*, *fuscus*, *monticola*, *ochrophaeus*, *quadramaculatus* and *wrighti*) are presently recognized by most authors (Conant 1958, Wake 1966, Brame 1966, Goin and Cochran 1970).

All of the above species, except *D. wrighti*, are polytypic. Of these *Desmognathus fuscus* has been split at one time or another into 11 subspecies (*auriculatus*, *brimleyorum*, *carolinensis*, *carri*, *conanti*, *fuscus*, *imitator*, *perlapsus*, *planiceps*, *ocoe*, *welteri*). *Desmognathus ochrophaeus*, *aeneus*, *monticola*, and *quadramaculatus* have each been considered ditypic. None of the last three names has ever been synonymized under *D. fuscus*, but *ochrophaeus* has been considered as a subspecies of *fuscus* (Allen 1901, Fowler 1906). For purposes of communication some of the above names will be grouped into three complexes, hereafter referred to as: (1) *auriculatus* complex (*auriculatus*, *carri*); (2) *fuscus* complex (*conanti*, *fuscus*, *welteri*); and (3) *ochrophaeus* complex (*caro-*

linensis, *imitator*, *perlapsus*, *planiceps*, *ochrophaeus*, *ocoeae*). *D. brimleyorum* will be treated as a full species.

Recently there has been disagreement on the number of subspecies in *D. fuscus* in the Coastal Plain of the eastern United States. Some workers have considered *auriculatus* and *brimleyorum* to be subspecies of *D. fuscus* (cf. Chaney 1958, Folkerts 1968, Harima 1969) but others have accorded them full specific rank (Valentine 1961, 1963, Wake 1966, Goin and Cochran 1970).

The reasons for the different interpretations probably stem from three major factors. First is the extensive geographic range of the forms involved. *D. f. fuscus* (nominate race of the type species of the genus; type locality, "northern New York") ranges northward to the St. Lawrence River drainage in New England and southeastern Quebec and into New Brunswick (Bleakney 1958). The *fuscus* and *ochrophaeus* complexes occur southward throughout the Appalachians (where they are represented by the most named forms: *ochrophaeus*, *fuscus*, *ocoeae*, *imitator*, *planiceps*), Piedmont (*fuscus*), and Coastal Plain physiographic provinces to Florida (*fuscus* and *auriculatus*). Thence, members of the *fuscus* or *auriculatus* complexes, or both, range westward to about the western limit of the Austroriparian Biotic Province in eastern Texas (Sanders and Smith 1949). The Ouachita Mountains of southeastern Oklahoma and southwestern Arkansas appear to be the northwestern limit of the range of the subfamily Desmognathinae, where it is represented by *brimleyorum*. No previous worker has dealt with *fuscus* or *auriculatus* throughout the entire range of either complex.

A second factor is the lack in salamanders of external, taxonomically utilizable meristic characters. Salamanders are smooth-skinned, usually lacking in epidermal accoutrements such as excrescences, tubercles, and scales. One of few such characters is costal groove number, but this is not variable infragenerically in *Desmognathus*.

The third, and most important, factor contributing to the difficulties encountered in determining systematic relationships in the genus is variation, both individual and populational. Mayr (1969:147) lists 17 types of variation that can be found within a single population. Members of *Desmognathus* under consideration in this study may be influenced by at least ten of these. Each is briefly discussed.

AGE VARIATION.—Members of the *fuscus*, *auriculatus*, and *ochrophaeus* complexes pass through a brief larval period of 2-6 months after hatching from the egg (Wilder 1913, Chaney 1949, Hairston 1949, Eaton 1956, Organ 1961, Tilley 1968). The larval morphology differs from the post-transformation morphology in several important respects: larvae possess external gills, undivided monocuspid teeth, distinct palatal mor-

phology, tail fins, "suctorial" mouth, and lack eyelids. Post-larval individuals lack gills and fins, and possess pedicillate, bicuspid teeth, eyelids, and reorganized mouthparts. After metamorphosis there is a 2-3 year juvenile state in which no dimorphism is apparent in any potential secondary sex character (Chaney 1949, Hairston 1949, Organ 1961, Tilley 1968). Sexual maturity is probably attained by most members of the *fuscus* complex after 2-4 years of age for males and 3-4 for females (Organ 1961, Tilley 1968). There is a very definite ontogenetic progression of color pattern from a dorsally spotted larval and juvenile pattern in all forms to old males and sometimes old females that are entirely dark. Males have a characteristic change in testicular lobing correlated with age (Kingsbury 1902, Humphrey 1922, Noble 1927).

SEASONAL VARIATION.—Males and females show seasonal variation in gonadal activity expressed as morphological change. Males undergo slight changes in the size of the mental gland and in the lining of the vent correlated with the advent of the breeding season (Noble 1931, Hays 1966). Gravid females become plump, and large white ova can be seen through the abdominal wall.

HABITAT VARIATION.—It has been experimentally demonstrated that individuals of *D. auriculatus* may undergo color change stimulated by differently colored substrates (Grobman 1950). In southern Alabama and northern Florida it has been suggested that *auriculatus* is an ecophenotype of the species *Desmognathus fuscus* found in mucky soils (Folkerts 1968).

DENSITY DEPENDENT VARIATION.—Although no studies are available demonstrating that interdeme size differences exist in desmognathines, some studies have shown that population densities, biomass production, fecundity, and spatial relationships of individuals in the habitat are such as to indicate that this type of variation is distinctly possible (Hairston 1949, Organ 1961, Spight 1967, Tilley and Tinkle 1968, Barbour et al. 1969). Mean size could vary from deme to deme, depending on age structure. Males that can be classed to age, utilizing the criterion of testicular lobing (Kingsbury 1902, Humphrey 1922), may vary considerably in snout-vent length between demes (pers. obs.). Several taxa in the *ochrophaeus* and *auriculatus* complexes have been partly characterized by their size differences (i.e., *perlapsus*, *ocoeae*, *planiceps*, *auriculatus*, *carri*).

ALLOMETRIC VARIATION.—Changes occur during ontogeny from larval through adult stages in the proportions of the head-to-body and leg-to-trunk lengths (Martof and Rose 1963, Rubenstein 1971).

NEUROGENIC COLOR VARIATION (=METACHROSIS).—Variation in the

color pattern caused by pigment dispersal in chromatophores is a common phenomenon among amphibians. All the forms under consideration in this study possess this variation. There may be a short-term change which takes place in a few minutes to half an hour, or a longer term change in response to a constant background color of the experimental substrate (Grobman 1950, this study).

PARASITE INDUCED VARIATION.—This is especially common in *D. brimleyorum* in which the digits of the manus and pes may be missing, fused, or otherwise altered from secondary infection caused by trombiculid mites (Acarina, Trombiculidae). Sometimes the infestation is so heavy that bumps are raised under the skin of the head and body (pers. obs.). Occasionally other members of the *fuscus* complex have similar infestations (Dunn 1926).

TERATOLOGICAL VARIATION.—Desmognathines have well-developed regenerative ability. Frequently specimens are encountered whose partial or entire appendage is undergoing regeneration. A leg may appear as a half-sized miniature of its counterpart. The tail is so often in a state of regeneration (sometimes for the second or third time), that it is of dubious value to include its length in any morphometric analysis.

SEX DIFFERENCES.—Aside from primary sex differences, variation is present in the form of marked secondary sexual differences in all species of the genus *Desmognathus*. Juvenile males are difficult to distinguish from juvenile and adult females without gonadal inspection. Adult males develop hedonic glands over the body surface (Noble 1931, Hays 1966), which are clustered into a pad in the mental area of the mandible. Males grow larger in length and in body bulk than do females. The depressor mandibulae muscle in males is greatly enlarged, giving a "jowly" appearance behind the angle of the commissure. Males often have a sinusoidal commissure, whereas in females it is straight. In *fuscus* and *ochrophaeus* both the structure of the dentary and the number of dentary teeth are different from those in females (Noble 1927, Noble and Pope 1929). The lining of the cloaca in all sexually mature males is papillaceous, and the vent appears swollen in the breeding season. These modifications are important during the deposition of spermatophores. The females have an invaginated sac in the dorsum of the cloaca called a spermatheca, which serves as a sperm storage compartment (Kingsbury 1895b, Marynick 1971).

CONTINUOUS VARIATION.—This is exemplified by infrademe pattern variation. Some demes contain individuals having all stages of dorsal patterns from a perfectly maculate condition through a pattern representing blotches that fuse ontogenetically into a median dorsal stripe. Colors may

also be variable on a more or less continuous basis within a given population.

TAXONOMIC HISTORY OF THE GENUS *Desmognathus* IN FLORIDA

Lönnberg (1894) was the first to list any species of the genus *Desmognathus* from Florida. He assigned a single specimen collected from a wet hammock in Orange County to *D. auriculata* Holbrook. Brimley (1910) listed three specimens from "Hastings, Florida," as *D. fusca auriculata*, apparently following Cope's (1869) referral of this form to a subspecies of *D. fuscus* based on color pattern differences. Only *D. f. auriculatus* was reported from Florida (Dunn 1917, 1926, Van Hyning 1933) until Carr (1940) listed populations from the Torreya State Park ravines as *D. f. fuscus*. Although Stejneger and Barbour (1943) followed Carr, Bishop (1943) apparently was not convinced of the presence of the latter race in Florida, as he reported only *D. f. auriculatus*.

The first worker to do a specific study of the genus in Florida was Grobman (1950). He concluded that, in addition to *fuscus* and *auriculatus*, a third subspecies (*D. f. brimleyorum*) was represented in the Florida panhandle whose range widely interdigitated with the other two. Shortly thereafter Neill (1951) described a fourth subspecies (*D. f. carri*) from spring habitats in central Florida. It was later placed in the synonymy of *D. f. auriculatus* by Rossman (1959).

Schmidt (1953) followed Grobman, but Carr and Goin (1955) differed from Grobman slightly in that they considered *D. f. brimleyorum* to be restricted to the Florida panhandle west of the Apalachicola River, with *auriculatus* ranging eastward from that drainage into peninsular Florida. They considered *D. f. fuscus* to range from the north only into the Apalachicola River basin. Conant (1958), without explanation, listed *D. f. carri* from central Florida and moved the eastern limit of *brimleyorum* westward to the state of Mississippi.

Valentine (1963) restricted the name *brimleyorum* to populations in the Ouachita Mountains of Arkansas and Oklahoma, but gave no reasons. In his study of the genus *Desmognathus* in Mississippi, he concluded that *auriculatus* was a valid species on the basis of larval morphology and adult color pattern. This was the first study of desmognathines from the Gulf Coastal Plain to utilize a new character, which was not based strictly on adult color pattern and size differences. Wake (1966) considered *fuscus* and *auriculatus* to be species in his osteological monograph of the family Plethodontidae. Folkerts (1968) agreed with Valentine in considering *brimleyorum* to be restricted to the Ouachita Mountains. He did not present data to support this.

Folkerts (1968), on the other hand, differed from Valentine in con-

sidering *auriculatus* to be a subspecies of *fuscus*, a conclusion subsequently followed by Harima (1969). Folkerts (*op. cit.*) proposed a band of intergradation between the two subspecies approximately 100 miles wide. Finally, Goin and Cochran (1970), without comment, listed all three forms (*auriculatus*, *brimleyorum*, *fuscus*) as distinct species.

Thus, 134 years after Holbrook's (1838) original description of *auriculatus*, the taxonomic status of desmognathine salamanders from the Coastal Plain of the southeastern United States was more confused than ever. The present study is an attempt to clarify that situation. This has been done by 1) comparing populations of desmognathine salamanders from the Ouachita Mountains of Arkansas with those from adjacent Coastal Plain populations, in order to establish an objective morphological basis for evaluating the *brimleyorum*-*fuscus* relationship; and 2) investigating intrademe variation in morphological and ecological characters of desmognathine salamanders from Florida and adjacent areas for the purpose of evaluating the *auriculatus*-*fuscus* relationship. More conservative morphological characters than those used in the past were sought for use as indicators of systematic relationships of the forms found within the geographical limits of this study.

METHODS

In the past many workers studying the genus *Desmognathus* have failed to examine variation in certain characters. Although it is well known that individuals of most species of *Desmognathus* tend to become uniformly colored (dark brown or black from melanophore invasion) with increasing age, most workers have relied heavily on color pattern in their taxonomic analyses. Furthermore, because the phenomenon of metachrosis is highly developed in these organisms (which also seems not to be well known), it is very difficult to assess systematic relationships on the basis of color pattern alone. Since age and sexual variation in the phenotype of an individual were perceived to be important early in this study, I felt it necessary to establish criteria by which age-classes could be delimited. This prevented attempts to compare characters between recently transformed juveniles of a large species with second-year, sexually mature individuals of a small species, for example.

All transformed males with a single testicular lobe were considered juveniles, even though some may have been in their first season of sexual maturity. Males with two or more testicular lobes were considered sexually mature (Kingsbury 1902, Humphrey 1922, Hairston 1949, Organ 1961, Martof and Rose 1963, Rubenstein 1969). Although the number of lobes may not necessarily specify an individual's exact age, males with the same number are probably closer in age than those with different numbers.

According to the state of their ovaries (determined by dissection and by season) females were judged to be juveniles, sexually mature, or spent following criteria utilized by Means and Longden (1970) and Tilley and Tinkle (1968).

Over 4,000 Florida specimens of the *fuscus* and *auriculatus* complexes used in this study were collected from September, 1969 to December, 1971. Approximately 10,000 others were examined from museums in the southeastern United States, U. S. National Museum, and Museum of Comparative Zoology. About 750 specimens of *Desmognathus brimleyorum* were collected by me from the Ouachita Mountains.

Specimens were killed in diluted chloral hydrate and preserved in a straight position in 10 percent commercial formalin. After one week most collections were soaked in water for at least 24 hours, then transferred to, and stored in 40 percent isopropyl alcohol. Skeletal preparations were obtained either by maceration in water or the use of dermestid beetles. One hundred eighty-four desmognathine skulls were cleaned by hand with jewelers forceps. Teeth were grossly examined with a Wild M4A dissecting microscope at 50X magnification. Detailed examination was made with a scanning electron microscope, up to 520X. All line drawings were made using a camera lucida.

A technique for examining the interior of the mouth cavity was developed. The atlas-mandibular ligament was severed near its insertion on the mandible by a scalpel incision along a line beginning at the posterior corner of the eye and continuing to just behind the angle of the gape. This eliminated damage to the crowns of the teeth and destruction of the quadrate and squamosal bones, allowing the mandible to be lowered to its full extent with ease.

Throughout the paper snout to vent measurements are indicated as "SVL."

STUDY AREA.—Specimens were collected personally from about 250 localities throughout the southern range of the genus *Desmognathus* (Fig. 1 [not all plotted]).

The study region includes the southeastern United States from eastern Texas to the Atlantic Ocean (Fig. 1). Within this area emphasis is placed on northern and western Florida (Fig. 1B) and the Ouachita mountain system in Arkansas and Oklahoma (Fig. 1A). Specimens have been examined from all areas peripheral to the study region, with material examined from a total of about 700 localities throughout the range of the subfamily. Only those specimens examined from the study region and a few other localities are listed in the "Specimens Examined" section.

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RESULTS

The Seal Salamander (*Desmognathus monticola* Dunn) was first discovered in Florida during the course of this study. The range of this species in the state is probably confined to northern Escambia County, where small populations inhabit mesic, spring-fed ravines along Canoe Creek, a tributary of Escambia-Conecuh River. Results of the discovery were published elsewhere (Means and Longden 1970) and will not be discussed further here.

The following characters were found to be of systematic value in this study: 1) tooth morphology; 2) jaw profiles of sexually mature males; 3) premaxillary fontanelle morphology; 4) prearticular spine morphology; 5) relative size (snout-vent length, SVL); 6) tail morphology; 7) color pattern; 8) degree of melanization; and 9) larval morphology. In addition, two ecological aspects of the forms studied, microhabitat selection and ecological associates, were found to be significant in assessing evolutionary relationships. Each will be discussed in order of occurrence.

TOOTH MORPHOLOGY

The gross morphology and structure of urodele teeth have been studied by many workers (Hilton 1951, Kerr 1960, Parsons and Williams 1962, Parker and Dunn 1964, Means 1971, 1972). Adults of Recent Amphibia are unique among vertebrates in possessing transversely divided jaw teeth. These teeth consist of an enamel-capped orthodentine crown attached to an orthodentine pedicel by a fibrous connection. The teeth are pleurodont, the pedicel being attached to the underlying bone along its base and labial side. In adult urodeles the crown is usually bicuspid, and the axis of each cusp is parallel to the long axis of the bone of attachment. The lingual cusp is usually apical and larger in mass than the labial cusp. Palatal and occasionally coronoid teeth are present in modern amphibians but will not be discussed in this study.

Analyses of tooth morphology have been attempted on a limited basis within the subfamily Desmognathinae in studies of sexual dimorphism (Noble 1927, Noble and Pope 1929). In his comparative osteology of the family Plethodontidae, Wake (1966) commented only on the morphology of pedicels in *Phaeognathus hubrichti*. Otherwise, he did not compare the morphology of teeth nor of maxillary and dentary bones infragenerically.

In this study sexually mature males of the species of *Desmognathus*, *Leurognathus*, and *Phaeognathus* were examined to determine interspecific differences in detailed crown morphology of dentary and maxillary teeth. Figure 2 illustrates the similarities between species of the three genera. Basically the amphibian bicuspid crown is retained, but a trend toward reduction and loss of the labial cusp is evident in the series A, B, C, G, D, E, F, respectively. *Desmognathus quadramaculatus*, *D. aeneus*, and *D. wrighti* have elongate crowns tapering to a more acute apex than the other species studied. I have investigated variation in crown morphology in this study only for desmognathines of the Gulf Coastal Plain and Ouachita Mountain provinces.

Figure 3 illustrates the sharp distinction between the crown morphology of *D. brimleyorum* (A-D) and all other forms in the subfamily Desmognathinae. Of note particularly is the contrast between Ouachita Mountain populations and the surrounding Coastal Plain forms (E-H). The rounded, fungiform crowns of the Ouachita specimens were found to be present on both maxilla and dentary throughout post-metamorphic development to adulthood. There was no significant infraspecific variation noted in crown morphology in populations throughout the Ouachita Mountain uplift.

Figure 4 compares the Ouachita crown morphology with the Coastal Plain type more closely. The Coastal Plain type (A) is a piercing tooth after the style of other desmognathines, which have a reduced labial cusp and a pointed lingual cusp whose apex terminates above the top of the former. In Ouachita Mountain specimens both cusps are reduced to thin enamel ridges of equal height lying on top of the dome-shaped crown. A conspicuous flat region lies between the two cusps, and the whole aspect of the tooth gives the impression that it serves a crushing function. Whether these are functionally molariform, however, has not been investigated.

Representatives of all described taxa of the subfamily Desmognathinae were examined in order to assess the significance of the distinctive crown morphology of the Ouachita Mountain populations (Means 1971). Desmognathines can roughly be placed into three groups according to the relation of the labial cusp to the lingual cusp (Table 1).

The first type is the least common in the subfamily; these teeth are decidedly fungiform, with both cusps about equal. Species of Type II (except *Phaeognathus hubrichti*) have the maxillary teeth crown shape similar to Type I (usually the labial cusp is slightly reduced), but Type II dentary teeth are uniquely different (the lingual cusp is strongly recurved posteriorly). This second type represents dimorphism within an individual, but it is more strongly expressed in males than in females

TABLE 1.—TOOTH MORPHOLOGY IN THE SUBFAMILY DESMOGNATHINAE.

Type I	Type II	Type III
Cusps Nearly Equal; Crown Fungiform, Non-Dimorphic	Lingual Cusp Recurved Posteriorly; Labial Cusp Present, Dimorphic	Labial Cusp Lost or Greatly Reduced, Non-Dimorphic
<i>D. brimleyorum</i> <i>D. fuscus</i> (NE U.S.)	<i>D. ochrophaeus</i> <i>D. "fuscus"</i> (SE U.S.) <i>D. auriculatus</i> <i>D. ocoee</i> <i>Phaeognathus hubrichti</i>	<i>D. aeneus</i> <i>D. monticola</i> <i>D. quadramaculatus</i> <i>D. wrighti</i> <i>Leurognathus marmoratus</i>

(Noble 1927, Noble and Pope 1929). This type of tooth morphology commonly occurs with commissure sinuosity (an external character sometimes used by others [Dunn 1917, 1926, Bishop 1943]). Type I teeth are not variable in morphology between jaws and have both cusps relatively well developed.

Type III teeth diverge from the typical amphibian bicuspid tooth morphology by reduction of the labial cusp. The loss of the labial cusp in some individuals of *D. wrighti* and *D. aeneus* is here judged to be a secondary one, as reported in the frog genus *Ceratophrys* (Lehman 1968, Schultze 1970).

The crowns of teeth in Ouachita Mountain populations are remarkably uniform morphologically in three ways: (1) maxillary and dentary teeth are similar, (2) infrademe variation is small, and (3) interdeme variation is small. Considering how little variation there is in the crown morphology of *brimleyorum*, and how distinctive it is when compared with that of most other members of the subfamily, I conclude that this tooth type must have a genetic basis and is not environmentally induced.

JAW PROFILES OF SEXUALLY MATURE MALES

Another osteological character, or complex of characters (apparently best developed in the *ochrophaeus* complex of the southern Appalachians), is the jaw profile of sexually mature males. Cope (1869) was the first to notice that males of *D. ochrophaeus* had the "... posterior half mandible concave and edentulous." Boulenger (1882) also mentioned the concave and edentulous condition of the mandible of males in his description of *D. ochrophaeus*. Me made no comment concerning the mandible of *D. fuscus*, therefore implying that it is not concave and edentulous. Dunn (1916, 1917, 1926) seems to have ignored this character altogether,

but Noble (1927) and Noble and Pope (1929) carried out castration and testicular transplant experiments which demonstrated that, once formed in the adult, the concave and edentulous structure of the mandible in males does not undergo any change induced by hormone treatment. Figure 5 illustrates jaw profiles in 12 species of the subfamily Desmognathinae. The line of the commissure is relatively straight between the maxilla and dentary in A-E and G-J. In marked contrast to this is the bowed condition of the maxilla and the notched (concave) dentary in southern *fuscus* (K), *ochrophaeus* (L), and *ocoeae* (F). It is significant that no population of *brimleyorum* (I) or *auriculatus* (J) examined showed any evidence whatever of this type of sexual dimorphism.

In Florida the marked sexual dimorphism in mandibular and maxillary morphology of *D. fuscus* is geographically variable. This type of dimorphism is constant and always present in populations in the Chattahoochee-Flint-Apalachicola River drainage and the lower Ochlockonee-Little River drainage of Florida (Fig. 6). Furthermore, specimens examined from ravine demes all the way to the headwaters of the Flint and the Chattahoochee rivers in the southern Appalachians are nearly identical in this condition. However, demes identified as *fuscus* from Gulf Coast drainages (Escambia to Choctawhatchee rivers) on the basis of other characters may possess jaw dimorphism somewhere along a gradient of expression from none to fully developed (Fig. 6).

In a number of Florida localities both *D. auriculatus* and *D. fuscus* can be collected within a few hundred meters of each other, and in two localities where I have taken specimens of both under the same debris, no intermediates have been found. Figure 7 illustrates the difference between both species in jaw profile dimorphism, viewed externally.

Within the geographical limits of this study, the significant facts involving this character complex are: (1) *D. brimleyorum* has no sexual dimorphism in jaw profile, whereas peripheral demes (northern Louisiana parishes and Crowley's Ridge physiographic region, Arkansas), here referred to *D. fuscus*, indicate slight to moderate dimorphism; (2) *auriculatus* has straight jaws in both sexes, whereas adjacent demes referred to *fuscus* possess strong profile dimorphism; (3) in Florida strong profile dimorphism is always present in *fuscus* demes throughout the Chattahoochee-Flint-Apalachicola River drainage, but in more westerly Gulf Coastal drainages (Escambia to Choctawhatchee rivers) demes referred to *fuscus* are variable in this character.

PREMAXILLARY FONTANELLE

Desmognathines have an axially oriented fontanelle between the two nasal processes of the premaxilla. The fontanelle is closed by fusion of the

two rami in *Phaeognathus hubrichti*, a terrestrial burrower, and in *Leurognathus marmoratus*, a subaquatic burrower. Presumably the loss of the fontanelle serves to add structural strength to the snout as a further adaptation of a burrowing morphology already well developed in other skull characters of the subfamily. This character has not previously been used in studies of interspecific variation.

In all species examined in the genus *Desmognathus*, the fontanelle is present and relatively similar among most forms (Fig. 8). It usually occurs between the two premaxillary processes for about two-thirds of their length, beginning at the mandibular portion and progressing well beyond the nasal constriction, terminating about the level of the anterior edge of the orbit. It is well developed in all skull preparations examined of specimens from Florida ravines that meet other criteria for the *fuscus* phenotype (Figs. 8, 9). However, swamp-muck forms of the *auriculatus* phenotype have nearly lost the fontanelle, it being confined to a tiny aperture between the nasal processes of the premaxilla just posterior to the *pars dentalis* (Figs. 8, 10). This reduction of the fontanelle is not subject to sexual dimorphism, and it is a constant character in all size classes of these demes and in every population examined for this study (Fig. 10).

PREARTICULAR SPINE

In desmognathines the head is used as a wedge for burrowing in the loose substrate. As a result, desmognathines have evolved a complex system of muscles, bones, and ligaments specifically adapted to this behavior. A large ligament (the atlas-mandibular ligament) has evolved in the levator mandibulae muscle which extends from a dorsal ridge on the atlas to the mandible (Baird 1849, Wake 1966, Hinderstein 1971). It serves to bring the skull down when the quadrato-pectoralis is contracted. Hinderstein (1971) apparently followed Wake (1966) in assuming that this ligament had its origin on the coronoid process (= spine) of the prearticular bone of the mandible. Both are incorrect in this assumption, however. The atlas-mandibular ligament actually is inserted on the dentary bone (Fig. 11C), with the dorsal spine lying along the lateral surface of the ligament just posterior to the insertion.

The prearticular spine serves as an additional surface for insertion of the levator mandibulae muscles. The main surface for muscular insertion on the mandible is the prearticular shelf. The muscles that insert here close the mandible. The prearticular spine may have some fascia attachment to the lateral side of the atlas-mandibular ligament, but tension on this ligament is transferred primarily to the surface of its insertion

on the posterior, lingual portion of the dentary immediately behind the teeth.

This spine is developed to a greater or lesser degree throughout the subfamily. However, it is most strongly developed in *Desmognathus brimleyorum*, and occurs as a high pinnacle pointing dorsally to the plane of the prearticular shelf (Figs. 11, 12). Thus it may serve as a qualitative character in partly delimiting *D. brimleyorum* from surrounding coastal plain populations of desmognathines.

TAIL MORPHOLOGY

Much has been said about the tail of desmognathines as a character serving to distinguish one form from another. Most authors (Cope 1889, Dunn 1917, Bishop 1943) have considered the cross section at the base of the tail to be important. Gross morphology of the whole tail and its length are often unreliable as characters, because salamander tails are commonly broken and undergoing regeneration. Usually a partially regenerated tail is recognizable externally, but completely regenerated tails often are not detectable.

In this study, tails examined using radiographs were found to be significant as indicators of taxonomic relationships in Florida (Figs. 13, 14). The fleshy portion of the tails of swamp and river floodplain muck inhabitants (*auriculatus*) is greater than those in ravine (*fuscus*) demes. A small, but distinct, dorsal keel is present and usually evident for the full length of the tail. The tails of swamp and floodplain, muck-inhabiting *auriculatus* are decidedly compressed and blade-shaped when compared to the slender, rounded aspect of ravine-inhabiting *fuscus*. Distally, on complete or fully regenerated tails, the blade aspect persists to the tip in swamp and floodplain desmognathines. The tail of ravine specimens tapers into a long, terete filament. The basal cross-section in Florida *fuscus* is rounded and for its entire length compares exactly with that of *ochrophaeus*. It is significant that the regenerating tails of ravine salamanders and those inhabiting floodplains regain the particular morphology of the original tail peculiar to the respective ecophenotype.

RELATIVE SIZE

Although size differences have been used by most authors in diagnoses of desmognathine taxa, no study has adequately compared the three species investigated herein. Grobman (1950) listed all three from Florida but did not comment on size differences.

Dunn (1917) presented data showing that *D. brimleyorum* (from the Ouachita Mountains) was larger than *fuscus* (northeastern U. S.),

but he gave no figures for *auriculatus*. In 1926 Dunn reported only the largest known sizes for these three taxa. He indicated that *brimleyorum* and *fuscus* reached approximately the same maximum length (65-68 mm SVL), but implied that *auriculatus* was smaller (49 mm SVL). Bishop (1941) presented more definite data on the size of adult *D. fuscus* from New York: males, \bar{x} = 48.6 mm SVL, N = 90; females, \bar{x} = 43.6 mm SVL, N = 65.

The average of maxima for adult *D. auriculatus* from seven localities in northern Florida and adjacent Georgia given by Rossman (1959, Table 1.) was 57.1 mm SVL. Neill (1951) and Valentine (1963) reported that adult males of *auriculatus* ranged between 45 and 60 mm SVL. Valentine (*op. cit.*) reported that adult males of *fuscus* in Mississippi ranged from 30-58 mm SVL, thus showing that *auriculatus* was larger than *fuscus* in that state.

Folkerts (1968) believed *D. fuscus* (35-65 mm SVL) was larger than *auriculatus* (33-61 mm SVL) in Alabama and western Florida. In this study *auriculatus* was found to barely enter southern Alabama along floodplains of the major rivers. My examination of specimens of *auriculatus* seen by Folkerts in Auburn University collections indicates that most were juveniles or small adults. Thus it became evident early in this study that a method for determining relative age of specimens was important to avoid confusion resulting from mixture of measurements taken from several age classes. Whenever possible specimens were dissected, and the gonads were examined when taking size measurements.

Figure 15 illustrates the size relationships between *D. auriculatus*, *brimleyorum*, and Florida *fuscus*. Although these samples are not large, I believe they are fairly representative and reflect the relative differences between the same age classes of the three biotypes.

The sample of 126 *D. brimleyorum* from the top of Rich Mountain, Arkansas (Fig. 15), is larger in all age classes than previously reported for this form (Chaney 1958). I believe this is because the Rich Mountain locality is at a very high altitude (ca. 2600 ft.) in the Ouachita Mountains, and Chaney's sample (114 postlarval specimens) is near the lowest altitude known for *brimleyorum* (ca. 400 ft.). Many ectothermic vertebrates show an increase in size correlated with an increase in altitude over the geographic range of the species.

It is readily seen that the mature male and female classes of *D. auriculatus* (from the Ochlockonee River drainage) are larger than the same classes of *fuscus* from the Torreya ravines in Liberty Co., Florida (Fig. 15). Furthermore, at one locality where both species occur together (Sweetwater Creek, Liberty Co., Florida) in the western Florida study area, the same relative size differences obtained (Fig. 16).

As an example of the problems that can arise from not comparing similar age classes (determined by direct gonadal inspection), Figure 17 compares paratypes of *Desmognathus fuscus carri* Neill with topotypes collected from the same Cabbage Palm hammock stream at Silver Glen Springs by Mr. Steve Christman in 1970. Included for comparison is the size-frequency distribution for *D. auriculatus* used in Figure 15. It is apparent that most of Neill's original series was composed of juveniles. Since relative size was diagnostic for *D. f. carri*, this character is invalid (Rossman 1959). More intensive collecting has turned up adults, which were missing from Neill's type series.

In this study *D. auriculatus* averaged larger than western Florida and southern Alabama *fuscus* in all age classes, including larvae. This is in agreement with Valentine (1963) and Rossman (1959), but not in accord with Folkerts (1968).

Color Pattern

Color pattern has figured heavily in earlier attempts to systematize salamanders of the genus *Desmognathus*. Largely because of the high degree of variability of this character complex, along with a great deal of overlap in gross appearance between variants of different forms, most species have several synonyms. Difficulty in identification of species is illustrated in a paper by Huheey (1966). Almost every study dealing with desmognathines from the Great Smoky Mountains National Park has listed *D. fuscus* as occurring there. Huheey reports that for every case he reinvestigated, specimens in question turned out to be either *D. monticola*, *quadramaculatus*, or *ochrophaeus*, and that in his opinion *D. fuscus* is not in the park. Conversely, some species are not widely acknowledged because of their gross similarity to a congener.

Cope (1896) assigned considerable taxonomic value to "mucous pores" in the development of the lateral pattern of the adult. He recognized two lateral series of pores, a superior and an inferior one. The three species he listed in 1889 were partly distinguished by the presence or absence of one or both series.

In his review of the genera *Desmognathus* and *Leurognathus*, Dunn (1917) stated, "I have been unable to use the lateral pores as diagnostic characters. This is largely because the distinctness of these pores is so dependent on the preservation." However, nine years later in his monograph of the family Plethodontidae, Dunn (1926) placed great importance on "... three rows of unpigmented areas on each side of the larva." His source was Banta and McAtee (1909), who showed the development of the color pattern of *Eurycea bislineata* to be dependent on these unpig-

mented areas. Apparently neither Dunn nor Banta and McAtee realized what the lateral unpigmented areas really were.

Kingsbury (1895a) was the first to recognize that the lateral rows of unpigmented areas were actually lateral lines of the vertebrate acousticolateralis system. The "unpigmented areas" of Dunn and Banta and McAtee surround free neuromast organs. These organs in Amphibia are usually at the bottom of a shallow pit or groove (Dijkgraaf 1962). I have examined every form in the subfamily Desmognathinae and find that the only "pores" along the side of the larvae and transformlings correspond to neuromast pits or their vestiges (Kingsbury 1895a, Hilton 1947). Thus, Cope's lateral rows of mucous pores correspond to the depressions of free neuromast organs in desmognathines.

Three rows of lateral-line organs are found in the larvae of salamanders (Kingsbury 1895, Hilton 1947, Eaton 1956). The development of adult pigment patterns in desmognathines is strongly influenced by the presence of the lateral lines. Eaton (1956) very accurately described the pigmentation of the larvae of *Desmognathus quadramaculatus* and *ochrophaeus* (*D. fuscus* according to Eaton; I tentatively follow Martof and Rose [1963] and Huheey [1966] in considering the form from Mt. Mitchell, N. C., as *ochrophaeus*).

In this study, all species examined during the larval stage possessed three lateral-line series that were usually obvious under magnification as rounded, light spots. I follow Eaton's (1956) terminology in recognizing dorsolateral (Row 1), lateral (Row 2), and ventrolateral (Row 3) lines (Figs. 18a, 19a, 20a, and 21a). Row 1 begins immediately above or just anterior to the insertion of the forelimbs on the trunk. It proceeds down the entire length of the trunk and out onto the dorsal sides of the tail for about two-thirds its length. Neuromast sites are located on approximately every second myomere. Row 2 begins in about the same place as Row 1 and proceeds along the trunk just below the level of Row 1. Often both lines appear to form a single line because neuromast sites of Row 2 usually alternate in position with those of Row 1. There occurs about one neuromast site per myomere in Row 2. This row diverges from Row 1, beginning above the insertion of the hind limbs, to form a well-marked system of neuromast sites mid-laterally on the tail.

Row 3 is the shortest, occurring only from the axilla to the groin, about one and one-half neuromast sites per two myomeres. In the above, it is seen that the number of neuromast sites in any given line does not exactly correspond to the number of myomeres (14 on the trunk, $20 \pm$ on the tail). This is probably because the lateral line neuromast sites are formed by nervous tissue that grows out from the acoustic tubercle in the dorsolateral wall of the medulla oblongata (Dijkgraaf 1962), invading

the trunk region during embryogenesis. These sites thus form independently of the metameric development of the trunk and the tail. Table 2 outlines the post-metamorphic fate of each lateral line (as each is apparent on transformed specimens in the form of a line of lightly pigmented spots, portholes, dots, etc.) for the three *desmognathines* of this study.

TABLE 2.—ONTOGENETIC FATE OF LATERAL-LINES IN *Desmognathus auriculatus*, *D. brimleyorum*, AND FLORIDA *D. fuscus*.

Taxon	Row #1	Row #2	Row #3
<i>Desmognathus auriculatus</i>	forms small, discrete, dorsal trunk spots that do not coalesce; same for tail.	becomes obscured by melanophore invasion on trunk; forms discrete portholes on sides of tail throughout life.	forms diagnostic rows of white spots between axilla and groin throughout life; not on tail.
<i>D. brimleyorum</i>	forms loose dorsal trunk pattern during juvenile stage, which dissipates to uniform coloration in adults of both sexes; same for dorsal tail pattern.	becomes obscured by melanophore invasion on trunk; forms rounded portholes on tail as juveniles become invaded postmaturity by melanophores.	becomes obscured by melanophore invasion on trunk following metamorphosis; not on tail.
Florida <i>D. fuscus</i>	forms strong dorsal trunk pattern (becomes obscured only in old males); forms strong dorsal tail stripe with scalloped borders.	barely discernible, even in larvae on trunk; forms rounded spots on tail, which become obscured following transformation.	becomes obscured by melanophore invasion on trunk during early post-metamorphosis; not on tail.

The color pattern of transformed *Desmognathus brimleyorum* develops from a typically *desmognathine* blotched condition present in most juveniles to uniformly brown dorsally (and laterally) in mature adults (Fig. 22). Some demes of *brimleyorum* have a high incidence of dorsal blotching, especially at lower elevation localities. All Ouachita Mountain collections examined contained a preponderance of patterned juveniles and none or only a few uniformly-colored, mature adults. These collections could easily be identified as *fuscus* without determination of age and close inspection of other characters (i.e., tooth and prearticular spine morphology). The venter in younger juveniles of *brimleyorum* appears immaculately white, but close inspection reveals a relatively uniform

suffusion of dark pigment cells, especially on larger juveniles. With increasing age the intensity of pigment becomes greater, giving a faintly soiled appearance. The venter is sometimes weakly mottled, but basically appears light tan to white when compared to the dark, uniformly colored dorsum.

Laterally, *D. brimleyorum* is distinguished by a nearly bicolored appearance. The light ventral color meets the dark dorsal color about mid-way along the side (between Row 3 of lateral-line light spots and a line above the division between the underlying epaxial and hypaxial musculature). The meeting of dorsal and ventral colors is relatively well-defined but not sharp. Considerable interdeme variation exists in the lateral pattern, however, due to the effects of melanization.

The pattern of *Desmognathus auriculatus* is best illustrated by specimens from Mississippi (Fig. 23). These are not so melanistic as individuals from Florida (Fig. 24) and southeastern Georgia (Fig. 25) demes, and a pattern is evident. Note particularly that the neuromast organs of lateral-line Row 1 do not repel melanophores nearly so strongly as those in *fuscus* (Figs. 21 & 27). Because of this, fusion of pigmentless areas surrounding the neuromast vestiges (so important in dorsal pattern development of *fuscus*) never occurs in *auriculatus*. Characteristically, *auriculatus* has a parallel pair of thin, light lines on the neck region that extend from the level of the insertion of the dorsalis trunci muscles on the underlying skull, posteriorly to the insertion of the forelimbs (Figs. 23 & 24). Lateral-line Row 1 forms discrete, punctate spots on the dorsolateral sides of the tail on either side of the fleshy dorsal fin (Figs. 23 & 24). The dorsal area between the rows of tail spots is usually less intensely pigmented than any other part of many specimens and it often appears deeply reddish (as do the trunk and tail "portholes" occasionally in some individuals in demes generally lacking red color on other parts of the body).

The ventral pattern of *auriculatus* is usually comprised of flecks of iridiophores over a dark (usually black) ground color. Some demes may lack the flecking entirely and others may have a reticulum of lighter and darker areas (Figs. 23 & 24). The opposite extreme from the light pattern of specimens pictured in Figure 23 is total absence of any pattern due to intense black pigmentation in some demes in Florida and southeastern Georgia (Figs. 25 & 26). The typical color scheme of *auriculatus*, when found in ravines in western Florida, is coal black with a wash of intense reddish color over the dorsum (Fig. 26; red lost in preservation). The red is usually obscured by black pigment and is only readily evident where it occurs on the light neuromast sites, dorsal base of the tail, or on the cheek. This color occasionally is so intense, however, that some in-

dividuals are quite red in gross appearance. The reddish color never occurs on the venter. In my opinion, the spring margin ecophenotype of central Florida described by Neill (1951) as *Desmognathus fuscus carri* is a local variation similar to the ravine ecophenotype of *auriculatus* found elsewhere during the course of this study.

The color pattern of transformed *D. fuscus* in the study area is also highly variable. Basically, juveniles and females are strongly marked dorsally by large light areas surrounding neuromast vestiges of lateral-line Row 1 (Fig. 27). These light areas exist in all states, from discretely isolated by fringing melanophores to broadly fused along the midline of the dorsum as a smooth, light stripe. The light areas were often differently colored in different individuals with red, yellow, or lighter shades of brown. Characteristically in *fuscus* the dorsal light spots are fringed laterally by a dense accumulation of pigment that sets the dorsal pattern off sharply from the sides of the specimen (Fig. 27a-c). Laterally, individuals are flecked with white iridiophores on a brown ground color.

Melanization, mostly present in older males, may or may not occur (Fig. 27c, e, f). When it does, the quality of the dark color in *fuscus* is decidedly brown as compared to black in *auriculatus*. This quality of color is often diagnostic by itself in identifying specimens of both species where they are found to occur together. The ventral color of *fuscus* also contrasts with that of *auriculatus*. In *fuscus* the ventral ground color is light but may be influenced by some degree of melanization (commonly appears peppered or mottled by clusters of melanophores). In *auriculatus* the ground color of the venter is black and often is generously sprinkled with white iridiophores.

Figure 28 illustrates a dorsal pattern variation in *fuscus* found in some demes of the Yellow, Escambia, and Choctawhatchee River drainages of western Florida. Dorsal light areas are not always present, and the dorsal pattern consists of fine lines of melanocytes in the shape of chevrons lying over myosepta. In a few localities where I found *auriculatus* and *fuscus* occupying the same habitat, mature males of *fuscus* were extremely similar to equally sized *auriculatus* in color and in the absence of a pattern (Fig. 29). However, inspection of tail morphology, jaw profile dimorphism, and close scrutiny of the vestiges of the juvenile pattern always effected a positive identification.

MELANIZATION AND METACHROSIS

The desmognathines investigated in this study exhibited a great deal of variation in external color pattern, depending mainly on the amount of melanization (deposition of melanin in the skin) occurring ontogenetically and geographically. Short-term (several hours to several days)

changes in individuals also occur, but are the result of another phenomenon, metachrosis (change in dispersion of melanin in pigment cells). The combination of the two darkening processes produces demes that are so different in gross inspection of color patterns that different individuals are hardly recognizable as the same species without reference to more conservative characters.

Desmognathus auriculatus provides a good example to demonstrate that the interaction of metachrosis and melanization leads to dramatic differences in color patterns. Grobman (1950) reported that light-colored individuals of *auriculatus* from Louisiana were experimentally induced to become darker by metachrosis when left on dark substrates for 10 days. Dark Florida specimens became lighter when left on light substrates. According to Grobman, Louisiana and Florida experimental specimens converged on a similar color quality (although he reported that they were still distinguishable).

Large series of specimens of *D. auriculatus* examined during this study from Louisiana (Tulane University collections) were found to be as lightly colored as some demes referred to *fuscus* from southern Mississippi, although basic pattern differences existed. Living specimens collected from southern Mississippi were also observed to be very light (Fig. 23). The reason for the decreased pigmentation of western Gulf drainage demes of *auriculatus* is not known precisely, but certain ecological correlations allow the following speculation. The very dark demes occurring in Florida inhabit black, swampy mucks derived mainly from cypresses (*Taxodium* spp.), gums (*Nyssa* spp.), and *Magnolia* spp. Muck in western Gulf localities in general appears to be lighter in color, possibly because a greater percentage of its composition is due to contributions from hardwood litter (species of the genera *Fagus*, *Quercus*, *Liquidambar*, *Carya*, *Alnus*, *Ulmus*, *Acer*, etc.). It is also noteworthy that, correlated with absence of black mucks west of the Pascagoula River system, large deposits of Pleistocene loess are found in western Mississippi. Whether the presence of these fine-grained aeolian sediments has some effect on the ecology of desmognathine salamanders is not known, but it is light in color and forms a pasty mud in the floodplains of streams in which it is reworked (pers. obs.).

It was often noted in the field that the overall darkness of a specimen was adjusted to that of the substrate upon which it was collected. Many demes of both *D. auriculatus* and *fuscus* collected on dark substrates were observed to have undergone a general decrease in intensity of dark pigment if kept in white plastic containers several hours after collection. Especially important in this regard are the observations made at Sweetwater Creek (Sec. 31, T2NR7W, Liberty County, Florida), where both

fuscus and *auriculatus* were collected in a few instances under the same debris in a mucky floodplain. Adults were very difficult to identify by color pattern alone at the time of capture (Fig. 29). However, as little as 30 minutes later, it was observed that, whereas *auriculatus* basically retained an intense black color, *fuscus* always became lighter overall. Even old males that had lost the juvenile blotching ontogenetically were recognizable because a brownish quality of their ground color was exposed by metachrosis (concentration of melanin particles in melanophores). These observations indicate that a considerable degree of the quality of external appearance of desmognathines in this study is environmentally influenced. This single phenomenon alone probably accounts for many of the different interpretations made by others in attempting to distinguish species in the Coastal Plain.

Although *D. fuscus* primarily inhabits streamsides, where it is found most abundantly in moist ravine situations in the area of this study, individuals nevertheless occupy mucky sites adjacent to ravine streams and also seepage sites in the ravine floodplain or along valley walls. At the headwaters of one upland stream this type of habitat was extensive and appeared suitable for *auriculatus* (i.e., Beaverdam Creek steephead, Sec. 8, T1NR7W, north of Bristol, Liberty County, Florida), but was populated by *fuscus*. In these situations all size classes of *fuscus* usually take on an overall dark wash due to the stellate condition of the melanophores. A collection of *fuscus* (UF/FSM-16240 through 16259) from Kolomoki Mounds State Park in southwest Georgia, and another from Calhoun County, Florida (UF/FSM-17793 through 17821) are especially noteworthy for this quality.

An important observation made in this study was a long-term (3-5 days) decrease in the intensity of black pigment in *auriculatus*, revealing the persistence of a weak, underlying pattern in black Florida populations. The pattern is similar to that in demes from Louisiana and Mississippi. On the basis of similarity of basal color pattern and of similarity in other morphological characters, I conclude that Louisiana, Mississippi, and Florida (swamp and floodplain muck) populations are conspecific. There is no good evidence at present to indicate that taxonomic recognition is warranted for light, western populations and dark, eastern populations.

Short-term (6-12 hours) color changes of dark individuals to a lighter condition were frequently noted in *D. fuscus* from northern Florida and southern Alabama (Figs. 30 & 31). Collections made in winter seemingly had higher percentages of dark specimens. Often in the field I initially identified intensely dark specimens of *fuscus* as *auriculatus*. Although positive field identification of these dark individuals was possible

by examination of other morphological characters, dark *fuscus* invariably became lighter if kept alive a few hours in collecting jars.

LARVAL MORPHOLOGY

Valentine (1963) was the first student of desmognathine taxonomy to use larval differences between *Desmognathus auriculatus* and *fuscus* as diagnostic characters. He described and compared larvae from Mississippi on the basis of body pattern, gill color and morphology, and relative size at transformation. However, Goin (1951) had earlier noted differences between hatchlings of these taxa.

In Florida, *D. auriculatus* larvae were found to be larger at transformation (*auriculatus*: \bar{x} =21.4 mm, N=10; *fuscus*: \bar{x} =13.5 mm; N=19); to be more intensely pigmented (*auriculatus*: Fig. 20a, b; *fuscus*: Fig. 21a); to possess bushy gills, dark in color (Fig. 20a, b), as opposed to tiny, iridiophore-populated gills of *fuscus* (Fig. 21a); and to be patterned dorsally by much smaller light areas around dorsal neuromasts of Row 1 (Fig. 20b) than *fuscus* (Fig. 21a). In all these characters examined in Florida material, the comparison between *auriculatus* and *fuscus* revealed differences similar to those reported by Valentine (1963) for these species in Mississippi.

Unquestionably, variation in the above characters exists. Drastich (1927) performed experiments demonstrating that the number of gill fimbriae decreases with availability of oxygen in larvae of *Salamandra salamandra*. Because of time limitations, no experiments were carried out on *D. auriculatus* during this study, but field observations established that ecological isolation is greater between the larvae of the two species in question than between transformed individuals from demes in the Apalachicola and Ochlockonee river drainages. However, in ravine habitats occupied by *auriculatus* in western Florida (which have not been open to colonization by *fuscus*), the gills of larvae remain luxuriant with fimbriae despite the presence of well-aereated water in which they were found. Thus, it appears that large bushy gills are diagnostic in serving to distinguish larvae of *auriculatus* from larvae of *fuscus*. At no time in the study was it as difficult to identify larvae or adults as it was to identify juveniles.

MICROHABITAT SELECTION

Desmognathus brimleyorum is confined to rocky, gravelly streams in the Ouachita Mountains. The adults were often difficult to collect because they were most often found under large rocks lying in the stream or at its edge. Rock falls along upper portions of mountain streams were

also good collecting sites for adults. On removal of the rocks, adults were found lying partially submerged in water. Rarely was one found totally out of water, and invariably each specimen attempted to escape into the stream. This species is one of the most aquatic in the genus.

The juveniles were readily collected by raking gravel along stream-sides, but especially where seepage or a small freshet drains over gravel and rock rubble. Thus, there appeared to be a microhabitat differentiation between adults and juveniles. Larvae were found in small grained gravel, under rocks in the stream, in small pools formed along stream courses, and in moss covering rock faces where these occurred with water flowing over them.

Desmognathus auriculatus was most often found under debris at the edge of mucky, floodplain sloughs, at mucky edges of swampy lakes (Lake Iamonia, Lake Miccosukee, Florida) and in other sites of decomposing muck associated with black waters. Individuals were often raked up from below several inches of wet muck. In southeastern Georgia this species was common in mucky streams draining the eastern flank of the Tifton Uplands.

Considerable seasonal fluctuation of water levels occurs in the habitat of *D. auriculatus* throughout the study area. When habitats are completely dry, the salamanders can be raked from under the surface of dried, peaty muck at the lowest point of the depression where they aggregate.

Although *D. auriculatus* was rarely taken from situations other than the above habitats, they were found in ravine streams in several places in the study area (Econfina Creek steepheads, streams emptying into the western end of Choctawhatchee Bay). These ravine environments, however, yielded specimens only where organic debris had accumulated along seepage sites. In such ravines, the basic muck microhabitat preference had not changed. There did not appear to be significant microhabitat differences between sex or age classes.

Those habitats primarily inhabited by *Desmognathus fuscus* in the study area are best described as sandy-bottomed, wooded, upland ravine streams. Usually the floor of a ravine valley is covered with multi-colored leaf litter (hardwood origin), and the streamside has mossy banks with accumulated organic debris supporting a large arthropod and oligochaete fauna. Numerous seepage sources occur near the stream head and along the downstream course, which maintains a relatively permanent flow.

Of the three species studied, *D. fuscus* appeared to be the most ubiquitous in its microhabitat selection. It was found in wet, mucky sites along lower reaches of upland streams where seepage areas were not well drained and partially decomposed hardwood litter had accumulated.

Although *fuscus* was not often found in river floodplain slough or swampy terrace stream habitats within the geographical range of *auriculatus*, it (*fuscus*) was taken from such habitats in southern Alabama, Louisiana, Mississippi, and from localities in Florida west of the Choctawhatchee River drainage. In Florida, these localities were always near or immediately adjacent to ravine habitats. Field observations indicated that at no time was *auriculatus* found occupying a ravine habitat if populated by *fuscus*, but as indicated above, *fuscus* could be found in some river floodplain habitats occupied by *auriculatus*. *D. fuscus* was never found in coastal flatwoods swamps and streams, or in the center of extensive floodplain swamps of larger rivers. Relative dispersal ability into a greater variety of habitats seemed to be higher for *fuscus* than for *auriculatus*.

ECOLOGICAL ASSOCIATES

Just as there are differences in microhabitat preferences between *D. fuscus* and *auriculatus* in Florida, there exists a similar relationship in the microhabitat preferences of two species of the genus *Pseudotriton*. Each species is an ecological associate of one of the desmognathines. Invariably, a species of *Desmognathus* and a species of *Pseudotriton* not only occurred together in the same habitat, but occupied similar microhabitats as well (differences in food habits and demography were at least two parameters that prevented these microhabitat cohabitants from sharing an identical ecological niche).

Pseudotriton montanus was found to be a muck dweller along swampy streams of floodplain terraces, coastal lowlands, and in upland mucky streams along the eastern flank of the Tifton Uplands. *Pseudotriton ruber* was found exclusively in deep, upland ravines. Whereas *D. fuscus* and *auriculatus* have higher population densities and wider dispersion throughout their respective habitats, the two species of *Pseudotriton* were comparatively less abundant in post-larval age classes and more highly localized in the different environments as far as it was possible to determine.

Desmognathus fuscus and *Pseudotriton ruber* are ecologically sympatric, forming a species pair largely confined to upland stream habitats. *D. auriculatus* and *P. montanus* form another pair, ecologically sympatric in river floodplains, coastal flatwoods streams, and in mucky streams draining the eastern slopes of the Tifton Uplands. It was found during the course of this study that these two pairs are also geographically sympatric in the study area, the geographic range of each member of both pairs coinciding almost exactly with the range of the other member.

SUMMARY OF DIFFERENCES BETWEEN NAMED ENTITIES OF THIS STUDY

Desmognathus brimleyorum Stejneger

1. large-sized (adults greater than 60 mm SVL)
2. fungiform crown morphology
3. no dimorphism between dentary and maxillary teeth
4. no sexual dimorphism in jaw profile
5. adults with no distinct pattern
6. large prearticular spine
7. premaxillary fontanelle about 50 percent of length of premaxillary spines (well developed)
8. neuromast vestiges of Row 2 and 3 surrounded by iridiophores, usually obvious as lateral lines of dots
9. tail cross-section round at base; tail keeled, compressed posteriorly
10. found in Ouachita Mountains of Arkansas and Oklahoma

Desmognathus auriculatus Holbrook

1. medium-sized (adults 45-60 mm SVL)
2. piercing, recurved dentary teeth
3. dimorphism between dentary and maxillary teeth
4. no sexual dimorphism in jaw profile
5. adults with a weak, but distinctive pattern in west (Louisiana, Mississippi), obscured in east (Florida, Georgia), but inducible by metachrosis
6. prearticular spine not well developed
7. premaxillary fontanelle nearly closed, spines fused posteriorly
8. neuromast vestiges of Row 2 (on tail) and Row 3 usually surrounded by iridiophores, usually obvious as lateral lines of dots in adults
9. tail cross-section round to trigonal at base; tail keeled; compressed to tip
10. range incompletely known to the northeast and west of Florida, but distinctly Coastal Plain

Desmognathus fuscus (Rafinesque)
from Florida

1. small-sized (adults 40-50 mm SVL)
2. piercing, recurved dentary teeth
3. strong dimorphism between dentary and maxillary teeth
4. extreme sexual dimorphism in jaw profile
5. adults usually with an elaborate pattern derived from juvenile blotched condition
6. prearticular spine moderately developed
7. premaxillary fontanelle well developed
8. neuromast vestiges usually not set off from lateral color pattern by iridiophores as lines of dots
9. tail cross-section round; tail not keeled, tapering to a terete filament at tip
10. ranges from at least Piedmont of Georgia to Florida, then westward at least to the Alabama River drainage (possibly to the Mississippi River)

Desmognathus fuscus (Rafinesque)
from New York

1. medium-sized (adults 45-60 mm SVL)
2. fungiform crown morphology
3. no dimorphism between dentary and maxillary teeth
4. no sexual dimorphism in jaw profile
5. adults usually with vestige of juvenile pattern

6. prearticular spine moderately developed
7. premaxillary fontanelle well developed
8. neuromast vestiges of Row 2 usually present on tail as line of dots
9. tail cross-section at base trigonal; tail compressed to tip
10. ranges from Ontario to at least the Piedmont of North Carolina (inaccurately known)

Desmognathus ochrophaeus Cope
from southern Appalachians

1. small-sized (adults 40-50 mm SVL)
2. piercing, recurved dentary teeth
3. strong dimorphism between dentary and maxillary teeth
4. extreme sexual dimorphism in jaw profile
5. adults usually with an elaborate pattern derived from juvenile blotched condition
6. prearticular spine moderately developed
7. premaxillary fontanelle well developed
8. neuromast vestiges usually not expressed in adult as lateral lines of dots
9. tail cross-section round; tail not keeled, tapering to a terete filament at tip
10. ranges throughout the southern Appalachians

DISCUSSION

STATUS OF *Desmognathus brimleyorum* STEJNEGER

In this study, Ouachita Mountain desmognathines were found to be distinguishable from adjacent Arkansas and Louisiana Coastal Plain populations on the basis of the following characters: tooth morphology, relative size, color pattern, prearticular spine morphology, larval morphology, and jaw profiles. Unpublished dissertation research of Chaney (1958, p. 84) indicates that Ouachita Mountain populations near Russellville, Arkansas are significantly different from Louisiana desmognathines in: "(1) head length/head width ratio; (2) size at hatching; (3) growth rate; (4) maximum size attained; (5) tail length; (6) time of attainment of sexual maturity; (7) number of eggs deposited; (8) color patterns possessed by the larvae and the adults." Thus, the results of both studies clearly indicate that populations in the Ouachita Mountains are strongly different from surrounding desmognathines in at least eleven morphological and developmental characters.

In the original description of *D. brimleyorum*, Stejneger (1895) pointed out that maxillary and mandibular teeth were "all very blunt." Other characters he mentioned are shared with one or more other species except one, "the anterior glandular prolongation of the lower lip," which Stejneger claimed was absent. All adult males I examined possessed a mental gland that is characteristic for all species in the genus *Desmognathus* and is responsible for an anteriorly directed protrusion of the fleshy portion of the mandible. However, Stejneger's observation that a "prolongation . . . is absent," is essentially correct. The mental gland is

proportionately smaller in *D. brimleyorum* males than in other species and is difficult to see without microscopic examination. Furthermore, the elongate, monocuspid premaxillary teeth (which occur in direct physical contact with the mental gland when the mouth is closed) of male *D. brimleyorum* are also proportionately less exaggerated.

In summary, populations of *Desmognathus* from the Ouachita Mountains area 1) differ from their congeners in the quality of at least 12 morphological and developmental characters, and 2) occur in rocky-bottomed streams in a unique geological and physiographic region on the periphery of the range of the subfamily Desmognathinae. I believe this constitutes sufficient evidence that these populations represent a valid species, in agreement with Stejneger's original evaluation. The approximate geographic range of *Desmognathus brimleyorum* is mapped in Figure 32.

THE RELATION OF *D. auriculatus* TO *D. fuscus* IN FLORIDA

MORPHOLOGICAL DIFFERENCES.—In Florida, desmognathines (except *Desmognathus monticola*) can be separated into two categories on the basis of differences in osteological and external morphological characters. *D. auriculatus* shows no sexual dimorphism in jaw profile, has a reduced premaxillary fontanelle, is larger than *fuscus* in comparisons between the same age-classes, possesses a compressed tail that retains a vestige of a dorsal fin in post-larval life, differs from *fuscus* in larval morphology, and attains an overall darker pigmentation that obscures an underlying pattern also different from that of *fuscus*.

D. fuscus may be characterized by having strong sexual dimorphism in jaw profile; a well-developed premaxillary fontanelle; small relative size; a terete, finless tail tapering to a round point; distinctive larval morphology; and strong dorsal pattern in post-larval life (except as sometimes obscured by melanization in old males).

All the above characters taken collectively allow positive identification of specimens as *fuscus* or *auriculatus*. However, jaw profile dimorphism, which is strongly developed and always present in *fuscus* in the Apalachicola and Ochlockonee River drainages, becomes less marked in western Florida drainages of the Choctawhatchee, Yellow, Blackwater, and Escambia Rivers. In some demes from western Florida, dimorphism is well developed, whereas it is nearly absent in others. This character alone serves to identify mature males of *fuscus* in the Apalachicola and Ochlockonee River drainages, but is less reliable when considered by itself in western Florida.

It is significant to note that in the entire subfamily the character of jaw profile dimorphism is most abundantly and consistently present in

populations of *D. fuscus* and *ochrophaeus* from the Piedmont and southern Appalachians, respectively. The only watershed in the area of this study that has its source in either the Piedmont or the southern Appalachians is the Apalachicola (=Chattahoochee) River. Variation in jaw profile dimorphism is negligible in Florida demes along this watershed, suggesting no recent barriers to gene flow. Equally significant is the fact that, while virtually no reduction of jaw profile dimorphism was observed from the southern Appalachians, variation in this character becomes greater as one moves westward in the upper reaches of the Alabama-Tombigbee River drainage, crossing drainage divides. Hence, it is logical that gene flow occurs more readily within drainage systems than between them. This assumption underlies all conclusions reached in this study concerning genetic relationship between demes of *fuscus* based on morphological similarity.

The other five characters mentioned that are significant in identification of *D. auriculatus* and *fuscus* do not exhibit consistent interdeme variation. Tail shape may be affected by the state of health or diet of individuals. Variation in relative size is possibly affected by density-dependent factors (no direct evidence of this was gathered). Occasionally individuals and populations were collected which were smaller than average for the species, but in general *fuscus* was smaller than *auriculatus* at any given age. Specimens occasionally were examined that fell into the range of variation in morphology of the premaxillary fontanelle of the other species, but in general this character is reliable. Color pattern is probably the one aspect of the phenotype most influenced by the local environment, and because of this it is the least reliable when taken by itself. Color pattern is so variable, depending on the substrate, that specimens of both species collected from the same locality were often nearly identical. However, metachrosis usually revealed basic differences if specimens were maintained alive several hours after capture on selected substrates. Larval morphology is also somewhat affected by the environment, but in this study larvae were always recognizable as either *auriculatus* or *fuscus*. The number of gill fimbriae may vary with oxygen and water available in the larval environment (Drastich 1927), but the presence or absence of iridiophores on gill rami and larval size, color, and color pattern still serve to distinguish *fuscus* from *auriculatus*.

ECOLOGICAL DIFFERENCES.—The most striking differences between *Desmognathus fuscus* and *D. auriculatus* within the geographical limits of this study were habitat and microhabitat preferences. In those drainage systems where both forms occurred, *auriculatus* was exclusively found in floodplain and coastal flatwoods swampy environments, where it was most often collected from sites of decomposing organic litter and from

along the margins of standing or slow-moving water. Usually specimens were discovered under the larger debris such as logs and leaf piles in muck. Often individuals were raked from under the surface of stagnant, shallow muck sites. Individuals invariably attempted to retreat into fluid muck or shallow, standing water.

D. fuscus was most commonly found in shaded, hillside ravines such as occur along the eastern escarpment of the Tallahassee Red Hills-Tifton Uplands physiographic region in Florida and adjacent Georgia. This type of environment offers a variety of microhabitats which were occupied by *fuscus*. The borders of ravine streams, especially where friable materials were present for burrowing, were teeming with *fuscus*. Density was highest, however, in hillside seepage sites where ground water and burrowing arthropods provided a wealth of anastomosing subterranean channels supplied with abundant moisture. *D. fuscus* was not often encountered more than a few inches from streamsides or seepage water. Some seepage sites (especially downstream from ravine heads where the gradient lessens and the ravine floor becomes wider) are somewhat mucky where leaf litter accumulates faster than it decomposes. These were also inhabited by *fuscus*.

In parts of the study area outside the geographical range of *D. auriculatus*, *fuscus* colonizes floodplain and other habitats where one would expect to find *auriculatus* (parts of western Florida and Coastal Plain Alabama). Metachrosis and possibly local selective pressures produce demes that resemble *auriculatus* in the degree of melanization of color pattern. Proper identification is dependent on other characters, especially the morphology of jaw profile, premaxillary fontanelle, and the tail.

There was greater latitude in habitat selection in *D. auriculatus* where this species occurred outside the geographical range of *fuscus* (Fig. 33) in southeastern Georgia and northeastern Florida. In the headwaters of tributaries of the Ochlockonee, St. Marks, Aucilla, Suwannee, and Satilla rivers, *auriculatus* was found in abundance (Fig. 34). *D. auriculatus* was also collected from steephead ravines of the Econfinia River and streams of similar aspect draining into western Choctawhatchee Bay. However, in none of the upland stream environments were microhabitat preferences significantly different from those where *auriculatus* and *fuscus* were geographically sympatric. Such upland streams are the headwater tributaries of the Ochlockonee, St. Marks, Aucilla, Suwannee, and Satilla rivers, which drain a gently seaward sloping, ancient plain (Tifton Uplands). These headwater streams do not dissect this plain deeply and most have wide, low-gradient floodplains. These are characteristically very swampy, containing large accumulations of decomposing organic litter derived mostly from gums (*Nyssa* spp.), cypress (*Taxodium* sp.),

Magnolia virginiana, *titi* (*Cyrilla racemiflora*), and other hydrophilic plants. True ravines occur along eastern escarpments of the larger rivers here, but these are notably depauperate in salamanders except where occasional mucky sites have developed.

The ravine steephead habitats along the Econfinia River and lower Choctawhatchee Bay are peculiar in their geological development (Sharp 1938), and differ significantly in biology from most ravine habitats along the eastern escarpment of the Apalachicola River. Ravines in the latter area develop from surface runoff over relatively impermeable clastic sediments of the Miocene Hawthorne Formation. These ravines are V-like in cross-section and have a fairly steep gradient in their upper reaches. These ravines contain a diverse hardwood forest comprised of many northern species, wide-ranging southern species, and a number of endemics. The unique northern aspect of these ravines is well known botanically. On the other hand, steephead ravines along the Econfinia River and lower Chochawhatchee Bay develop in loose sands of younger age which are relatively permeable to water. Surface runoff is much reduced. Steepheads form from lateral sapping of the water table (Sellards and Gunter 1918, Sharp 1938, Vernon 1942). Valley formation is U-shaped since erosion is headward along the base of valley walls. The plant communities common to these ravines differ in many ways from those along the Apalachicola River eastern escarpment. Two of the dominants are *titis* (*Cyrilla racemiflora* and *Cliftonia monophylla*). The ravine sides are very dry upslope from the stream bottom, and support a number of xerophilic plants. The muck and soil of these ravines are derived from different plant species than those dominants found in the Apalachicola-Ochlockonee ravines. This type of ravine contains a great many mucky seepage sites, and the gradient near the ravine steephead is not too different from downstream. This particular type of habitat seems equally suitable to colonization by muck-"loving" *auriculatus* or by ubiquitous *fuscus*. In fact, this study has indicated that *fuscus* competitively displaces *auriculatus* from these ravines when both species have the opportunity to colonize them (Fig. 35).

The northward flowing ravine steephead tributaries of the Yellow River, whose watershed divide is common to southward flowing steephead ravines along Choctawhatchee Bay, are nearly identical to the latter geologically and biologically. Figure 35 shows that *D. auriculatus* occurs exclusively in these habitats at the western end of the bay. *D. auriculatus* is also found in the swampy floodplain of the Yellow River at the confluences of ravine steephead streams there and thus is capable of colonizing the upper reaches of these tributaries. However, the headwaters of these ravines are instead populated by *D. fuscus* (Fig. 35).

It is my belief that *fuscus* has not yet invaded the ravines occupied by *D. auriculatus* that drain into western Choctawhatchee Bay because physical barriers exist to the dispersal of *fuscus* (which ranges northward throughout the Choctawhatchee River drainage to its headwaters). One such barrier may be the discontinuous connection of the ravines between the eastern and western ends of the bay. During Pleistocene glacial maxima all tributaries of the lower Choctawhatchee River may have been ravines, but the presence in western ravine streams of the endemic darter, *Etheostoma okaloosae*, and the absence of its close relative, *E. edwini*, in these same drainages (Collette and Yerger 1962) indicates that there may never have been a connection between streams at both ends of the present bay. Although *fuscus* is not present in ravine streams along the western end of Choctawhatchee Bay, it occurs in those draining into the eastern end. A similar distribution is recorded for *Etheostoma edwini* (Collette and Yerger 1962).

As already mentioned, *D. fuscus* is assumed to disperse within drainages more readily than between them. This is because stream divides become well-defined barriers of inhospitably dry habitats for salamanders in the area of this study (usually pine-turkey oak, sand ridge communities). Swampy habitats of low elevation along the Gulf Coast also act as effective barriers to the dispersal of *fuscus*, inasmuch as aquatic, larval individuals appear to be more strictly adapted to the ecology of ravine habitats than transformed, terrestrial specimens; in contrast, however, such habitats are virtual highways for *auriculatus*. Hence *auriculatus* is capable of colonizing tributary ravine streams by immigration upriver from alluvial plains and coastal swamps that are continuously connected along the Gulf Coast of Florida from the peninsula to Pensacola Bay (i.e., ravines and steepheads along Econfinna Creek, which has probably never been connected with either the Apalachicola or the Choctawhatchee Rivers; *fuscus* presently occurs on both sides of this small, independent drainage system, but not in it).

Desmognathus fuscus disperses downstream from upland population centers initially, and displaces *auriculatus* whenever *fuscus* is able to surmount ecological barriers to its dispersal. Furthermore, in the few localities found in this study where optimum habitats for both species were immediately adjacent (i.e., Sweetwater Creek and Ocklawaha Creek localities), the two species did not hybridize and were mutually exclusive in their respective microhabitats except along the zone of contact.

I consider the above to constitute evidence for the validity of *D. auriculatus* and *D. fuscus* as full species within the study area. This is in agreement with Valentine's (1963) conclusions regarding the relationship between *auriculatus* and *fuscus* in Mississippi. Also, Chaney (1949,

1958) reported that his studies of desmognathines from southern Louisiana and Mississippi revealed two larval and adult morphotypes. He did not venture a speculation as to the taxonomic identity of the morphs. During examination of his extensive collections, I concluded that *fuscus* and *auriculatus* both are present in the Florida parishes of Louisiana. However, it is important to note that Mississippi and Louisiana specimens are the most difficult of all to distinguish morphologically in the entire range of sympatry between *auriculatus* and *fuscus*. All the characters investigated in this study and found to be significant in separating the two species in Florida converge in specimens of the two forms from those states.

GEOGRAPHICAL DISTRIBUTION.—Both *Desmognathus fuscus* and *auriculatus* range widely beyond the geographical boundaries of this study. The evolutionary relationships between these species in other parts of their ranges may be different from those postulated herein. Hence, Figures 33 and 35 represent the distribution of *fuscus* and *auriculatus* strictly as determined for specimens directly examined (and in most cases collected) by me. Extralimital studies are presently under way.

D. fuscus ranges throughout the Apalachicola-Flint-Chattahoochee river system from the Piedmont of Georgia to the ravines dissecting the western escarpment of the Tallahassee Red Hills physiographic region. It is found eastward to ravines along Lake Talquin (an artificial impoundment of the Ochlockonee River) and throughout the Little River, a tributary of the Ochlockonee. All efforts to collect *fuscus* in the Ochlockonee above the confluence of the Little River were unsuccessful. I do not believe *fuscus* occurs above this confluence for the following reasons: the Ochlockonee River formerly flowed southward to the coast through the Lake Bradford chain and the abandoned valley on which the old Tallahassee Municipal Airport was built. The Ochlockonee has been captured by a tributary of the Little River (Hendry and Sproul 1966) so recently that *fuscus* has not yet dispersed northward through the wide, swampy floodplain above the site of stream capture. As evidence of this, only *auriculatus* is commonly collected in stream habitats above the level of capture in the Ochlockonee River, but only *fuscus* is found in similar situations in northern tributaries of the Little River immediately to the west (Fig. 33).

Desmognathus fuscus has entered the lower Chipola River drainage where that stream breaches the remnant uplands that used to form a continuous connection between the Western Highlands and the Tallahassee Red Hills physiographic regions (Fig. 33). In general, a hiatus in the range of *fuscus* seems to occur between the Choctawhatchee and the Apalachicola rivers in Florida (probably due both to inadequate collect-

ing and scarcity of ravines). A few *fuscus* were found in western ravines of the Holmes Valley Escarpment, but none on other remnant highlands between these two rivers. Geologists (Puri and Vernon 1964) speculate that the Apalachicola River once flowed westward across the Marianna Lowlands, joining the ancestral Choctawhatchee to breach the highlands along the present course of the latter river. The occurrence of *fuscus* in the Choctawhatchee River drainage may be due to colonization during this past connection with the Chattahoochee-Apalachicola River. Headwater stream capture or fortuitous migration over drainage divides shared with the Alabama or Chattahoochee systems, or both, also may explain the presence of *fuscus* throughout the Choctawhatchee drainage. It may be significant that *fuscus* demes from this system are variable in some morphological characters that do not vary in *fuscus* in the Apalachicola-Chattahoochee system. It is possible that after colonization of west Florida river systems, reduced or discontinued gene flow with the parent population, coupled with a change in selective pressures, allowed gene frequencies to change. This would account for increased variation in otherwise strongly conservative characters.

Desmognathus fuscus occurs throughout the Escambia-Conecuh River drainage in Florida and Alabama. Demes were sampled in this study from ravines emptying directly into Escambia Bay below the mouth of the Escambia River. Also, *fuscus* was collected in the floodplain of the Escambia and Conecuh tributaries where *auriculatus* was expected. Much variation in size, melanization, jaw profile dimorphism and other characters was noted between demes, especially in Florida localities. Demes sampled from deep ravines in the Red Hills of southern Alabama (headwaters of the Escambia-Conecuh system) were less variable relative to each other and more closely approximated the phenotype of *fuscus* from the Apalachicola-Chattahoochee drainage. I feel this is due to the closer proximity of the Escambia-Conecuh headwater populations to the Apalachicola-Chattahoochee River populations (Fig. 36), where gene flow may still occur. An even more convincing argument, however, may be made for the possibility that because these headwater populations in Alabama inhabit the deepest and most continuous ravines in the system, selective pressures still favor strong expression of character states.

Probably no greater interdeme variation in *fuscus* was observed than that from the Blackwater and Yellow River drainages. I hypothesize that *fuscus* has met with somewhat different selective pressures in adapting to the microhabitats available to it in these two river systems. The ravine habitats are different because the underlying geology of permeable Plio-Pleistocene clastic sediments has allowed steephead types of ravines to develop near the coast. Shallow, young valleys have developed in

headwater tributaries. The vegetation is unique in these streams because of the presence of both titis (*Cliftonia monophylla* and *Cyrilla racemiflora*), pitcher plants, sphagnum, and a host of other plants most commonly found in flatwood bays and not in upland stream valleys.

Desmognathus fuscus probably entered the Blackwater and Yellow River drainages via past connections of their floodplains with that of the Escambia River during lower sea levels in the Pleistocene. Examination of drainage patterns in Figure 36 reveals that the Escambia and Choctawhatchee drainages surround those of the Blackwater and Yellow rivers. Because of the youth of the latter systems, headwater stream capture has probably not occurred. *D. fuscus* demes in the Blackwater and Yellow rivers not only have become adapted to somewhat different ecological conditions from those of ancestral Escambia River stock, but have probably been protected from the homeostatic effect of gene flow with the Escambia gene pool during the high stand of seas in Recent times.

THE RELATION OF FLORIDA *D. fuscus* TO SOUTHERN APPALACHIAN *ochrophaeus*

Skulls and preserved series of specimens from the type locality of *Desmognathus fuscus* (northern New York) were examined to determine the characteristics of the nominate race. These states were used as standards with which the morphology of populations of Piedmont and Coastal Plain desmognathines was compared to assess taxonomic relatedness.

It is now apparent that the category of *D. fuscus* is a heterogeneous one if all southern populations of desmognathines heretofore referred to this species remain lumped under this name. All the Florida, Georgia, and Alabama Piedmont and Coastal Plain specimens examined in this study agreed on a morphological basis more closely with *ochrophaeus* from the southern Appalachians than with *fuscus* from New York. The southern limit of specimens examined that agree with New York *fuscus* was about Uwharrie National Forest in the Piedmont of North Carolina. The exact delimitation of the southern limit of the range of *fuscus* has yet to be determined. A study of what happens in the zone of contact of northern *fuscus*, southern *fuscus*, and *auriculatus* in North and South Carolina would go far to elucidate evolutionary relationships between these three taxonomic entities.

The most readily observed features of *D. fuscus* (New York) are fungiform tooth morphology, compressed tail, and absence of sexual dimorphism in jaw profiles. All literature accounts of *fuscus* clearly indicate that little or no jaw sinuosity (external commissure somewhat re-

flects the profile between jaw bones) and a compressed, keeled tail (Cope 1889, Dunn 1917, Bishop 1943) are present in specimens from New York and adjacent northeastern states.

Specimens examined by me that previously were assigned to *D. fuscus* from Piedmont localities of Georgia typically have jaw profile dimorphism strongly developed in adults, teretely tapering tails, and teeth dimorphic between maxilla and mandible. These character states are also found in adjacent populations of *ochrophaeus* from the southern Appalachians. This may partly explain why other workers have been unable to distinguish some populations of *fuscus* from *ochrophaeus* in this region (Martof and Rose 1963).

The major conclusion obtained from comparisons of New York *D. fuscus* with southern material previously referred to by that name is that Florida and Georgia "*fuscus*" very strongly resemble *ochrophaeus* from the southern Appalachians of Georgia and not topotypic specimens of *fuscus*. It is notable that relative size and color pattern is also more closely alike between southern *fuscus* and *ochrophaeus* than between southern and northern *fuscus*.

CONCLUSIONS

1. *Desmognathus brimleyorum* Stejneger is a valid species confined to the Ouachita Mountains of Arkansas and Oklahoma.

2. *Desmognathus auriculatus* in Florida is considered to be a valid species; *D. fuscus carri* is considered to be an ecophenotype of *D. auriculatus*.

3. *Desmognathus "fuscus"* ranges throughout Florida west of the Ochlockonee River.

4. *Desmognathus "fuscus"* in the Apalachicola and Ochlockonee river drainages is closely similar morphologically to demes of this species upstream in the Flint-Chattahoochee rivers. These resemble *D. ochrophaeus* more closely than the nominate race of *D. fuscus* from northern New York and adjacent states.

5. Intensive study of qualitative characters indicates strong, localized variation in *D. fuscus*. This variation, and peripheral populations examined, indicates a critical need for further study of southern "*fuscus*" and *ochrophaeus*, using a multidisciplinary approach.

SPECIMENS EXAMINED

SKELETAL PREPARATIONS

Desmognathus aeneus

Georgia—Dawson Co.: UF/FSM*-27271 (1m).

Desmognathus auriculatus

Florida—Bay Co.: DBM-1488 (1m, 1f), DBM-1620 (2m, 1j); Columbia Co.: UF/FSM-4076-1 (1m); Gadsden Co.: DBM-1660 (1m); Jefferson Co.: no # (1m); Leon Co.: FSU-598 (1m), DBM-1229 (1m, 2j), DBM-1511 (1m), no # (1m, 1f, 1j); Liberty Co.: DBM-1527 (1m); Marion Co.: DBM-1649 (1m), no # (1m); Okaloosa Co.: FSU-645 (1m), DBM-1255 (1m), DBM-1563 (1m), DBM-1725 (1m); Wakulla Co.: FSU-785 (1m); Washington Co.: DBM-1519 (1m).

Georgia—Charlton Co.: DBM-1551 (1m, 1f); Grady Co.: DBM-1281 (1m); Irwin Co.: DBM-1626 (1m); Liberty Co.: DBM-1545 (1m); Thomas Co.: DBM-1634 (1m).

Louisiana—Washington Parish: TU-11832 (1m, 1f).

Mississippi—Forrest Co.: DBM-1537 (1m).

South Carolina—Berkeley Co.: DBM-1546 (1m).

Desmognathus brimleyorum

Arkansas—Clarke Co.: DBM-1295 (12 juv - ad); Garland Co.: NELSC-2350 (1m); Polk Co.: DBM-1245 (1m, 1f), DBM-1246 (2m, 1f, 1j), no # (1m); ?Co.: USNM-118476 (1m).

Oklahoma—LeFlore Co.: DBM-1476 (1m), DBM-1711 (1m, 1j).

Desmognathus cf. fuscus

Alabama—Baldwin Co.: DBM-1219 (1m); Butler Co.: DBM-1232 (1m), DBM-1428 (2m); Clay Co.: DBM-1607 (1m); Cleburne Co.: DBM-1186 (1m); Conecuh Co.: DBM-1427 (2m); Dale Co.: DBM-1189 (1m); Houston Co.: UF/FSM 9316-2 (1m); Tuscaloosa Co.: UAIC 49-1241 (1m).

Arkansas—Cross Co.: DBM-1589 (1m).

Florida—Escambia Co.: DBM-1240 (1m), DBM-1241 (1m), DBM-1242 (1m), no # (1m); Gadsden Co.: DBM-1171 (1m, 1j); Leon Co.: DBM-1490 (1m); Liberty Co.: DBM-69CC (2m, 1f, 1j), DBM-1154 (1m), DBM-1527 (2m); Okaloosa Co.: DBM-1263 (1m), DBM-1558 (1m); Santa Rosa Co.: DBM-1220 (1m), DBM-1259 (2m, 2f), DBM-1260 (1m), DBM-1667 (1m); Walton Co.: DBM-1222 (1m), DBM-1235 (1m), DBM-1236 (1m).

Georgia—Bibb Co.: UF/FSM 14019-2; Clarke Co.: UG-60 (1m); Fulton Co.: no # (1m); Randolph Co.: DBM-1291 (2m).

Louisiana—Ouachita Par.: NELSC-17147 (1m); St. Tammany Par.: TU-2870 (1m); Union Par.: NELSC-24002 (1m).

Kentucky—Harlan Co.: NELSC- (no #) (1m).

Massachusetts—Franklin Co.: MCZ A-82583.

Mississippi—Benton Co.: DBM-1592 (1m); Forrest Co.: DBM-1537 (1m); Lawrence Co.: TU-14136 (1m); Tishomingo Co.: DBM-1188 (1m), TU-14635 (1m); Walthall Co.: DBM-1534 (1m).

*Collection abbreviations are explained in the Acknowledgments (p. 8); DBM-numbers are collections made by the author expressly for this study.

North Carolina—Bladen Co.: DBM-1547 (2m); Caswell Co.: DBM-no # (1m);
Montgomery Co.: DBM-1601 (1m); Orange Co.: DBM-1704 (1m).
New York—Orange Co.: USNM-23222 (1m), USNM-23227 (1f); Warren Co.:
USNM-80232 (1m), USNM-80234 (1m), USNM-80237 (1f).
Tennessee—Giles Co.: JWR (1m); Montgomery Co.: NELSC-15658 (1m), NELSC-
19503 (1m); Sevier Co.: NELSC-10588 (1m), NELSC-11812 (1m), NELSC-
12001 (1m), NELSC-12154 (1m).
Texas—Tyler Co.: RW-627 (1m).

Desmognathus monticola

Alabama—Butler Co.: DBM-1232 (1m), DBM-1575 (1m); Clay Co.: DBM-1607
(1m); Randolph Co.: DBM-1185 (1m, 1f, 1j).
Georgia—Lumpkin Co.: UAIC 68-(179-220) (1m, 1f).
North Carolina—Avery Co.: MCZ-6463 (1m).
Tennessee—Sevier Co.: NELSC-11809 (1m), NELSC-12154 (1m).
Virginia—Grayson (?) Co.: MCZ-6558 (1m).
West Virginia—Greenbrier Co.: no # (1m, 1f).

Desmognathus ochrophaeus

Georgia—Rabun Co.: TTRS-10 (1m), USNM-147576 (1m), USNM-147577 (1m),
USNM-147579 (1f), USNM-147597 (1f); Towns Co.: USNM-147668 (1m),
USNM-147683 (1f).
Maryland—Garrett Co.: USNM-101903 (1m), USNM-101905 (1f).
New York—Cattaraugus Co.: MCZ-33834 (1m), MCZ-33868 (1f), MCZ-65690
(1m).
North Carolina—Buncombe Co.: UG-1314-4 (1m); Cherokee Co.: USNM-147688
(1m); Swain Co.: DBM-1398 (1m).
Tennessee—Polk Co.: USNM-147802 (1m), USNM-147804 (1f).

Desmognathus "ocoe"

Tennessee—Polk Co.: USNM-147802 (1m), USNM-147804 (1f).

Desmognathus quadramaculatus

Georgia—Fannin Co.: UG-677 (1m); Habersham Co.: UG-96 (1m), no data (1m);
Haywood Co.: DBM-1400 (1m), no data (1m).

Desmognathus wrighti

North Carolina—Avery Co.: UF/FSM-8241-1 (1m).

Leurognathus marmoratus

Georgia—Rabun Co.: USNM-155979 (1m), USNM-155985 (1f), USNM-156484
(1m), USNM-156508 (1f).
North Carolina—Haywood Co.: DBM-1399 (1m).
South Carolina—Oconee Co.: AUM-12109 (1m).

Phaeognathus hubrichti

Alabama—Butler Co.: DBM-1232 (1m, 2f), DBM-1413 (2m, 1f), no # (1).

ALCOHOLIC SPECIMENS

Desmognathus auriculatus

Alabama—Baldwin Co.: AU-10543, AU-13008, USNM-57226, USNM-57227; Houston Co.: AU-2173?; Mobile Co.: USNM-57228, -57232 to -57236, UF/FSM-3039 (4).

Florida—Alachua Co.: UF/FSM-14111, -333, -600 (23), -1460 (4), -1522 (2), 2031 (1), -3086 (6), -3675, -8073, -9218, -55 (6), -173 (4), -1094 (8), -14030, -14230 (2), -16046, -17178, -18311 to -13, -25869, -25872 to -75, SRT-572; Baker Co.: UF/FSM-256 (2), -2958, -2368 (12), -26076, -26078, -26080, -26082, -26084, -26087, -26077 to -86, USNM-136950 to -136954; Calhoun Co.: UF/FSM-27249 to -55, DBM-1179 (3), FSU-35 (3), FSU-154 (5), FSU-440 (2), FSU-167 (8), RW-3061 (1); Bay Co.: DBM-1488 (25), DBM-1499 (2), DBM-1517 (ca. 5), DBM-1620 (23), DBM-1621 (9), DBM-1662 (ca. 10), DBM-1663 (1), DBM-1664 (1), DBM-1685 (1), DBM-1696 (5); Columbia Co.: UF/FSM-4076 (17); Clay Co.: UF/FSM-1078 to -80; Dixie Co.: UF/FSM-387 (6); Duval Co.: Vockell (1); Escambia Co.: TU-16572 (20); Franklin Co.: UF/FSM-9258 (4); Gadsden Co.: DBM-1153 (13), DBM-1283 (ca. 10), DBM-1340 (ca. 15), DBM-1538 (ca. 10), DBM-1539 (1), DBM-1544 (1), DBM-1622 (9), DBM-1635 (7), DBM-1654 (5), DBM-1660 (4), DBM-1700 (2); Gulf Co.: UF/FSM no # (4), -7833 (1), -9147 (2), -2676 (7), 9143 (7); Hillsborough Co.: UF/FSM-3036 (3), -18316, SRT-1126 (2), SRT-1127 (3), SRT-1174 (1), SRT-1176 (1); Holmes Co.: UF/FSM-2680 (2), AUM-10531, -2, -3; Jackson Co.: DBM-1595 (6), DBM-1596 (ca. 15), DBM-1656 (10), UF/FSM-6566, -6760 (6), -6761, -7761, -7762 (25), -7763, -9395 (3), -391 (4), -704 (3), -2646 (2), -1233 (19), -26068 to -74, TU-13631 (8), RW-2997 (1), TU-13395 (73), TU-14909 (1), TU-13320 (1), TU-13374 (1), TU-13424 (13); Jefferson Co.: DBM-1305 (ca. 20), DBM-1541 (4); Lake Co.: UF/FSM-18292 to -18310, SRT-512, SRT-278; Leon Co.: DBM-1152 (2), DBM-1206 (ca. 8), DBM-1221 (ca. 10), DBM-1229 (ca. 20), DBM-1276 (10), DBM-1391 (ca. 10), DBM-1494 (1), DBM-1511 (1), DBM-1512 (1), DBM-1560 (43), DBM-1619 (10), FSU-38 (7), FSU-818 (8), FSU-473 (6), FSU-193 (8), FSU-240 (1), FSU-152 (2), FSU-40 (1), FSU-643 (10), FSU-508 (2), FSU-827 (2), FSU-205 (4), FSU-681 (4), FSU-525 (1), FSU-662 (7), FSU-339 (9), FSU-276 (1), FSU-428 (3), FSU-816 (1), FSU-511 (1), FSU-600 (2), FSU-444 (1), FSU-602 (2), FSU-168 (2), FSU-39 (2), FSU-39 (2), FSU-37 (2), FSU-598 (6), FSU-53 (1); Liberty Co.: DBM-1233 (ca. 5), DBM-1234 (3), DBM-1354 (7), DBM-1484 (1), DBM-1527 (ca. 5), DBM-1528 (ca. 6), DBM-1611 (11), DBM-1657 (28), DBM-1659 (2), UF/FSM-10111 (7), -10157 (6), -10159 (3), -10166 (3), -10138, -10116, -17784, -17787, -9141 (4), 9144 (4), -9138 (3), -6837, -6900 (3), -7760 (3), FSU-817 (19), FSU-235 (3), FSU-424 (3); Marion Co.: UF/FSM-18292 to -18310, S. Christman (78), -3076 (15), -3077 (10), -7133 (6), -17446 to -17463, DBM-1648 (8), DBM-1649 (9), DBM-1650 (10); Okaloosa Co.: DBM-1223 (10), DBM-1255 (ca. 50), DBM-1562 (2), DBM-1563 (ca. 6), DBM-1567 (1), DBM-1568 (2), DBM-1699 (23), DBM-1716 (17), DBM-1717 (4), DBM-1723 (3), DBM-1724 (5), DBM-1725 (44), DBM-1726 (8), DBM-1729 (ca. 20), NELSC-19952 to -19956, NELSC-17175 to -17177, UAH-68-1193 to 68-1195, FSU-645 (10); Polk Co.: UF/FSM-7378, -26068 to -26074, -2962 (2), -2963, SRT-28 (6), SRT-317 (3), SRT-278 (3), SRT-1177 (4); Putnam Co.: UF/FSM-1079; Santa Rosa Co.: DBM-1666 (8), TU-15839 (3); Taylor Co.: DBM-1651 (2); Volusia Co.: UF/FSM-18317; Wakulla Co.: DBM-1553 (6), DBM-1554 (8), DBM-1570 (9), DBM-1613 (1), DBM-1671 (2), FSU-785 (10), FSU-767 (8), FSU-36 (6), FSU-33 (29); Walton Co.: DBM-1653 (11), DBM-1665

- (1), UAHC-68-646 to 68-675, FSU-87 (3), UAHC-68-774, -68-775; Washington Co.: DBM-1519 (2), UF/FSM no # (8), AUM-15703 to -15705 (3).
- Georgia—Berrien Co.: DBM-1645 (14), USNM-104554 (2), USNM-62097 to -62102, USNM-62181; Bullock Co.: UF/FSM-1569 (4); Camden Co.: DBM-1550 (5), UF/FSM-2062 (1), UF/FSM-7813 (1); Charlton Co.: DBM-1551 (1), USNM-129943 to -129946; Chatham Co.: USNM-21379 to -80; Coffee Co.: DBM-1644 (10); Decatur Co.: UF/FSM-1407-2, -1410 (3); Glynn Co.: USNM-92160 (1); Grady Co.: DBM-1281 (4), DBM-1565 (1), DBM-1623 (3), DBM-1672 (9); Liberty Co.: DBM-1545 (ca. 15), USNM-3901 (12), UF/FSM-8072 (1); Irwin Co.: DBM-1626 (15), DBM-1642 (11), UG-1331, -2, -3, -7, UG-1079; Mitchell Co.: DBM-1674 (12); Thomas Co.: DBM-1634 (16), DBM-1673 (4), TTRS-12, -13; Ware Co.: AUM-10012 (1), USNM-92247 (1); Wilcox Co.: TU-14890 (6); Worth Co.: DBM-1676 (11), DBM-1678 (6), DBM-1680 (5).
- Louisiana—Jefferson Par.: TU-13671 (23); St. Charles Par.: DBM-1688 (11), TU-18518 (5); St. Tammany Par.: DBM-1691 (2), USNM-8874 (1), USNM-113252, -3; Tangipahoa Par.: DBM-1692 (4), USNM-115964 (1); Washington Par.: TU-11832 (17).
- Mississippi—Forrest Co.: DBM-1537 (ca. 20); Harrison Co.: USNM-51142 to -51151; Jones Co.: DBM-1535 (ca. 25); Perry Co.: DBM-1583 (ca. 8); Walthall Co.: DBM-1533 (1).
- North Carolina—Brunswick Co.: DBM-1548 (1).
- South Carolina—Jasper Co.: RW-2626 (1); Berkeley Co.: DBM-1546 (72).
- Texas—Wood Co.: DBM-1684 (19).

Desmognathus brimleyorum

- Arkansas—Clark Co.: DBM-1295 (ca. 15); Combs Co.: USNM-118475 to -118483; Garland Co.: TU-16801 (4), USNM-22157 (holotype), USNM-22158 to -22169 (paratypes), MCZ-2598 (2 paratypes), USNM-57214 to -57225; Hot Springs Co.: DBM-1296 (36), TU-16795 (10), TU-16803 (18); Howard Co.: Nash (1); Montgomery Co.: DBM-1297 (ca. 20), DBM-1298 (27); Pike Co.: TU-16794 (5); Polk Co.: DBM-1245 (122), DBM-1246 (55), DBM-1481 (2), DBM-1707 (ca. 40), DBM-1708 (ca. 150), TU-18299 (7), TU-17993 (36), TU-18291 to -18297, TU-18287 to -18289, NELSC-7350 to -7352, NELSC-16445 to -16451, Nash (7), OU-25550 to -25571; Pope Co.: AM-A60759 to -A60762; Scott Co.: DBM-1479 (9), TU-16793 (1); Yell Co.: DBM-1480 (4).
- Oklahoma—LeFlore Co.: DBM-1476 (ca. 15), DBM-1477 (2), DBM-1478 (5), DBM-1709 (ca. 10), DBM-1710 (ca. 10), DBM-1711 (ca. 300), OU-6601, -3, -4, OU-6609 to -6617, OU-6874 to -6877, OU-6881, -2, OU-6972, USNM-99409 to -99436; McCurtain Co.: DBM-1475 (1), OU-27233 to -27256, OU-31414 to -31419; Pushmataha Co.: DBM-1473 (ca. 20).

Desmognathus cf. fuscus

- Alabama—Baldwin Co.: DBM-1219 (ca. 60), DBM-1581 (ca. 10), DBM-1582 (1), DBM-1686 (11), DBM-1693 (55); Barbour Co.: AUM-6434, -5, AUM-13009 to -18, AUM-13101, -2, AUM-16796 to -800; Butler Co.: DBM-1413 (ca. 10), DBM-1428 (ca. 25), DBM-1575 (10), AUM-5062 to -8, AUM-5727, AUM-9524; Clarke Co.: DBM-1482 (ca. 10), AUM-11136, -37, AUM-12702 to -25, AUM-14816 to -21, AUM-15698, -99, AUM-15706 to -10; Clay Co.: DBM-1607 (2); Cleburne Co.: DBM-1186 (ca. 12); Conecuh Co.: DBM-1232 (ca. 5), DBM-1414 (5), DBM-1427 (ca. 30), AUM-16784 to -95; Covington Co.: AUM-5010, -5061, AUM-14735 to -44; Crenshaw Co.: AUM-6459 to -64, AUM-7530 to -3; Dale Co.: DBM-1189 (ca. 10), AUM-14868 to -76, AUM-15118 to -75, AUM-15278 to -80, AUM-15295 to -306; Geneva Co.: AUM-77, AUM-245; Henry Co.:

- DBM-1322 (ca. 10), AUM-7765 to -83, AUM-10013 to -15, AUM-10029 to -31, AUM-15190, AUM-15236 to -40, AUM-16933 to -35; Houston Co.: AUM-1464, AUM-15292 to -94, UF/FSM-9316; Monroe Co.: AUM-6943, -6946, -6961, -6977, -7028, -7196, -7234, -7239, -7248, -7249, -7254 -7257, AUM-15202 to -12, AUM-18750 to -53; Pike Co.: AUM-15155 to -72; Randolph Co.: DBM-1184 (ca. 12); Russell Co.: AUM-5372, -5449, -5470, -11469, -15265 to -70, -15272 to -77.
- Arkansas—Cross Co.: DBM-1588 (3), DBM-1589 (ca. 35), DBM-1590 (8), DBM-1591 (24), UF/FSM-16091 to -16112.
- Florida—Calhoun Co.: DBM-1265 (ca. 20), DBM-1661 (11), UF/FSM-11793 to -17821; Escambia Co.: DBM-1193 (ca. 25), DBM-1218 (ca. 20), DBM-1239 (ca. 50), DBM-1240 (ca. 50), DBM-1241 (53), DBM-1242 (ca. 20), DBM-1248 (ca. 30), DBM-1258 (1); Gadsden Co.: DBM-1162 (ca. 50), DBM-1171 (ca. 35), DBM-1227 (ca. 10), DBM-1228 (ca. 15), DBM-1230 (ca. 30), DBM-1231 (ca. 15), DBM-1384 (ca. 30), DBM-1515 (ca. 15), DBM-1538 (1), DBM-1654 (1), DBM-1706; Leon Co.: DBM-1152 (6), DBM-1160 (ca. 15), DBM-1168 (ca. 15), DBM-1210 (ca. 20), DBM-1211 (6), DBM-1226 (ca. 40), DBM-1282.5 (9), DBM-1490 (1); Liberty Co.: DBM-1154 (7), DBM-1161 (2), DBM-1177 (ca. 20), DBM-1203 (ca. 15), DBM-1207 (27), DBM-1212 (ca. 50), DBM-1213 (ca. 30), DBM-1214 (ca. 30), DBM-1215 (ca. 20), DBM-1233 (ca. 15), DBM-1234 (3), DBM-1253 (ca. 105), DBM-1264 (50), DBM-69-CA (ca. 35), DBM-69-CB (ca. 15), DBM-69-CC (ca. 30), DBM-69-CD (ca. 25), DBM-1334 (ca. 35), DBM-1341 (ca. 20), DBM-1388 (ca. 30), DBM-1527 (ca. 10), DBM-1528 (ca. 6), DBM-1611 (9), DBM-1658 (5); Okaloosa Co.: DBM-1224 (6), DBM-1257 (5), DBM-1262 (3), DBM-1263 (ca. 70), DBM-1558 (15), DBM-1606 (1), DBM-1718 (ca. 20), DBM-1727 (ca. 50), DBM-1728 (6); Santa Rosa Co.: DBM-1220 (ca. 30), DBM-1225 (ca. 20), DBM-1259 (ca. 50), DBM-1260 (ca. 75), DBM-1261 (ca. 20), DBM-1667 (25), DBM-1670 (11), DBM-1695 (15), DBM-1698 (22); Walton Co.: DBM-1216 (ca. 15), DBM-1217 (ca. 10), DBM-1222 (ca. 15), DBM-1235 (ca. 20), DBM-1236 (ca. 20), DBM-1243 (ca. 15), DBM-1715 (26), DBM-1719 (4), DBM-1720 (3), DBM-1721 (5), DBM-1722 (4); Washington Co.: DBM-1238 (4), DBM-1594 (4), DBM-1652 (10).
- Georgia—Bibb Co.: UF/FSM-1408 (7), -14019 (6) -14020 (2), -14021 (3); Clarke Co.: UG-204 (72), UG-60 (50); Clay Co.: DBM-1183 (ca. 60), UF/FSM-16240 to -16259; Cobb Co.: UG-207 (6); Decatur Co.: DBM-1170 (ca. 25), DBM-1180 (ca. 40), DBM-1403 (1); Fulton Co.: no # (15); Harris Co.: UG-280, UG-887; Pike Co.: UG-1158 (12); Randolph Co.: DBM-1291 (ca. 15); Twiggs Co.: DBM-1641 (ca. 20); White Co.: UG-154 (2).
- Louisiana—Natchitoches Par.: TU-16797 (11); Sabine Par.: TU-13291 (35), TU-13732 (146), TU-14105 (20); St. Tammany Par.: TU-13672 (111), TU-16441 (71), TU-2642 to -2860 (ca. 200), TU-2861 to -2975 (114) (possibly mixed with *auriculatus*); Union Par.: NELSC-23995 to -24003.
- Mississippi—Benton Co.: DBM-1592 (18), DBM-1187 (ca. 10); Forrest Co.: DBM-1536 (ca. 15), DBM-1537 (14); Jones Co.: DBM-1535 (22); Lawrence Co.: TU-14136 (35); Tishomingo Co.: DBM-1188 (4), TU-14635 (31); Walthall Co.: DBM-1534 (38).
- North Carolina—Bladen Co.: DBM-1547 (73); Durham Co.: DBM-1702 (1), DBM-1703 (11); Gaston Co.: DBM-1604 (4); Montgomery Co.: DBM-1597 (6), DBM-1598 (8), DBM-1599 (1), DBM-1600 (12), DBM-1601 (ca. 30); Orange Co.: DBM-1704 (12).
- South Carolina—York Co.: DBM-1605 (4).
- New York—Cattaraugus Co.: MCZ-65702 to -12; Erie Co.: MCZ-33133 to -51; Orange Co.: USNM series; Warren Co.: USNM series.

Desmognathus ochrophaeus

Most of the approximately 5500 specimens examined by Martof and Rose (1963) are now in my care and were referred to in this study. Also, voluminous material in the Museum of Comparative Zoology, Harvard University, and in the U. S. National Museum, Washington, D. C., was examined for this study from the entire range of this form.

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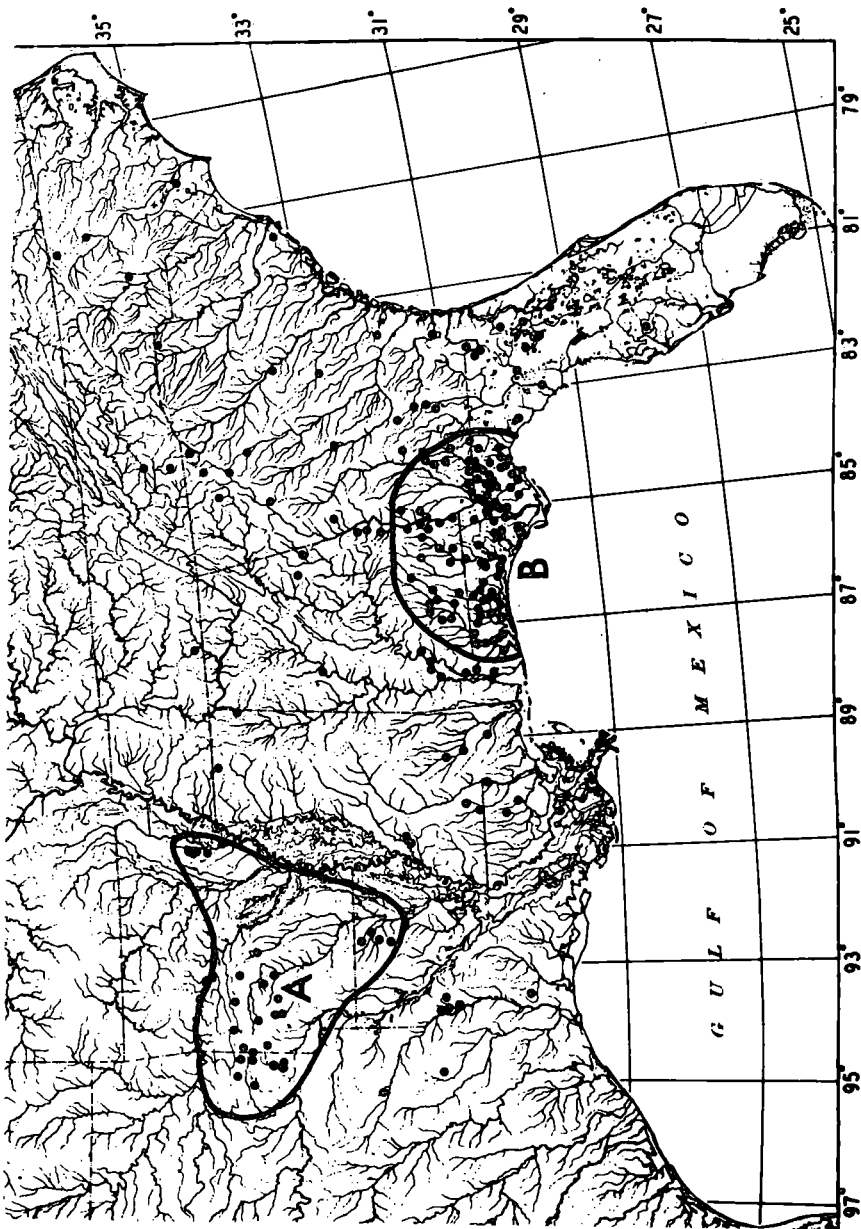
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FIGURE 1.—Map of study areas. A) Ouachita Mountain Uplift of Arkansas and Oklahoma, and peripheral portions of Coastal Plain Arkansas and Louisiana. B) Florida west of the Suwannee River drainage. Dots represent localities from which specimens were examined during this study.



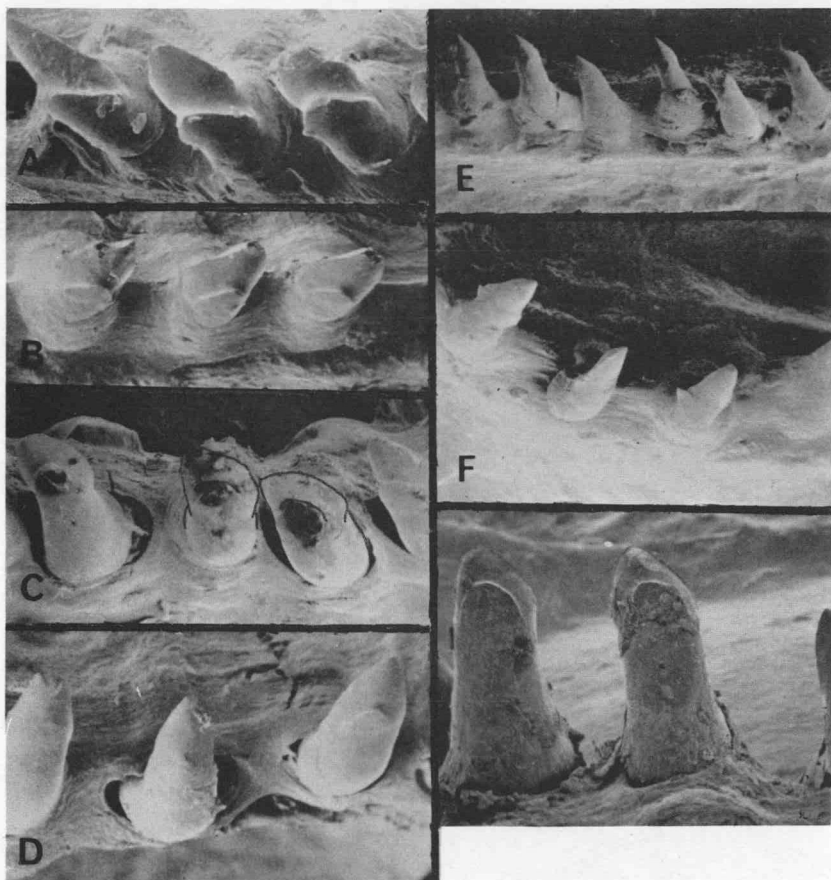


FIGURE 2.—Crown morphology in the subfamily Desmognathinae. A) *Phaeognathus hubrichti*; B) *Leurognathus marmoratus*; C) *Desmognathus monticola*; D) *D. quadramaculatus*; E) *D. aeneus*; F) *D. wrighti*; G) *D. fuscus* (Fulton Co., Ga.). All are dentary teeth prepared from 2-lobed males at 100X except G, which is 120X.

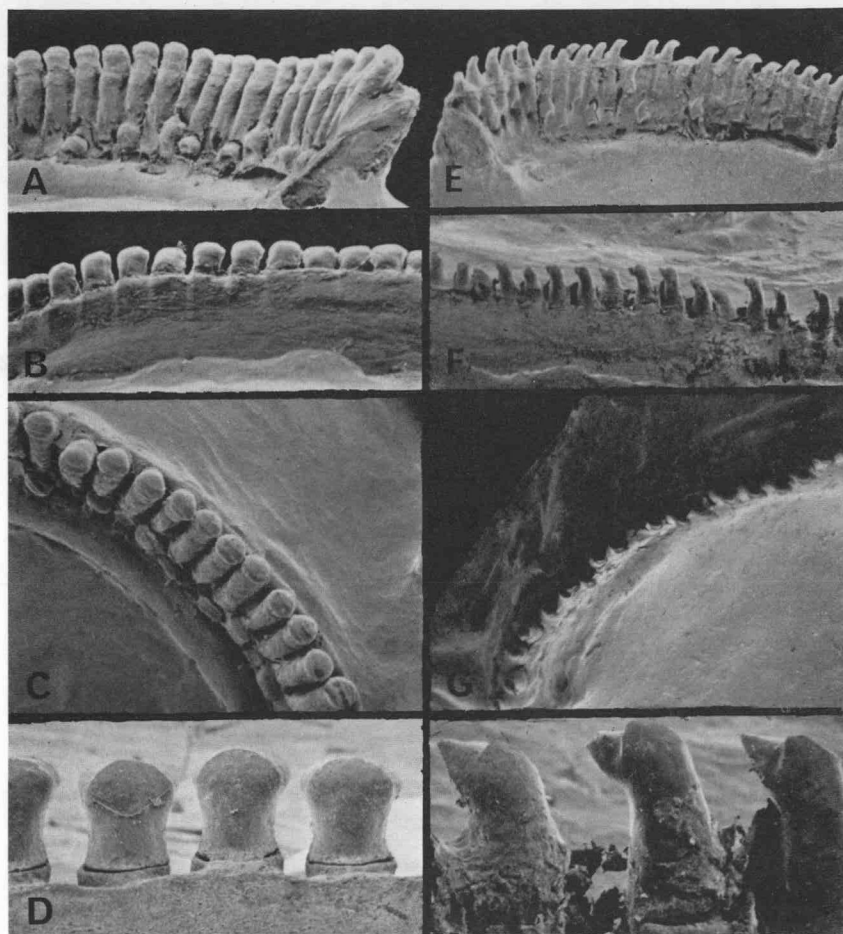


FIGURE 3.—Crown morphology of Ouachita Mountain and northern Louisiana desmognathines. A-D) *Desmognathus brimleyorum* Stejneger dentary teeth of 2-lobed male from Rich Mountain, Polk Co., Arkansas; E-H) *Desmognathus cf. fuscus* dentary teeth of 2-lobed male from Union Par., Louisiana. A, E) (20X, 24X) lingual view; B, F) (20X, 24X) labial view; C, G) (both 20X) occlusal view; D, H) (124X, 120X) labial view.

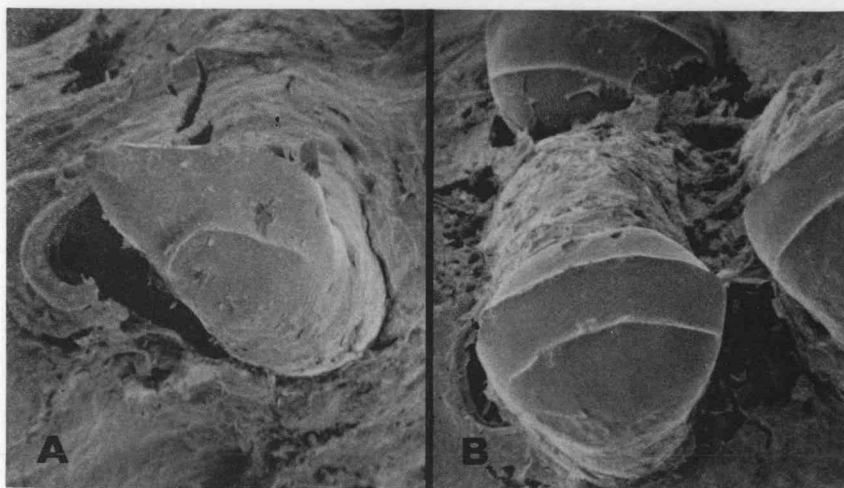
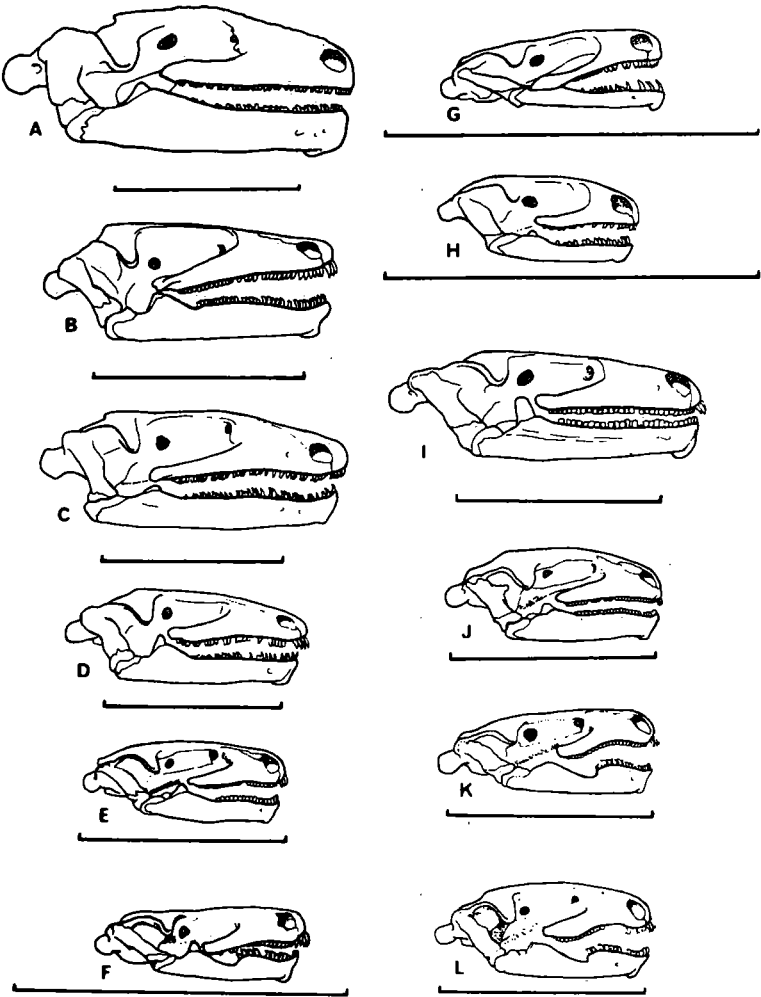


FIGURE 4.—Detailed occlusal crown morphology. A) *Desmognathus* cf. *fuscus* from Union Par., La (320X), 2-lobed male; B) *D. brimleyorum* from Polk Co., Ark. (110X), 2-lobed male. Both dentary teeth.

FIGURE 5.—Jaw profile in sexually mature males of species in the subfamily Desmognathinae. A) *Phaeognathus hubrichti* (DBM-1413), Butler Co., Alabama; B) *Leurognathus marmoratus* (USNM-155979), Rabun Co., Ga.; C) *Desmognathus quadramaculatus* (DBM-1400), Haywood Co., N. C.; D) *D. monticola* (DBM-1185), Randolph Co., Ala.; E) *D. fuscus* topotype (USNM-80232), Warren Co., N. Y.; F) *D. ocoee* (USNM-147802), Polk Co., Tenn.; G) *D. wrighti* (UF/FSM-8241), Avery Co., N. C.; H) *D. aeneus* (UF/FSM-27271), Dawson Co., Ga.; I) *D. brimleyorum* (DBM-1476), Polk Co., Ark.; J) *D. auriculatus* (DBM-1551), Charlton Co., Ga.; K) *D. ochrophaeus* (UG-1314-4), Yancey Co., N. C.; L) *D. cf. fuscus* (DBM-69CC), Liberty Co., Fla. All are 2+ lobed males drawn in same position with camera lucida (scale = 10 mm).



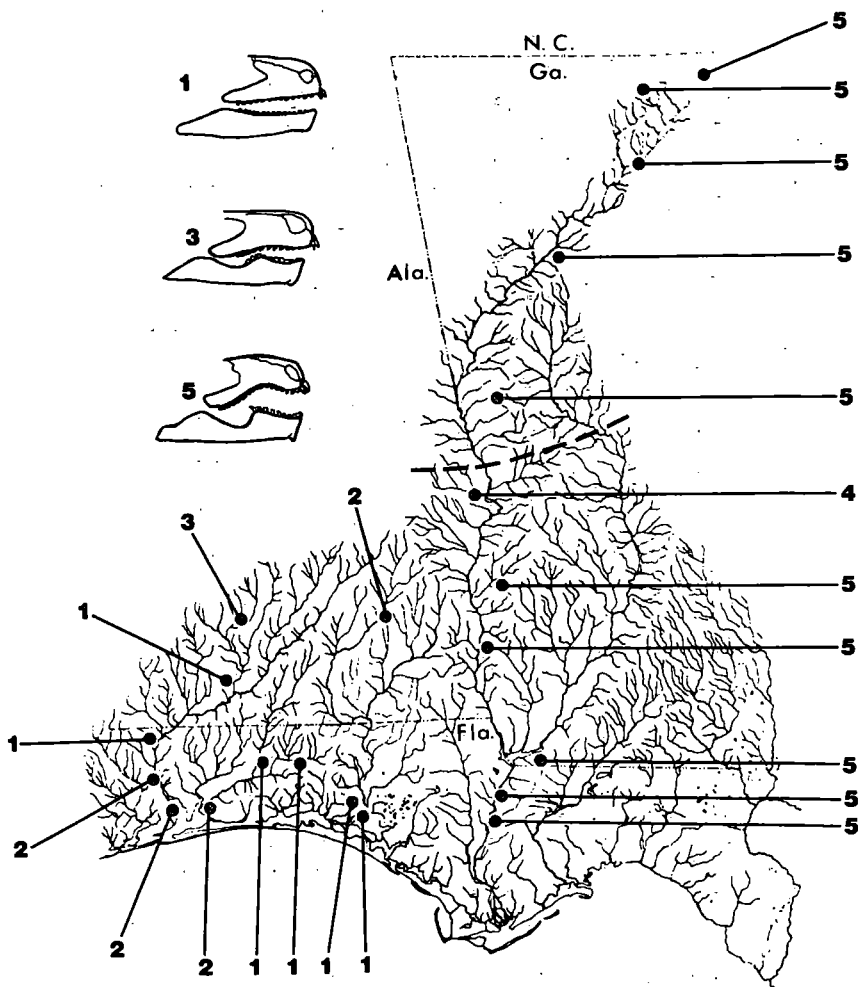


FIGURE 6.—Variation in jaw profile dimorphism of Florida *Desmognathus* cf. *fuscus*. Skulls from each locality depicted were rated from 1 to 5 in profile dimorphism as compared to standards (1=*D. auriculatus* males from Florida which show no dimorphism; 5=*D. ochrophaeus* males from Swain Co., N. C. which possess profile dimorphism in the extreme).

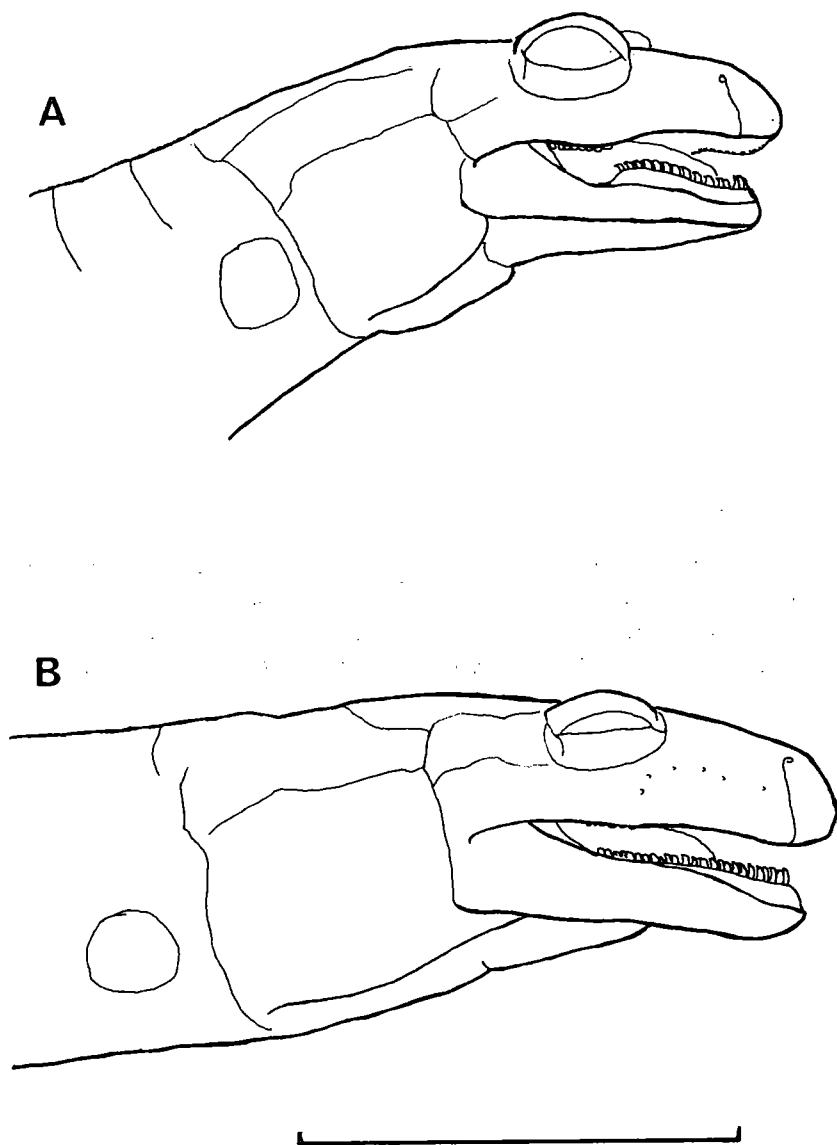
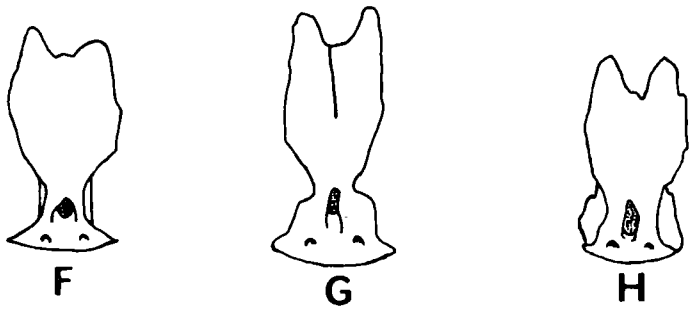
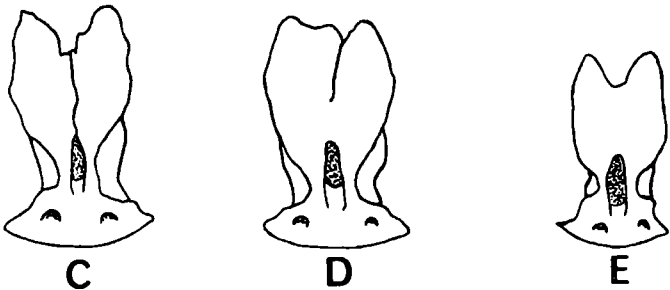
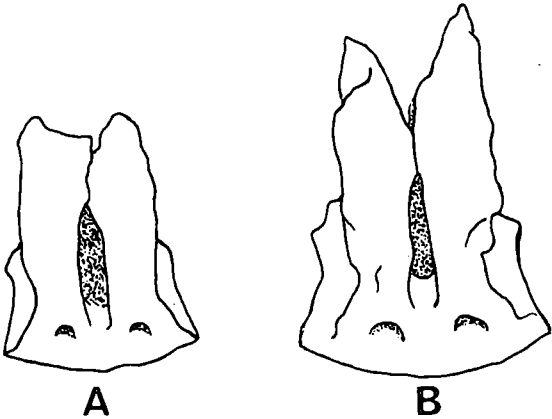


FIGURE 7.—External jaw profile in adult Florida males. A) *Desmognathus* cf. *fuscus*; B) *D. auriculatus*. Both 2-lobed males from Sweetwater Creek, Liberty Co., Florida where they are sympatric in the same habitat (but not in the same microhabitats).

FIGURE 8.—Premaxillary fontanelle morphology. A) *Desmognathus bremsleyorum* adult female, B) 3-lobed male from Rich Mountain, Arkansas; C,D) *Desmognathus* cf. *fuscus* 2-lobed males, E) adult female from Florida, F,G) *D. auriculatus* 2-lobed males, H) adult female from Florida.



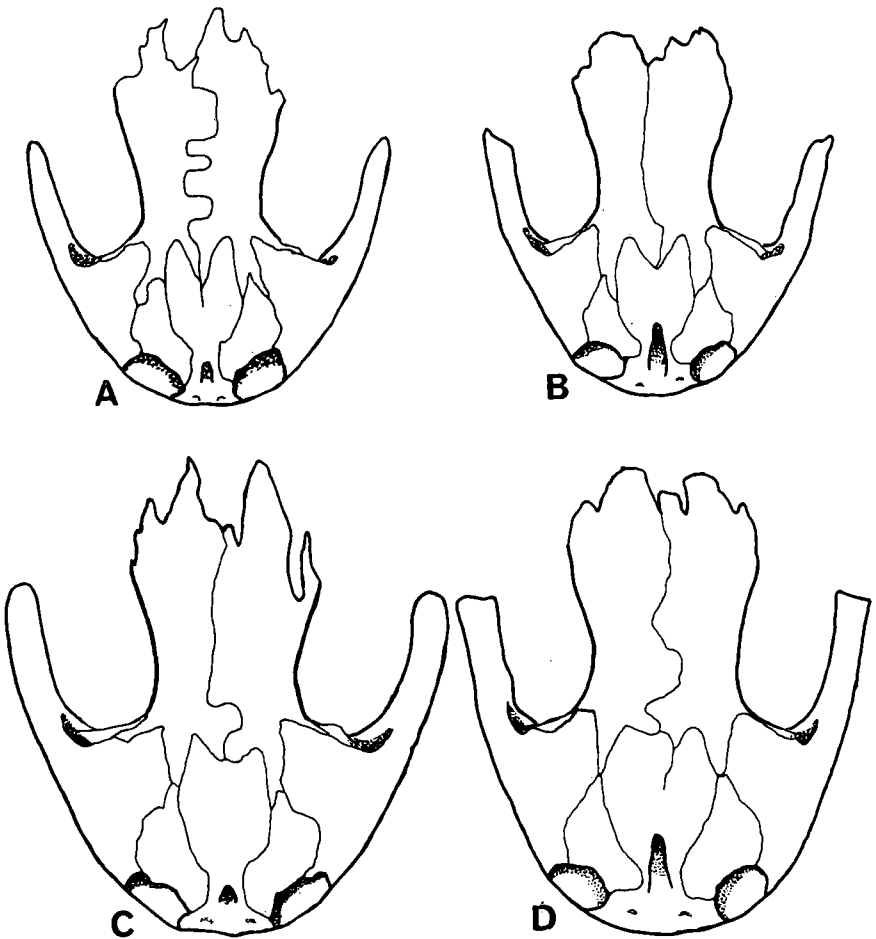


FIGURE 9.—Premaxillary fontanelle morphology. These and the following figure show wide variation in bone shape along suture lines, but conservatism both in the shape of the skull as a whole and in the degree of fusion of the posterodorsal projections of the premaxilla which form the premaxillary fontanelle. *Desmognathus auriculatus*: A) female; C) 2-lobed male. *D. cf. fuscus*: B) female; D) 2-lobed male. All are from Florida.

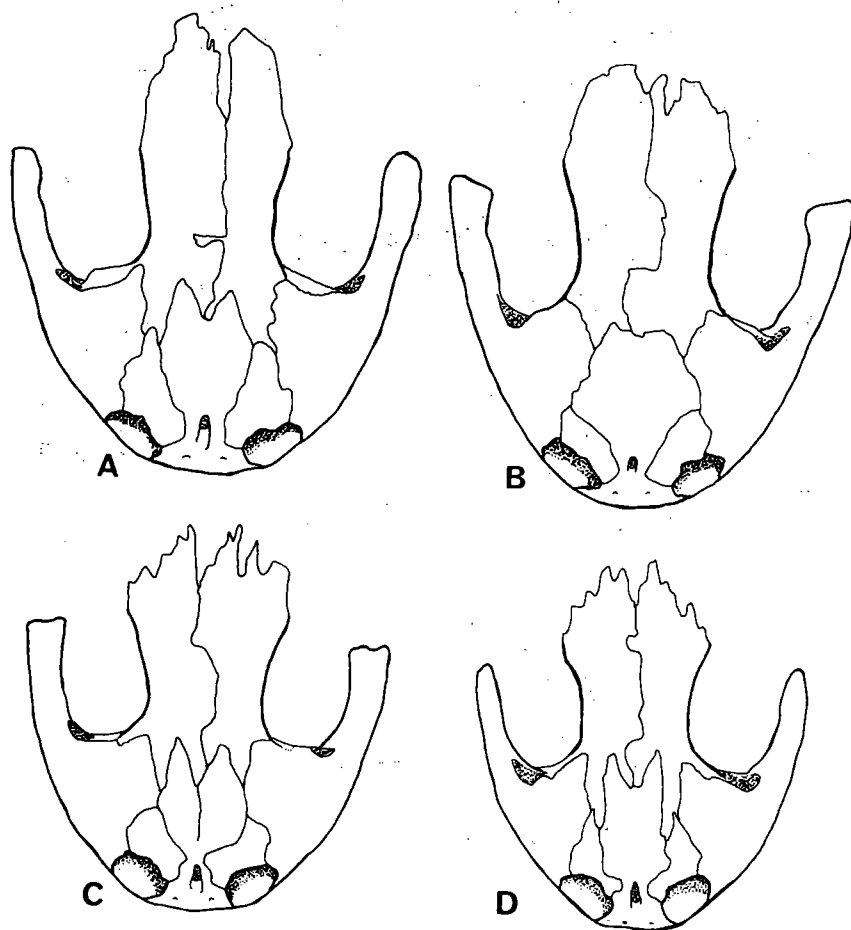


FIGURE 10.—Premaxillary fontanelle morphology. Variation in *Desmognathus auriculatus* along suture lines of bones of the skull is great, but size of the premaxillary fontanelle and shape of skull remain constant. A) 2-lobed male from Marion Co., Fla.; B) 3-lobed male from Bay Co., Fla.; C) 3-lobed male from Wakulla Co., Fla.; D) 2-lobed male from Grady Co., Ga.

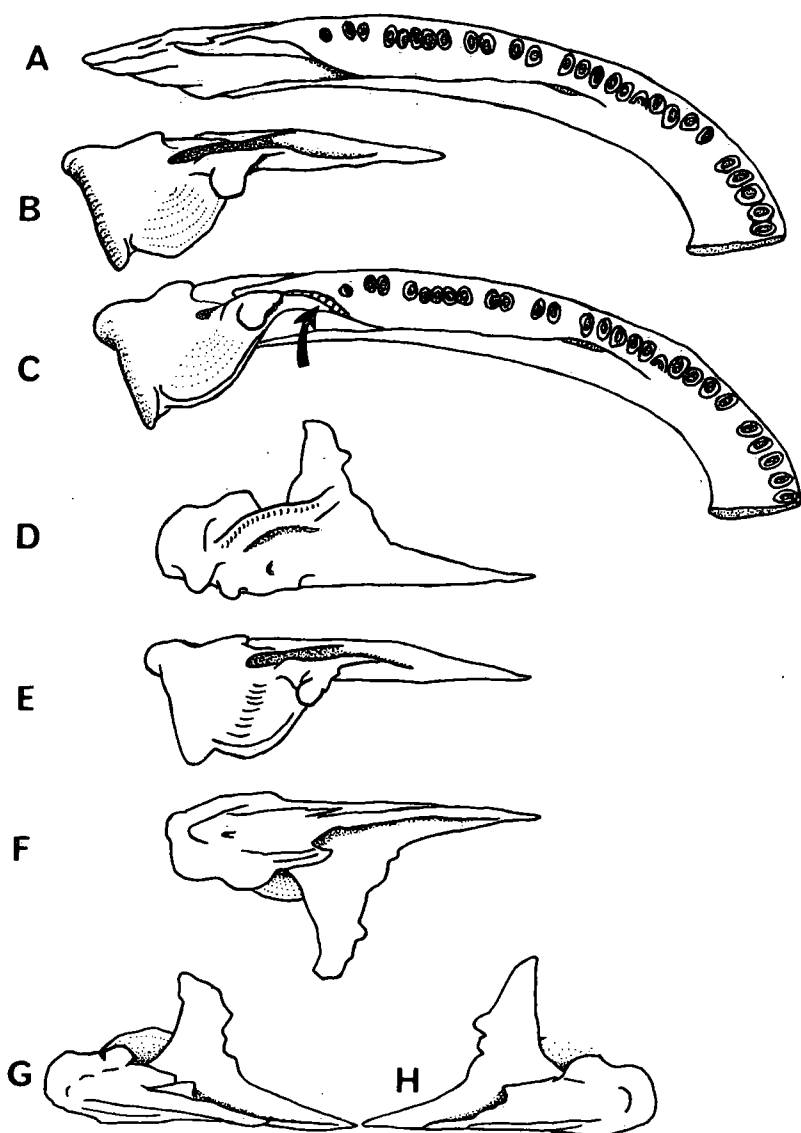


FIGURE 11.—Preaticular spine morphology. Mandibular bones of an adult male *Desmognathus brimleyorum* Stejneger. A) Occlusal view of macerated dentary; B) occlusal view of prearticular; C) A and B combined; D-F) lingual, occlusal, and labial views respectively of prearticular bone illustrating the high dorsally pointing spine. A female is represented in G, H. Arrow indicates surface of insertion of atlas-mandibular ligament on dentary (crosshatched).

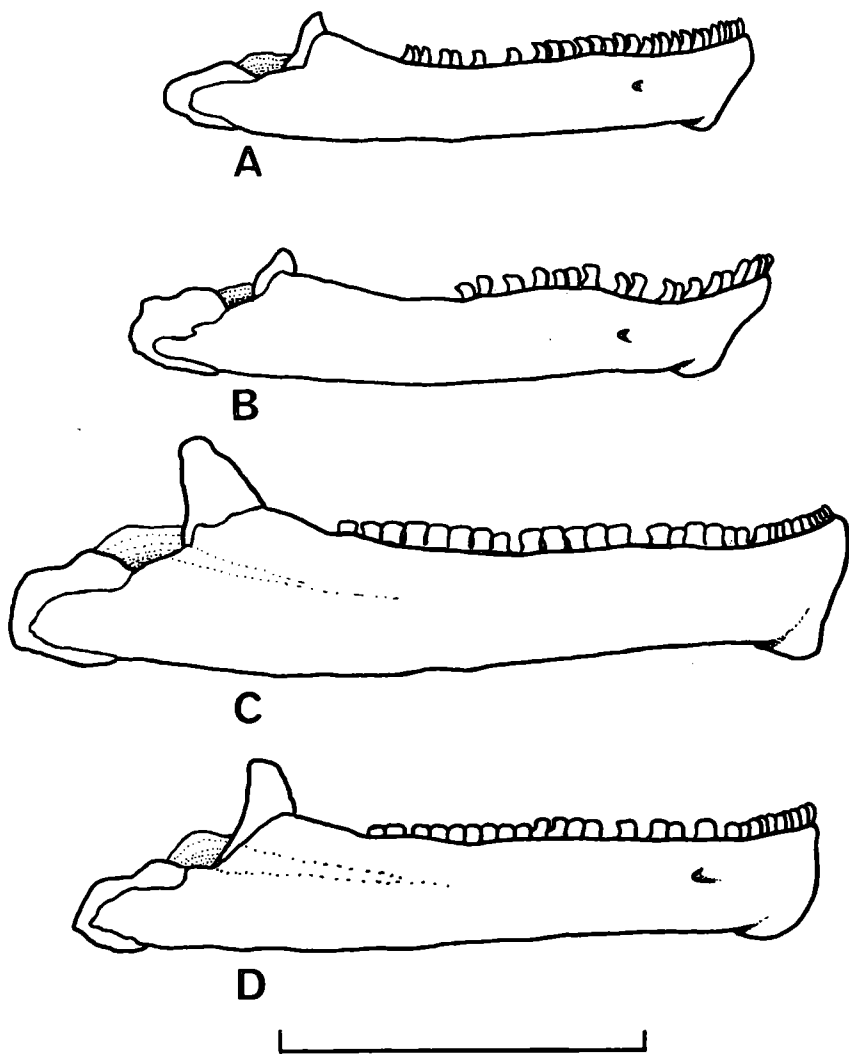


FIGURE 12.—Prearticular spine morphology. Comparison of *Desmognathus brimleyorum* with *D. cf. fuscus* from the adjacent Coastal Plain of Arkansas and Louisiana. A) *D. cf. fuscus* male from Union Par., La.; B) *D. cf. fuscus* male from Cross Co., Arkansas; C) *D. brimleyorum* male from Polk Co., Ark.; D) *D. brimleyorum* female from Polk Co., Ark. (Scale = 10 mm).

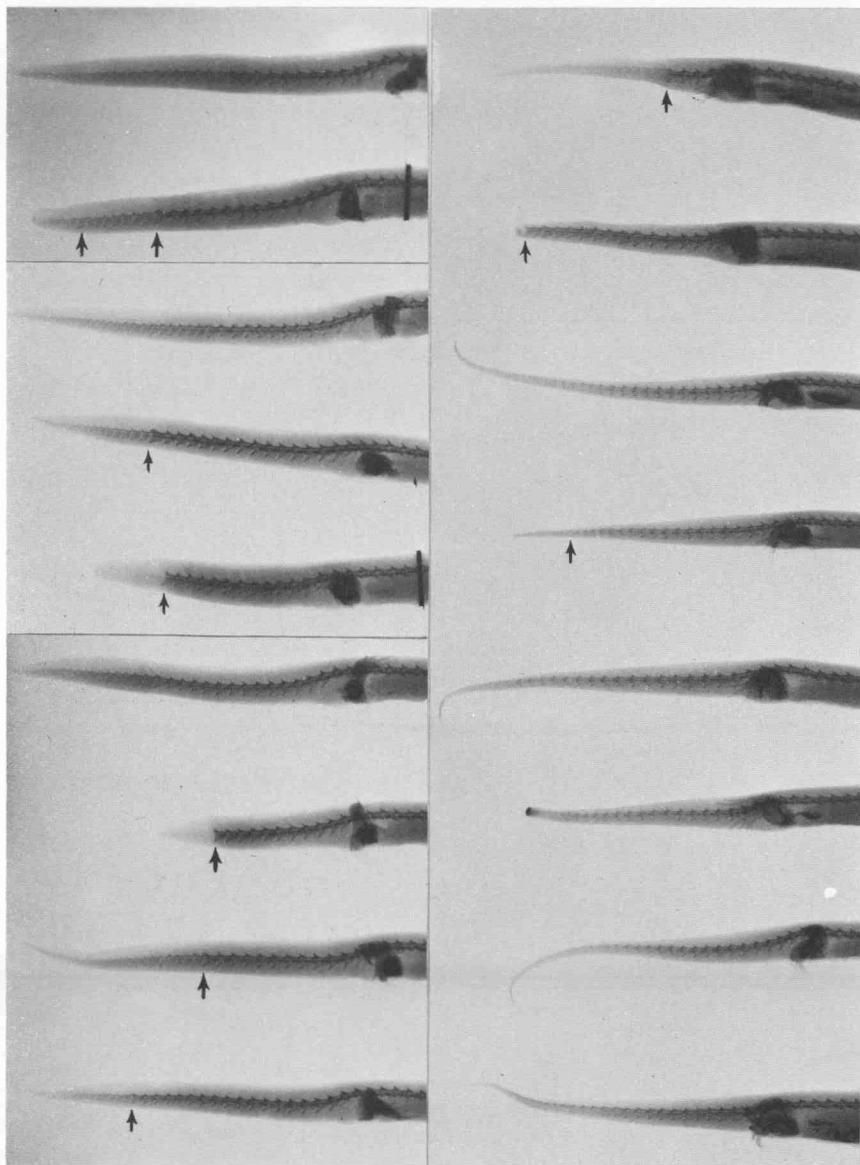


FIGURE 13.—Tail morphology. X-rays of *Desmognathus auriculatus* males on the left, *D. cf. fuscus* males on the right. Arrows mark the beginning of regenerated tail tips.

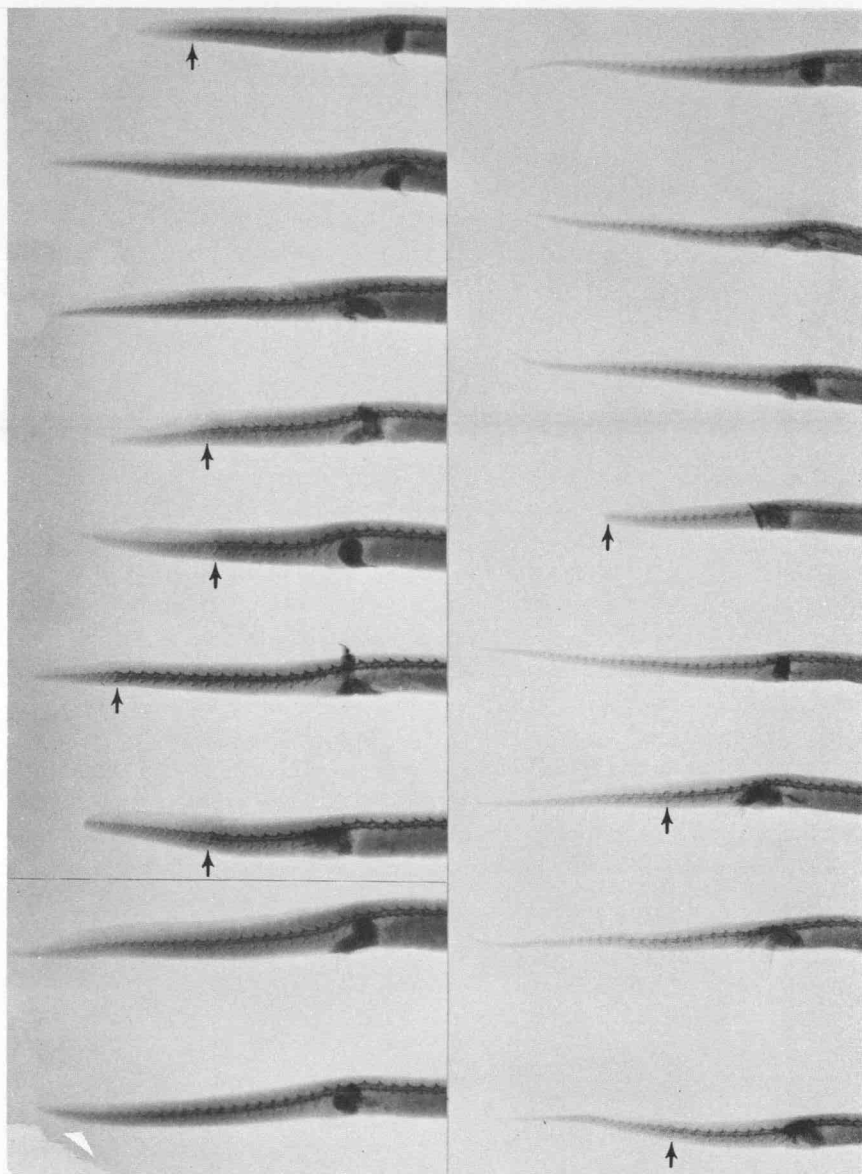
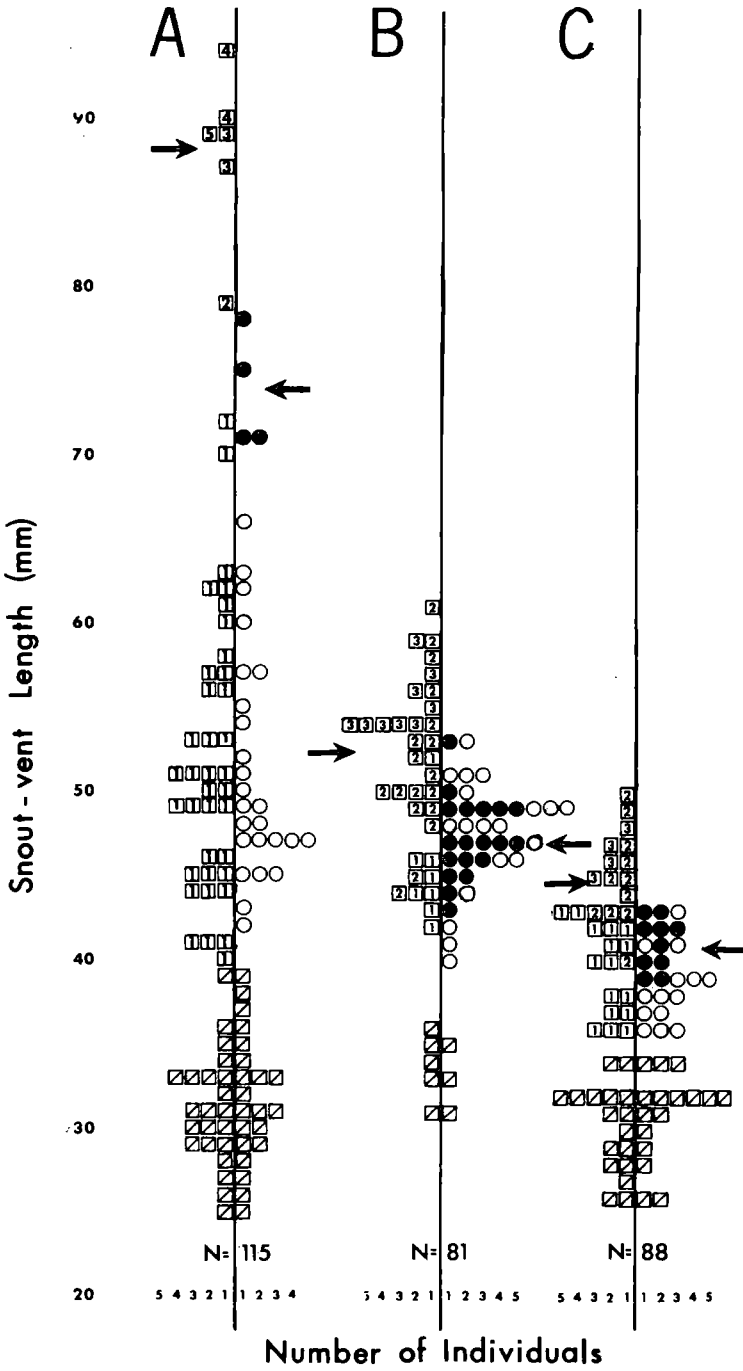


FIGURE 14.—Tail morphology. X-rays of *Desmognathus auriculatus* females on the left; *D. cf. fuscus* females on right. Arrows indicate beginning of regenerated tail tips.

FIGURE 15.—Size comparison between equivalent age classes of representative populations of *Desmognathus auriculatus*, *D. brimleyorum*, and *D. fuscus* (Fla.). Squares with numbers=mature males, numbers indicate lobes per testis; squares with slash=undissected juveniles of either sex (arbitrarily divided equally on diagram); open circles=spent or juvenile females (ova less than 1.5 mm diameter in ovaries); filled circles=gravid females (ovarian ova greater than 1.5 mm diameter). Arrows indicate mean snout-vent length of sexually mature males (2 lobes or more per testis) and gravid females. *D. brimleyorum* collected December, 1969 from top of Rich Mountain (2600 ft. elev.), Polk Co., Arkansas; *D. auriculatus* collected spring, 1971, 1972 from Ochlockonee River drainage, Leon Co., Florida; *D. cf. fuscus* collected spring, 1968 from ravine in Gadsden Co., Florida.



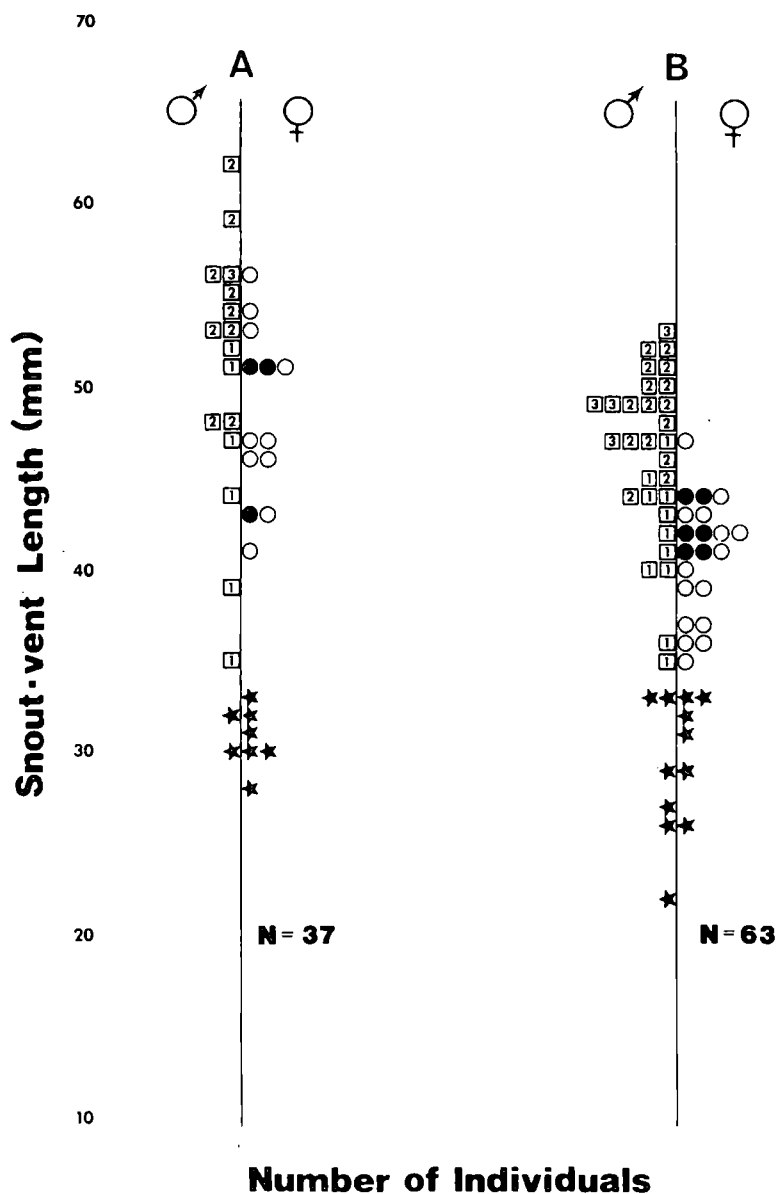


FIGURE 16.—Comparison of equivalent age classes of *Desmognathus auriculatus* (A) and *D. cf. fuscus* (B) collected at the same time from the same locality. Stars indicate undisseminated juveniles of either sex. Floodplain and escarpment toe of Sweetwater Creek in Sec. 21 T2N R7W, Liberty Co., Florida. (Symbols as in Fig. 15.)

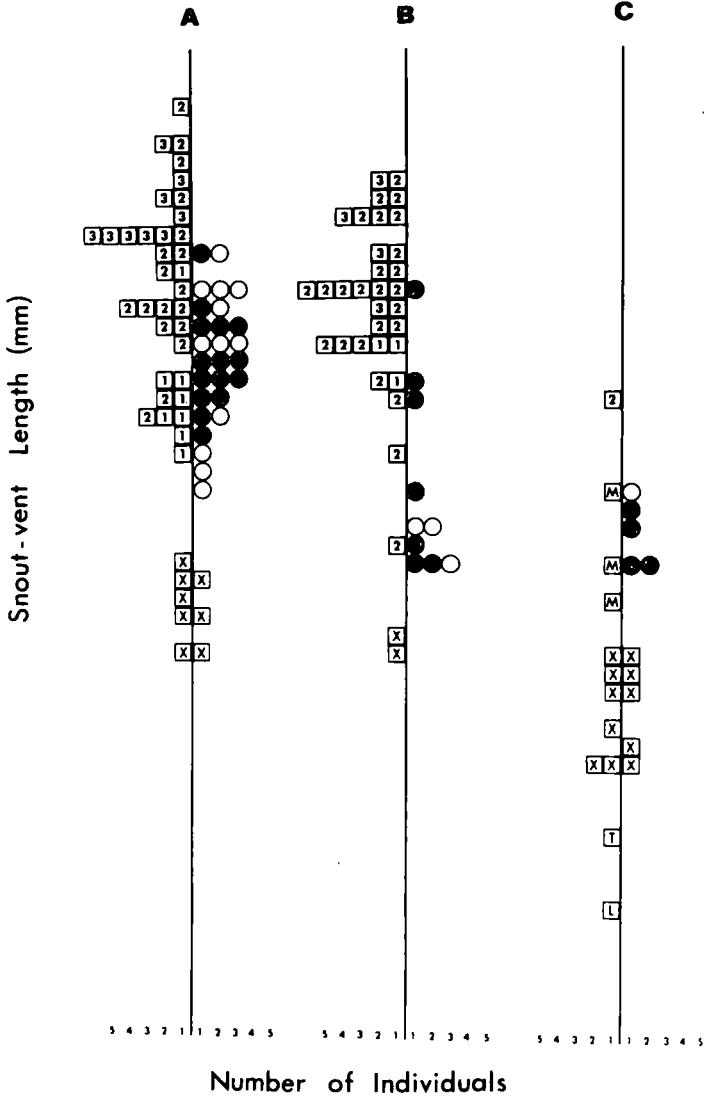


FIGURE 17.—Size-frequency distribution of *Desmognathus fuscus carri* Neill. A representative size-frequency distribution for *D. auriculatus* from Ochlockonee River drainage (A) is compared with *D. f. carri* topotypes collected from Silver Glen Springs by S. Christman (B) and paratypes (C). Males are designated by squares with numbers signifying lobes per testis; squares with X indicate undissected juveniles; filled circles = gravid females; open circles = spent or juvenile females (ovarian ova less than 1.5 mm diameter); squares with M indicate 1-lobed mature males.

FIGURE 18.—Development of color pattern in *Desmognathus brimleyorum* Stejneger. A) larva; B) juvenile of previous year's larva; C, D) 1+ year old juveniles. Lateral line rows 1-3 become obscured on the trunk by melanophore invasion after transformation (B-D); row 2 (on the tail) persists in *D. brimleyorum* longer than any lateral line row, but is eventually lost in sexually mature specimens.

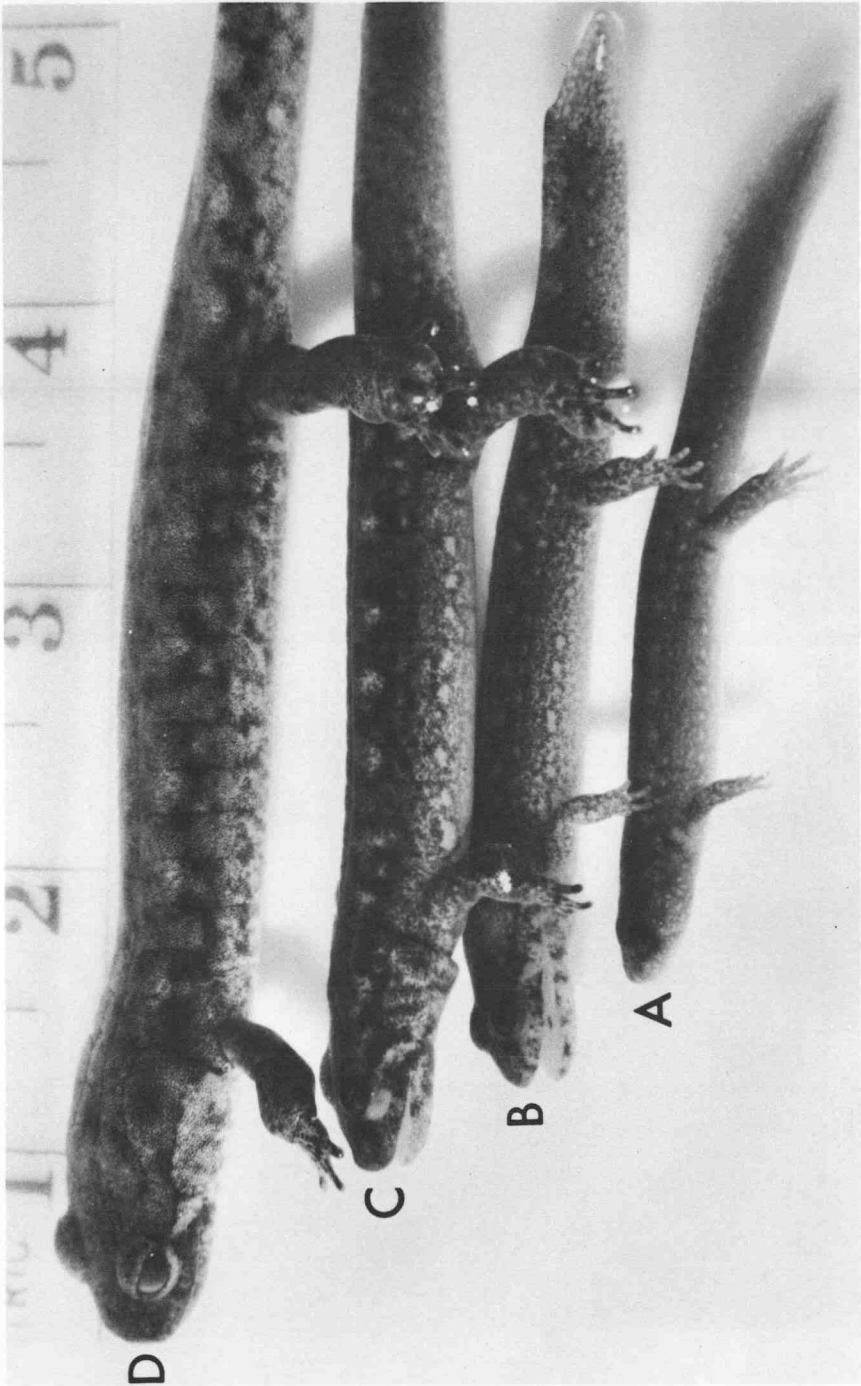


FIGURE 19.—Development of color pattern in *Desmognathus auriculatus* from Mississippi. A, B) larvae; C) recent transformling. Note uncoalesced, pigmentless areas surrounding neuromast sites of lateral line rows, especially on dorsum of transformling. Collected 26 March 1971 from floodplain of Leaf River, Forrest Co., Miss. (DBM-1537).

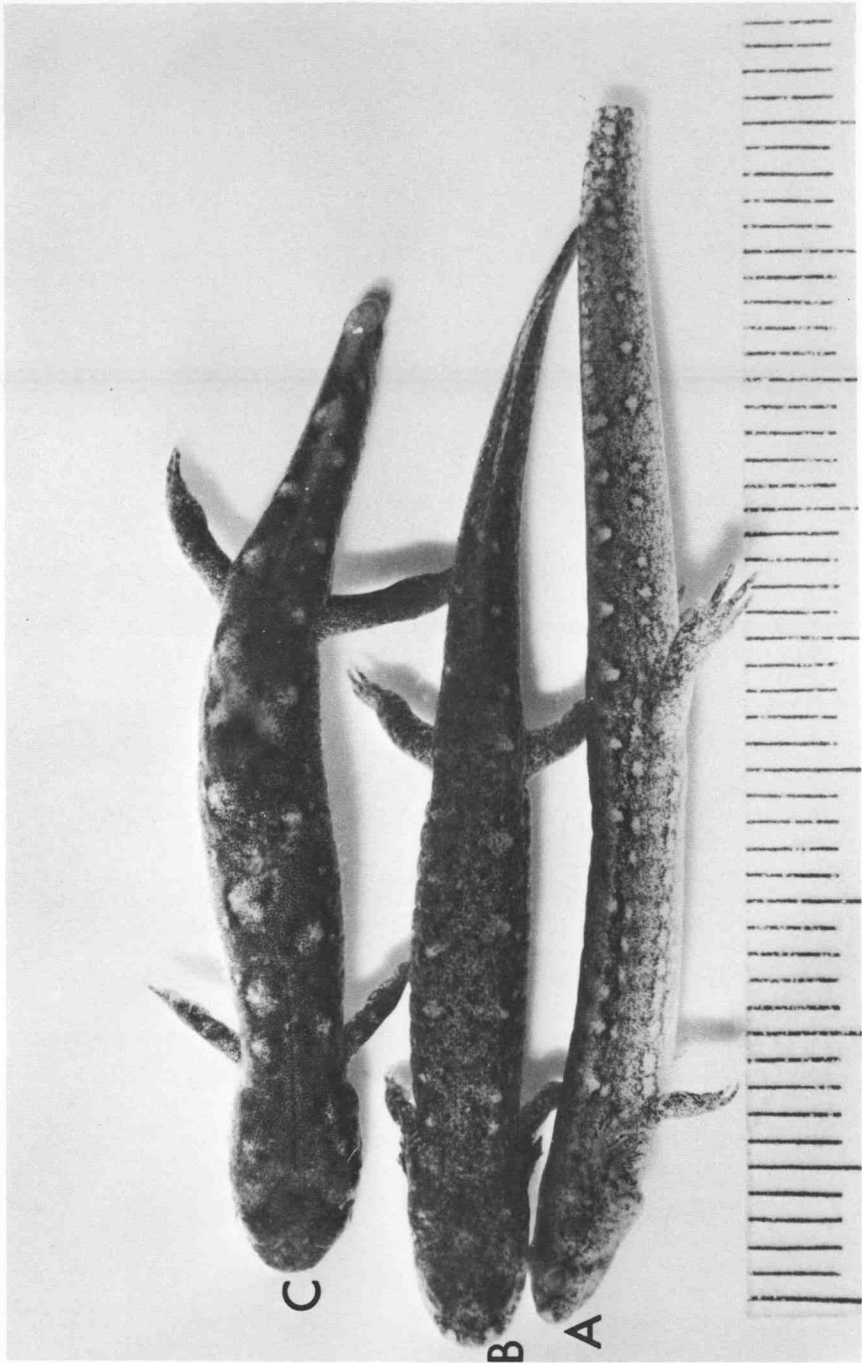


FIGURE 20.—Development of Color Pattern in *Desmognathus auriculatus* from Florida. A, B) larvae; C) transformling. Note extensive dark pigment surrounding neuromast sites, and swamped-out pattern in transformling. Collected 28 March 1971 from mucky depression in Ochlockonee River tributary, Gadsden Co., Fla. (DBM 1538).

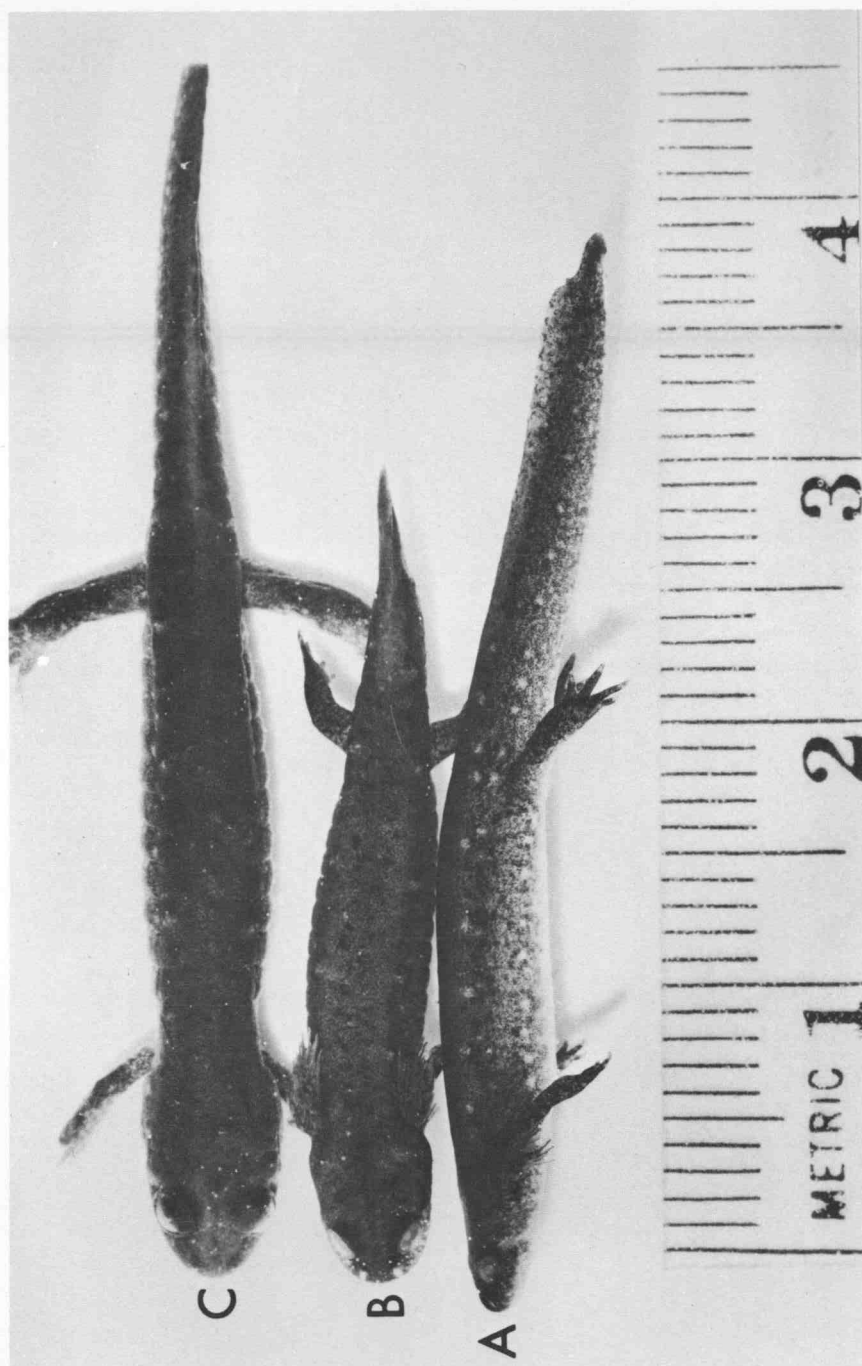


FIGURE 21.—Development of color pattern in *Desmognathus fuscus* from Florida. A) Larva; note obvious presence of lateral line rows 1 and 3, but absence of row 2 on trunk. Row 2 is present on tail. B-D) first year transformlings; B and D illustrate variation in fusion of light dorsal blotches; C illustrates a faint persistence of row 3 on the trunk and row 2 on the tail (these become obscured by melanophore invasion with increasing age). Collected 16 December 1969 from Apalachicola escarpment ravine in Liberty Co., Fla. (DBM-1253). Scale = 1 mm.

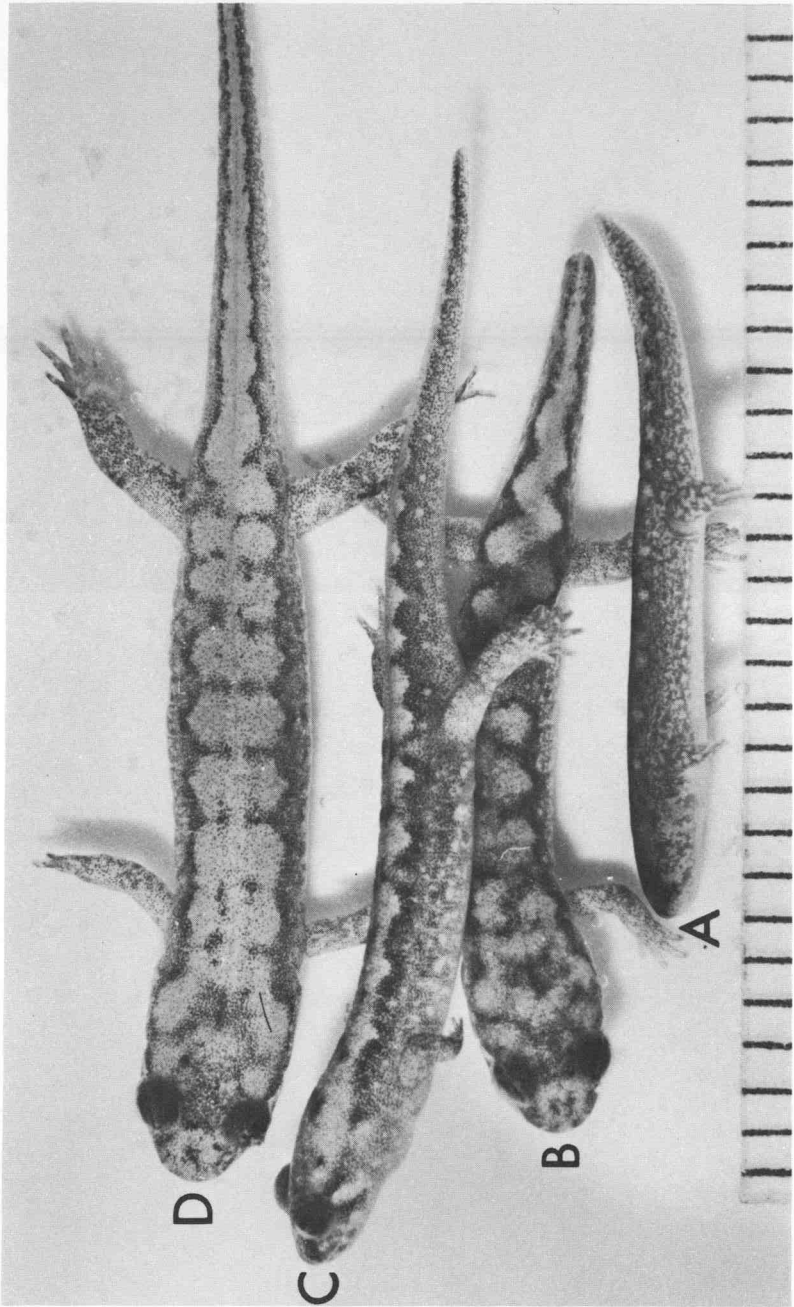


FIGURE 22.—Ontogenetic fate of dorsal pattern in *Desmognathus brimleyorum*. A) larva; B-D juveniles; E) small adult female; F) adult male. Collected 28 November 1969 from top of Rich Mountain, Polk Co., Ark. (DBM-1245).

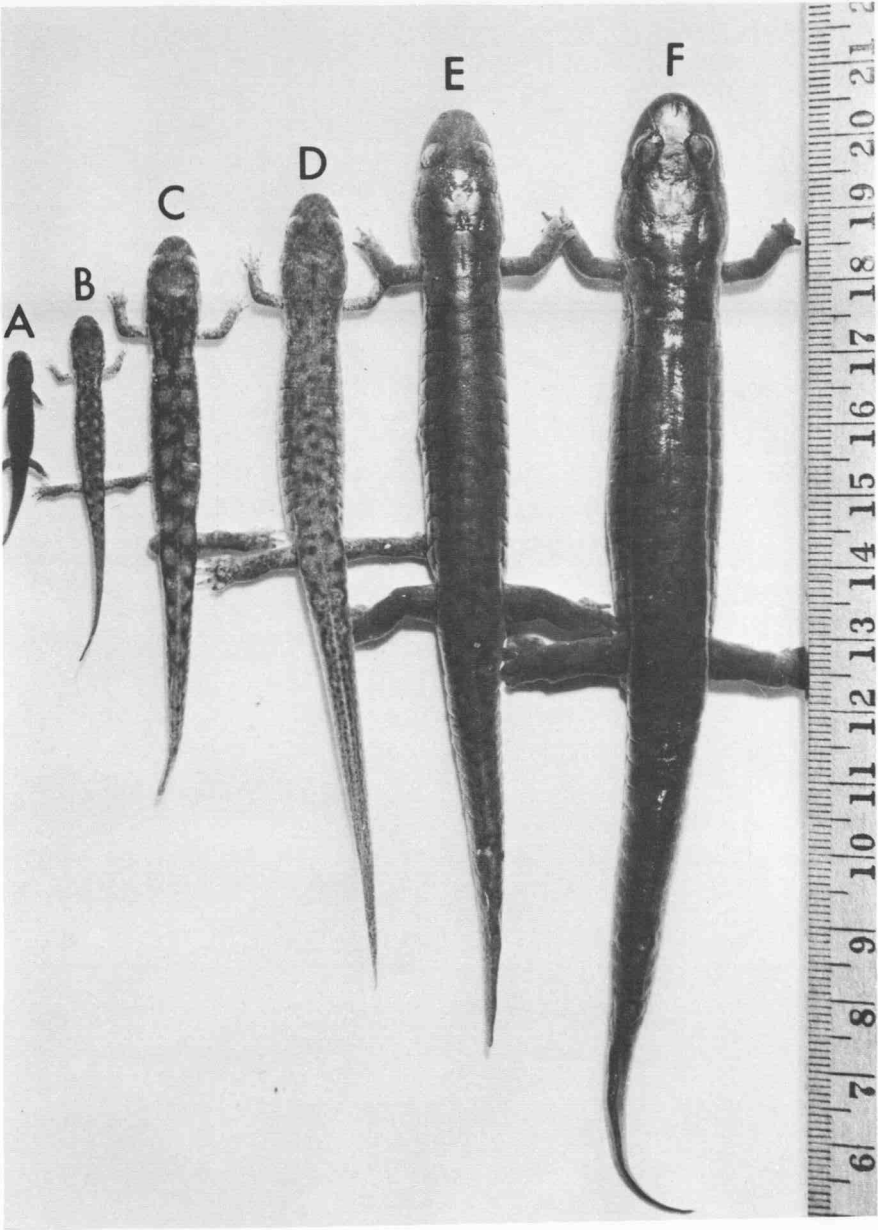


FIGURE 23.—Color pattern in adult *Desmognathus auriculatus* from Mississippi. A, B) juveniles; D) adult female; C, E, F) adult males. Note dorsal pattern of uncoalesced light spots surrounding neuromast sites on the trunk and tail; also, note presence of faint lines on "neck." Collected 25 March 1971 from ox-bow lake of Leaf River, Jones Co., Miss. (DBM-1535).

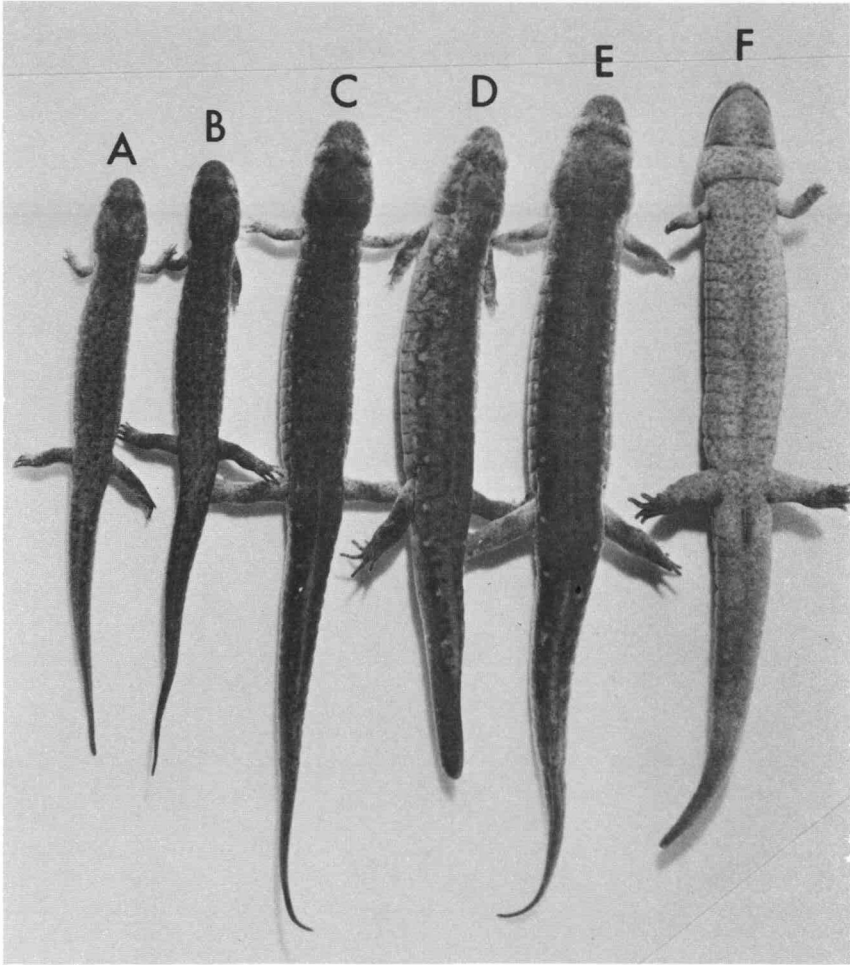


FIGURE 24.—Color pattern of adult *Desmognathus auriculatus* from Leon Co., Fla. Note overall dark color and presence of lighter neuromast sites on B; faint “neck” lines are present on B. Dorsum of tail is lighter medially and has light spots surrounding neuromast vestiges in some. A, B) juveniles; C) adult male; D-F) adult females. Collected 1 May 1971 from mucky margin of cypress pond in Leon Co., Fla. (DBM-1560).

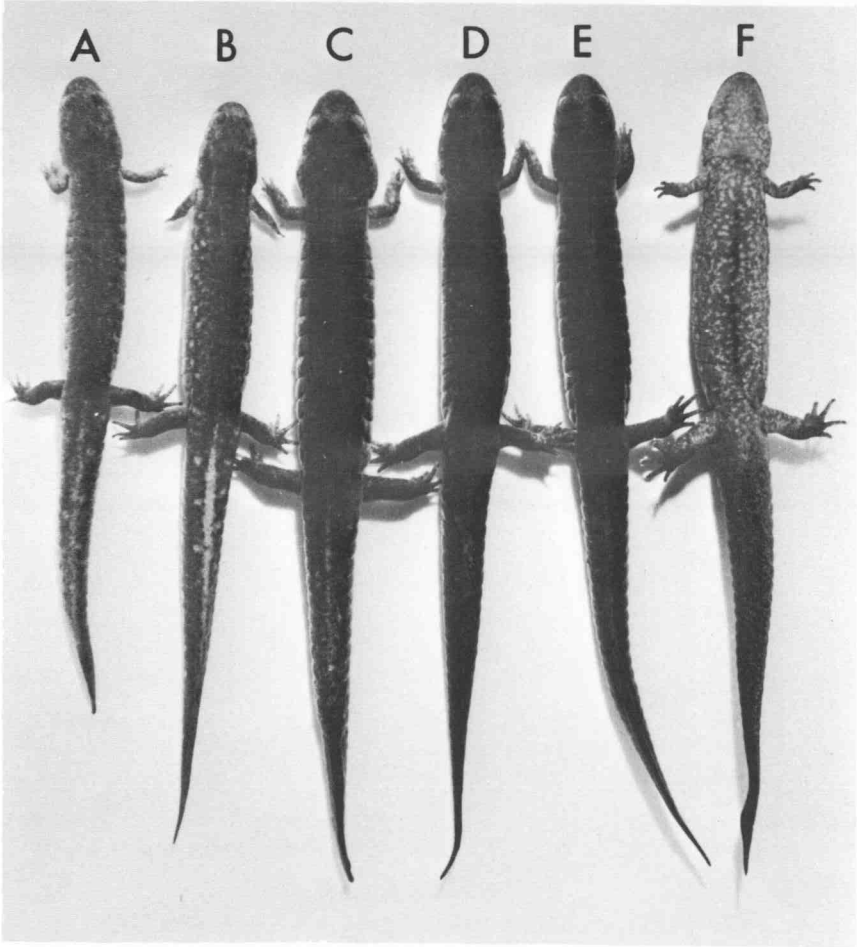


FIGURE 25.—Color pattern of adult *Desmognathus auriculatus* from Liberty Co., Georgia. Note overall darkness of topotypes. A) juveniles; B, C, E) adult females; D) adult male. Collected 13 April 1971 from Riceboro, Liberty Co., Ga. (DBM-1545).



FIGURE 26.—Color pattern of postlarval *Desmognathus auriculatus* from ravine in Okaloosa Co., Florida. These specimens have lost a strong wash of brick red color due to preservation. The red color is evident on the dorsum on close examination of living specimens; but where it is superimposed on "portholes" (neuromast sites of row 3 on trunk and row 2 on tail) and other less intensely pigmented areas, it shows up brightly. Collected 17 December 1969 from Rogue Creek head, Okaloosa Co., Fla. (DBM-1255).

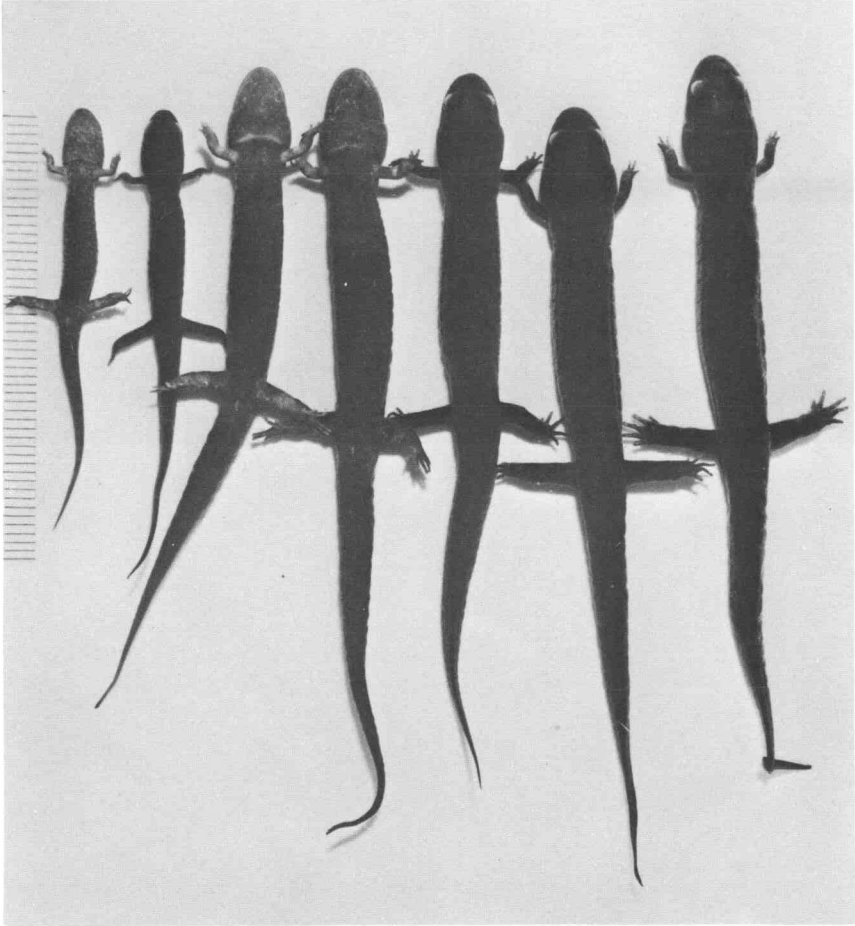


FIGURE 27.—Color pattern of postlarval *Desmognathus fuscus* from Liberty Co., Florida. Note scalloped-edge pattern on dorsum of juvenile males and adult female (A, B, D) and effect of melanization on adult males (E, F). One adult male (C) retains the juvenile pattern of coalesced light spots. Collected 17 December 1969 from head of Beaverdam Creek, Liberty Co., Fla. (DBM-1215).

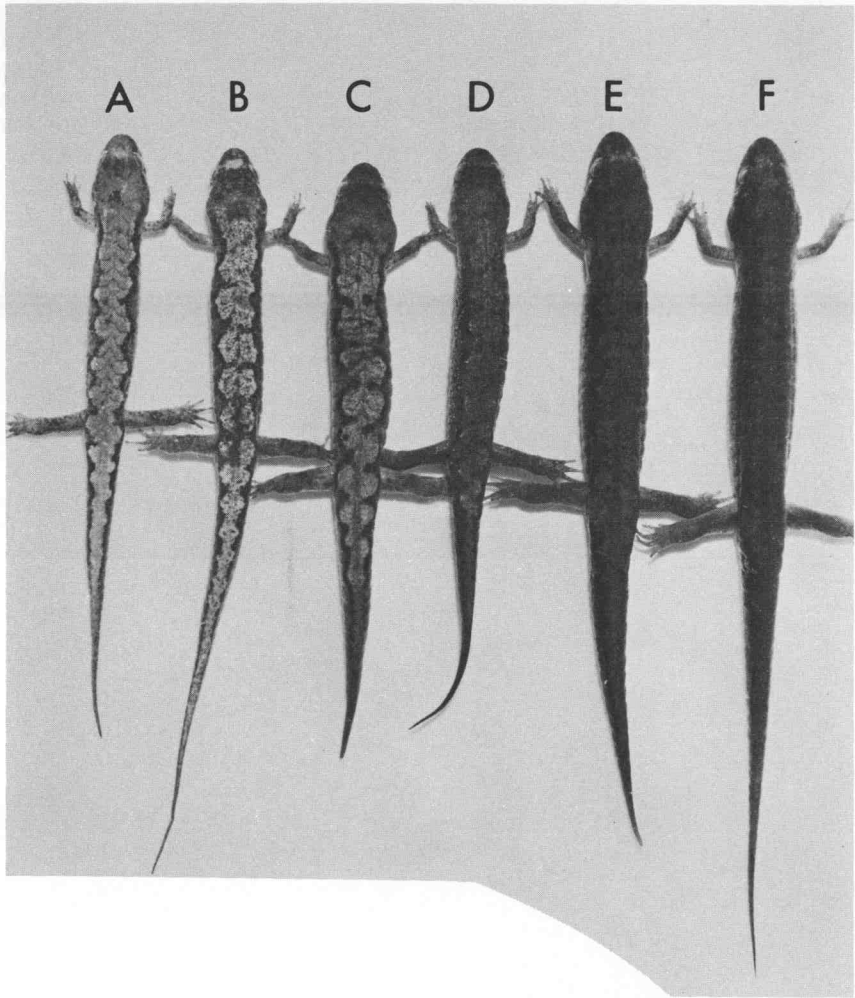


FIGURE 28.—Color pattern of postlarval *Desmognathus fuscus* from Walton Co., Florida. Note the thin lines of melanophore concentration on dorsa. These appear to result from ontogenetic breakup of dorsal blotches (e.g., in the series A-D-F). Collected 14 November 1969 from ravine tributary of Bruce Creek, Walton Co., Florida (DBM-1236).

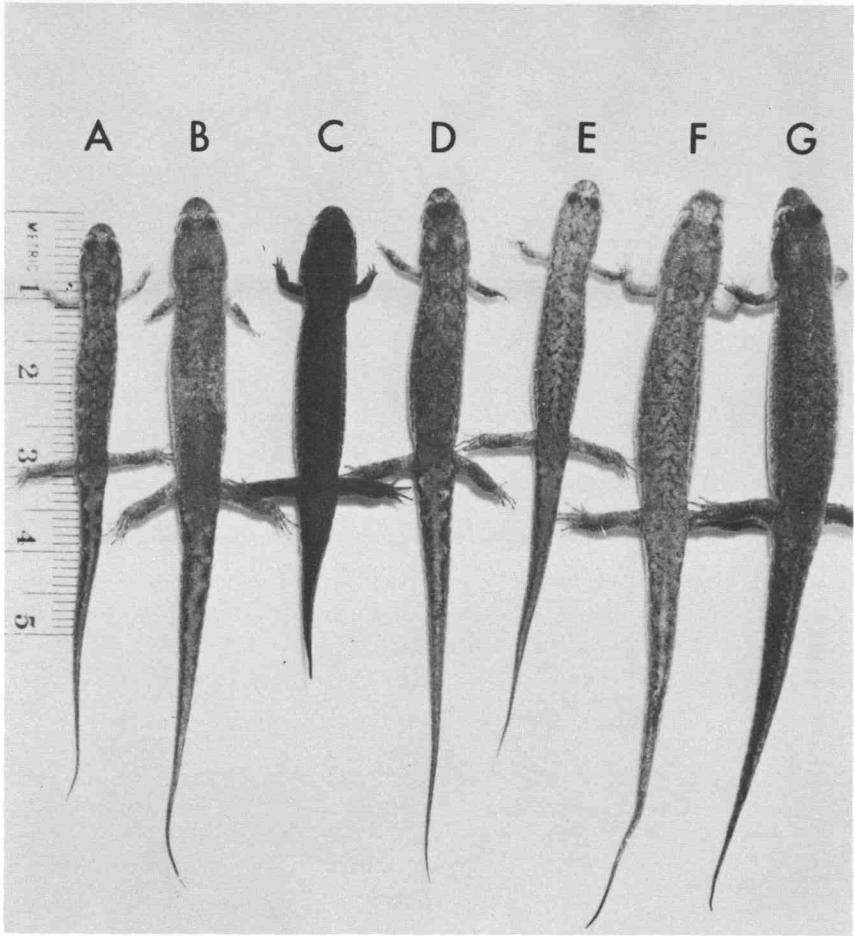
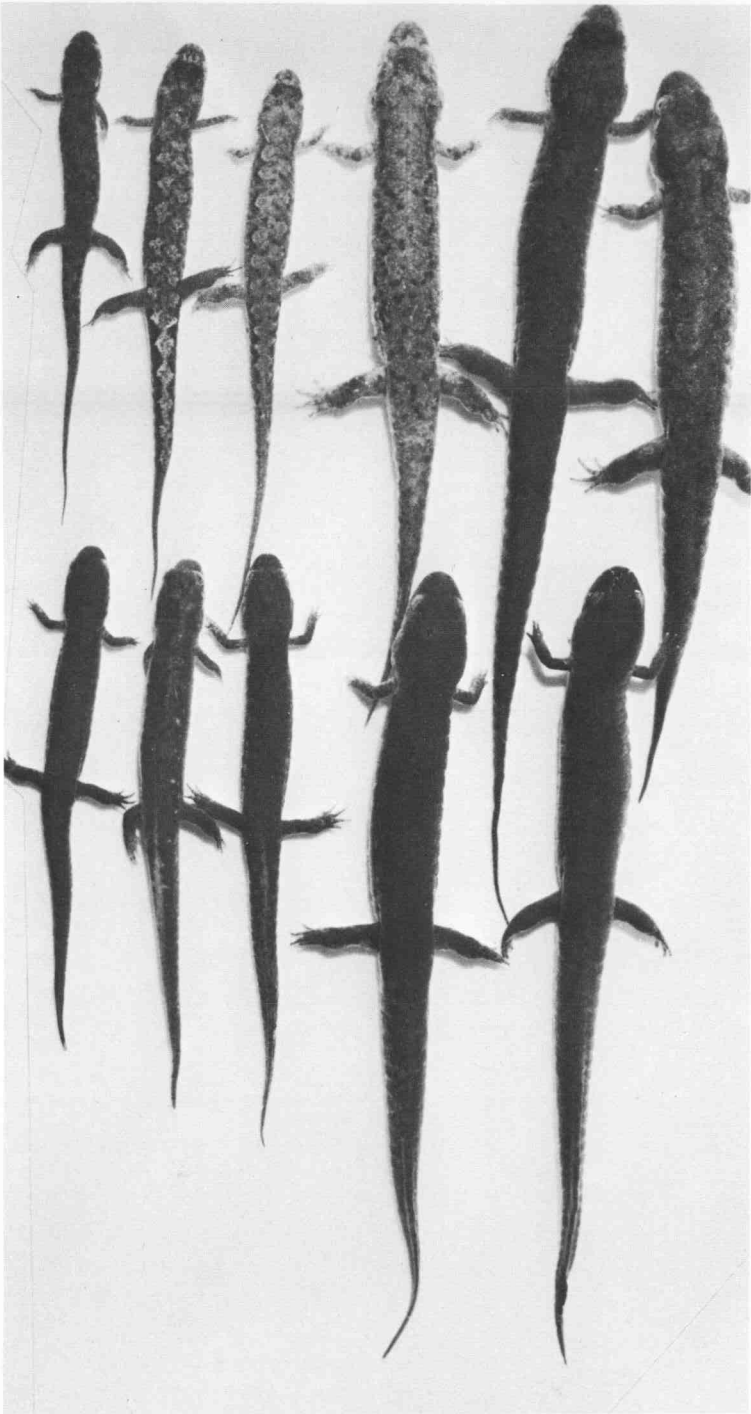


FIGURE 29.—Color pattern of *Desmognathus auriculatus* and *D. fuscus* collected at the same time from the same locality. Top row, *D. fuscus*; bottom row, *D. auriculatus*. Note the close similarity of adult males (largest specimens) of *fuscus* to *auriculatus* at first glance. Closer inspection reveals externally visible differences in tail morphology, head shape, qualitative differences in color. Collected 31 August 1971 from floodplain of Sweetwater Creek, Liberty Co., Florida (DBM-1611).



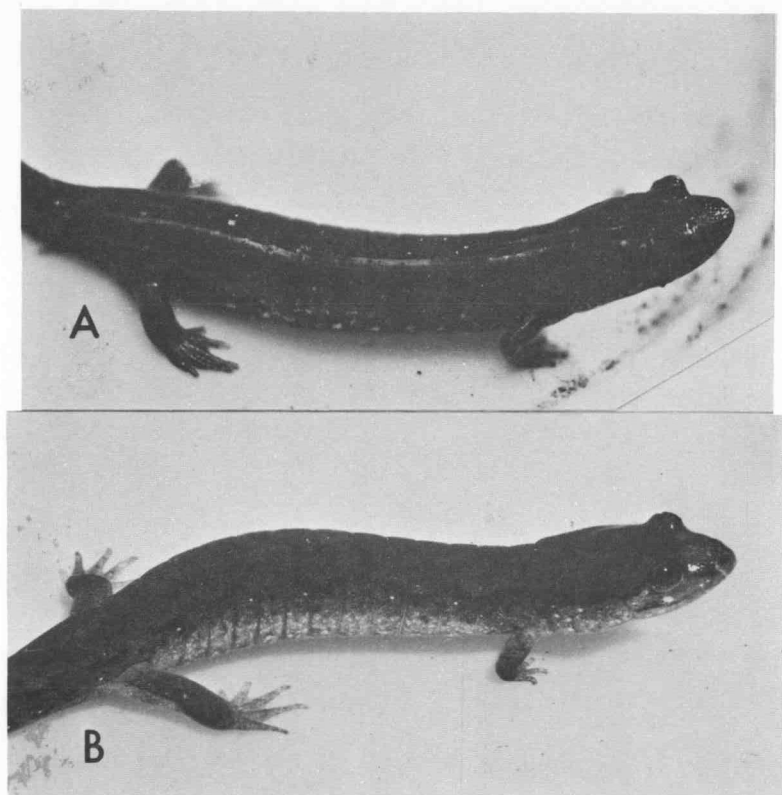


FIGURE 30.—Color change in *Desmognathus fuscus* from Liberty Co., Florida. Adult male (A) photographed immediately after capture in the field, and six hours later in lab (B). Collected 26 February 1972 from an acid hillside seepage site in ravine dissecting Apalachicola escarpment, Liberty Co., Florida (DBM-1658). Differences in proportions due to refraction of light (B photographed through water).

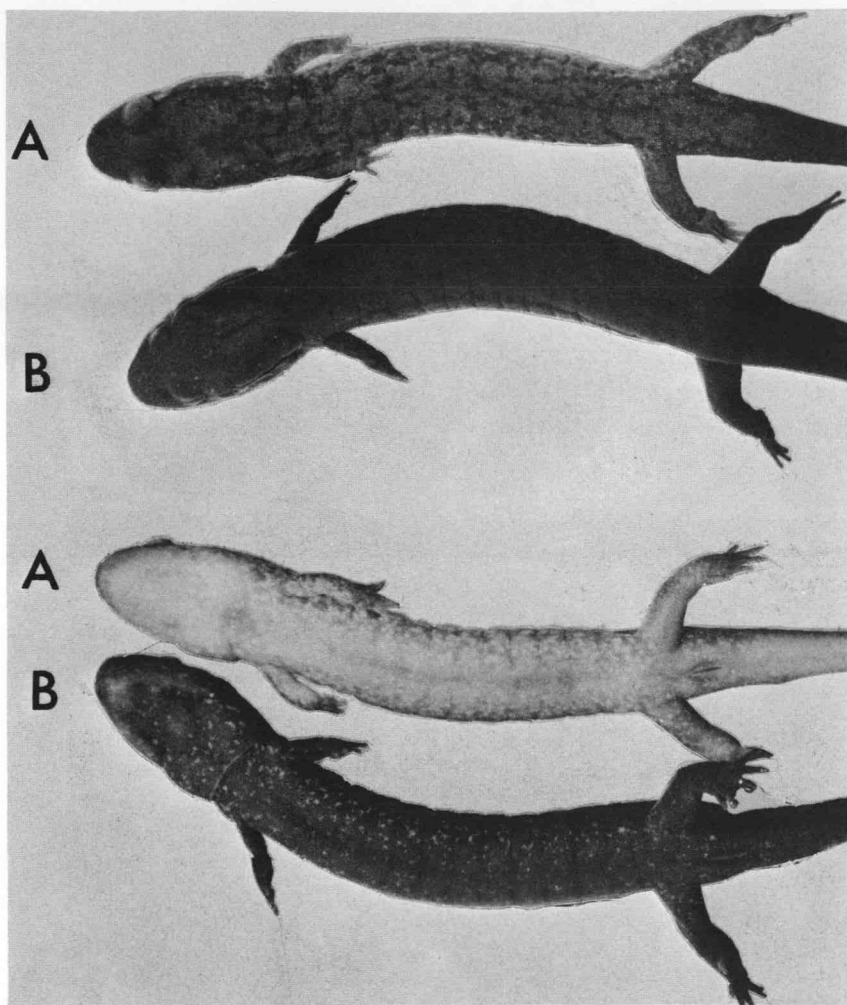


FIGURE 31.—Color change in *Desmognathus fuscus* from Baldwin Co., Alabama. A) Adult male preserved 36 hours after collection (kept in white plastic container in field); B) Adult male preserved immediately in the field. Specimen A was collected from the same site as B and was identical in color at the time of collection. Collected 6 April 1972 (DBM-1686) and 10 April (DBM-1693) from mucky ravine draining into east side of Mobile Bay, Baldwin Co., Alabama.

FIGURE 32.—Geographical range of *Desmognathus brimleyorum* Stejneger. Solid circles represent localities from which specimens of *D. brimleyorum* were examined for this study. Triangles represent the closest localities from which other species were examined.

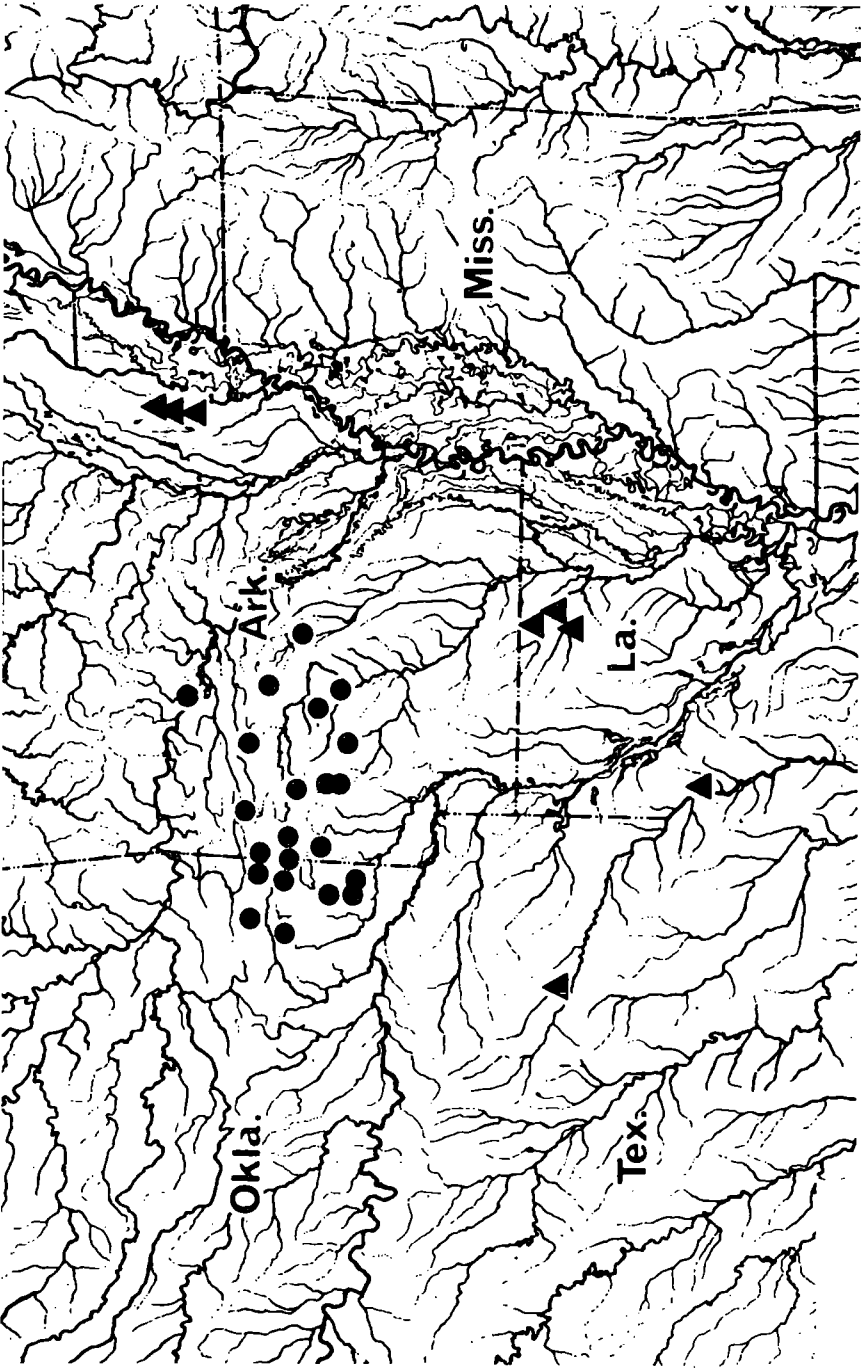


FIGURE 33.—Geographic range of *Desmognathus fuscus* in Florida drainages. Solid line represents probable boundary of range to the south and east.

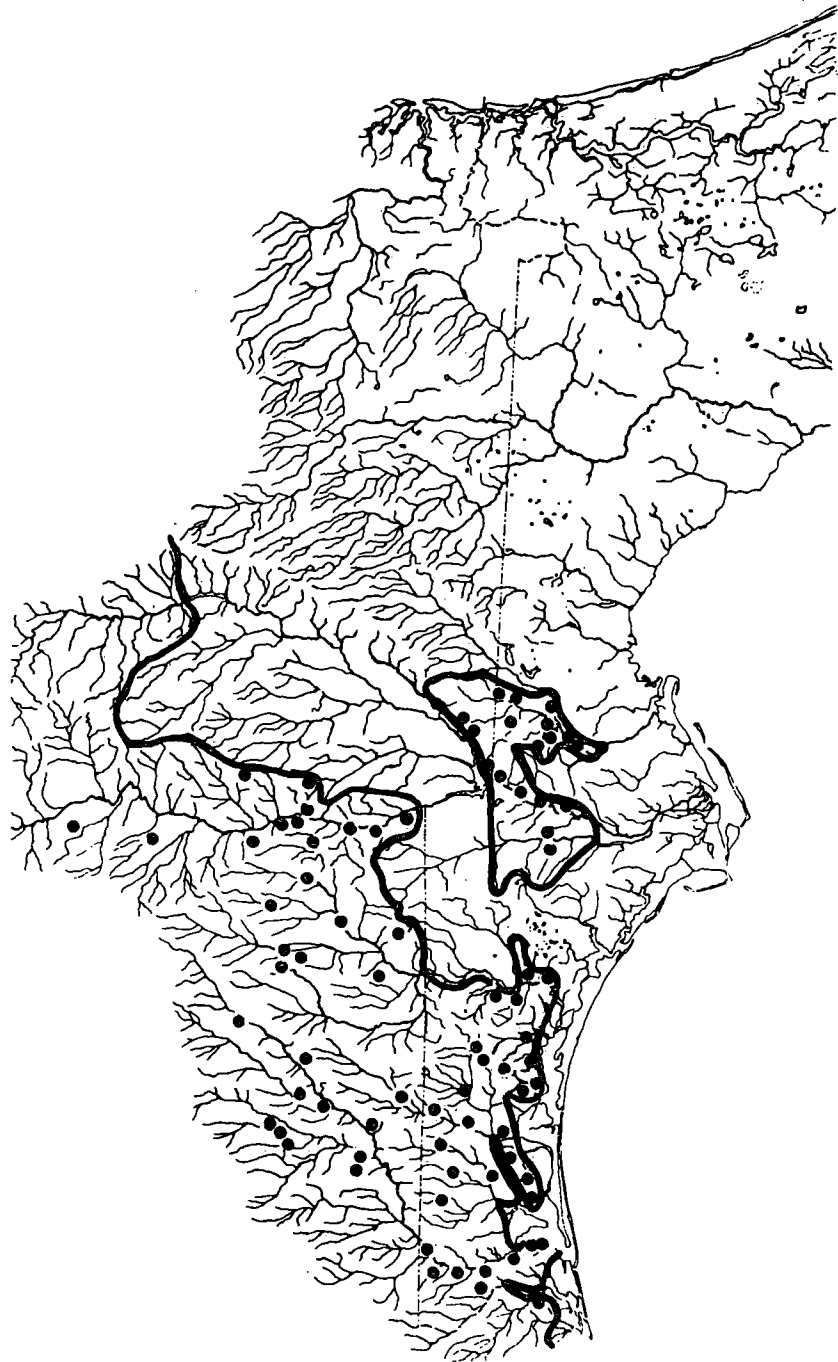


FIGURE 34.—Geographic range of *Desmognathus auriculatus* in Florida drainages. Solid line represents probable boundary of range to the north.

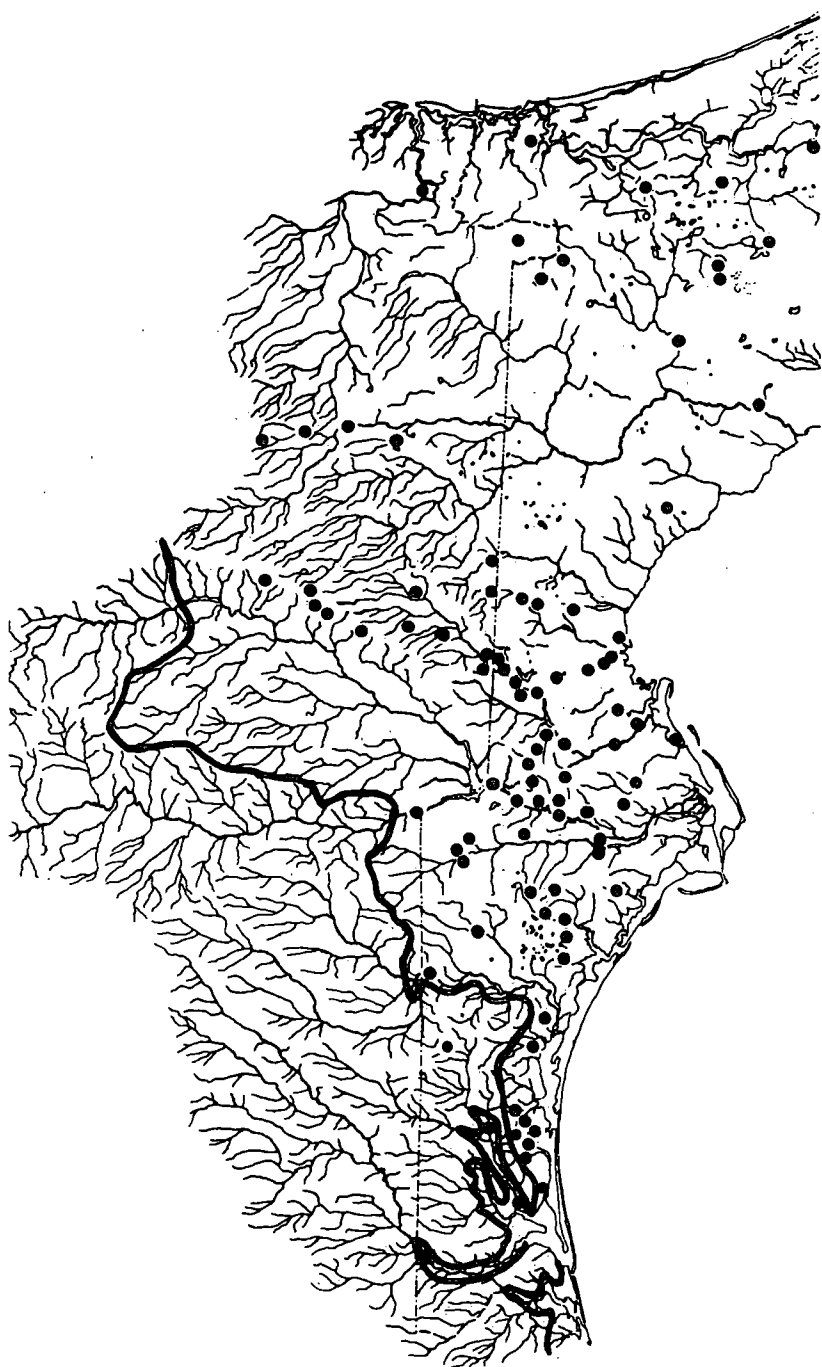
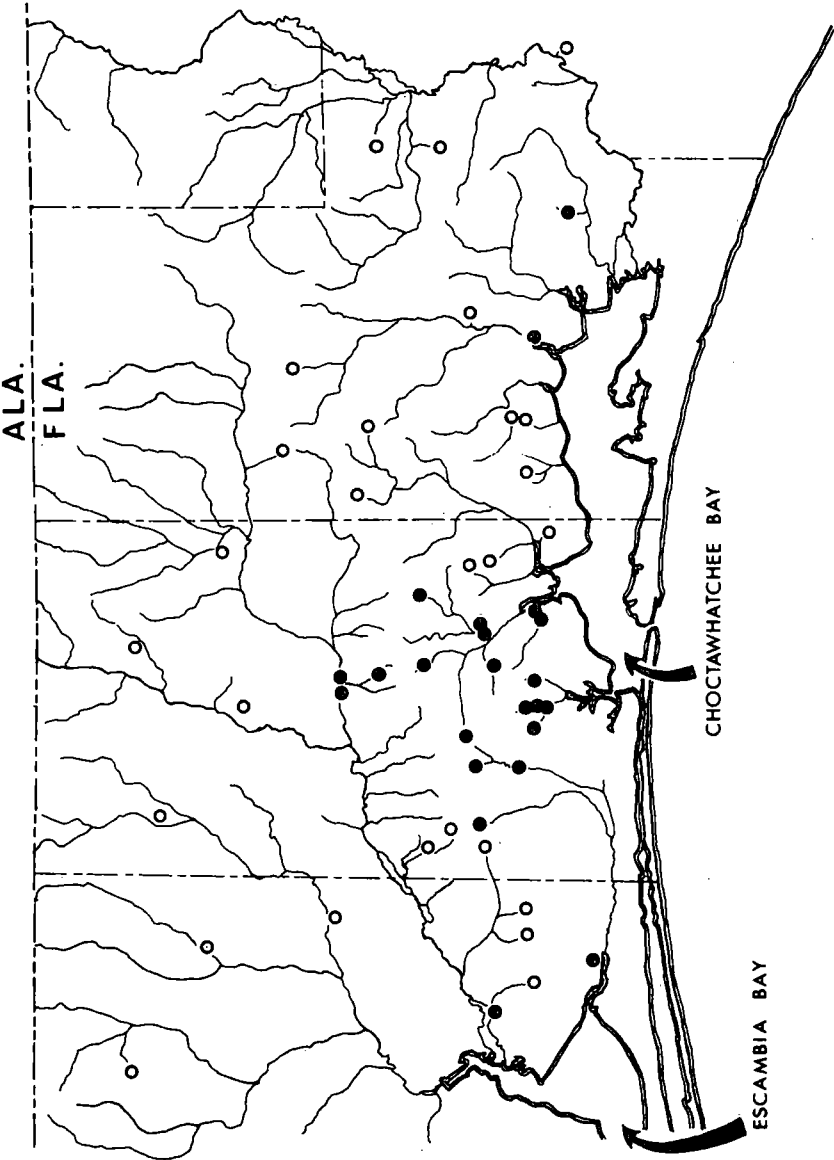


FIGURE 35.—Distribution of *Desmognathus auriculatus* and *D. fuscus* in ravines of western Florida. Filled circles represent ravine populations of *D. auriculatus*; open circles represent ravine populations of *D. fuscus*.



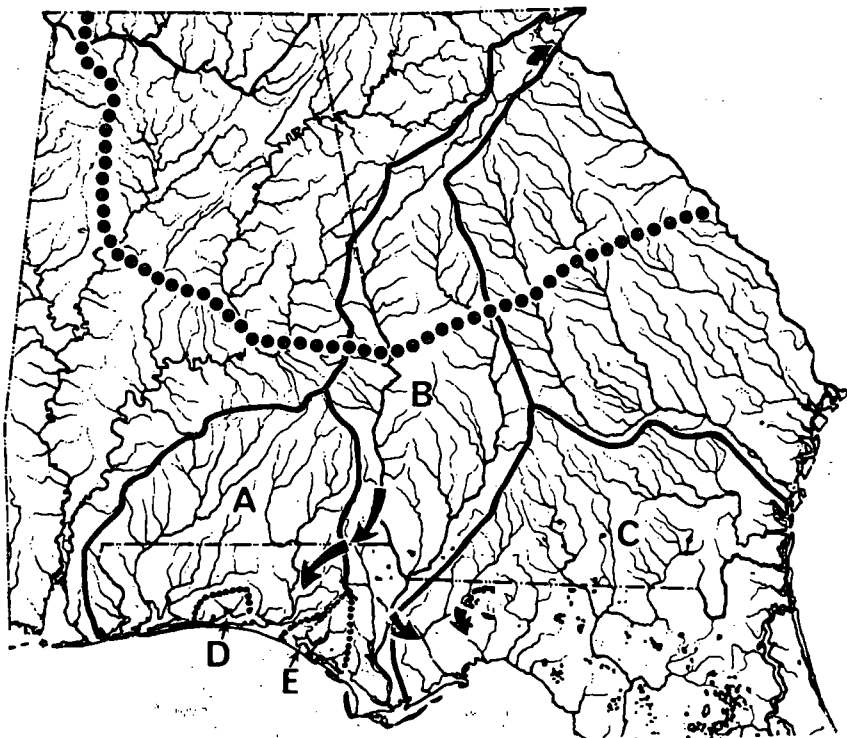


FIGURE 36.—Physiography and drainage map of northern Florida and adjacent states. A) Escambia-Conecuh River basin on west, Choctawhatchee-Pea River on east; B) Apalachicola-Chattahoochee-Flint River basin with origin above Fall Line (heavy dotted line); C) drainages whose heads drain Tifton Uplands plateau (west to east: Ochlockonee, Aucilla, Suwannee system, Satilla River); D) steephead streams emptying into the western end of Choctawhatchee Bay; E) Econfinia Creek and steephead tributary ravines. Arrows mark major stream course changes which may have affected dispersal of desmognathines under consideration in this study.

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