Catalogue of American Amphibians and Reptiles.

TILLEY, STEPHEN G. 1973. Desmognathus ochrophaeus.

Desmognathus ochrophaeus Cope Mountain dusky salamander

- Desmognathus ochrophaea Cope, 1859:124. Type-locality, "Susquehanna County, Pennsylvania." Holotype listed by Dunn (1917b) as destroyed.
- Desmognathus haldemanni: Strauch, 1870:74. Suppression to synonymy under D. haldemanni Holbrook.
- Plethodon ochrophaeus: Smith, 1877:71. Transfer to the genus Plethodon Tschudi.
- Desmognathus ochrophaeus: Boulenger, 1882:77. Emendation. Desmognathus fusca: Fowler, 1906. Suppression to a synonym of D. fuscus Rafinesque.
- Desmognathus ochrophaea carolinensis Dunn, 1916:74. Typelocality, ". . . spring near top of Mt. Mitchell, North Carolina, altitude over 6500 feet." Holotype, an adult male, collected October 5, 1902 by H. H. Brimley and F. Sherman, Jr., U.S.N.M. 31135, examined by author.
- Desmognathus ochrophaea ochrophaea: Dunn, 1917b:415. Emendation.
- Desmognathus ochrophaeus ochrophaeus: Stejneger and Barbour, 1917:22. Emendation.
- Desmognathus ochrophaeus carolinensis: Stejneger and Barbour, 1917:23. Emendation.
- Desmognathus fuscus carolinensis: Pope, 1924:4. Transfer of D. o. carolinensis to D. fuscus.
- Desmognathus fuscus ochrophaeus: Dunn, 1926:114. Suppression to a subspecies of D. fuscus.
- Desmognathus fuscus imitator Dunn, 1927:84. Type-locality, "Indian Pass, Great Smoky Mts., N.C." Holotype collected by J. E. Benedict, Jr., June, 1927, U.S.N.M. 72762, not examined by author. Synonymized with D. o. carolinensis by Pope (1928).
- Desmognathus carolinensis: Brimley, 1928:21. Elevation of D. o. carolinensis to specific status.
- Desmognathus aureatagulus Weller, 1930: page unnumbered. Type-locality, "... trail between Newfound Gap and Indian Pass, altitude 4400-5000 ft." Holotype collected by R. Dury, W. Wyss, A. Loring, S. Loring, and W. H. Weller, June 26, 1930, Cincinnati Museum of Natural History no. 656, not examined by author. Synonymized with D. f. imitator by Weller (1931).
- Initiator by Weiler (1931).
 Desmognathus ocoee Nicholls, 1949:127. Type-locality, "Ship's Prow Rock, in Ocoee Gorge, beside U. S. Highway 64, nine miles airline west of Ducktown, in Polk County, Tennessee." Holotype collected by J. C. Nicholls, Jr., November 14, 1948, U.S.N.M. 128007, not examined by author. Considered a synonym of D. ochrophaeus by Martof and Rose (1963) and Huheey (1966a). See Comment.
- Desmognathus perlapsus Neill, 1950:1. Type-locality, "a rocky outcropping on the western wall of Tallulah Gorge, near the town of Tallulah Falls, Rabun County, Georgia." Valentine (1964) quotes Huheey as stating in a letter that the type-locality is in Habersham County, Georgia. Holotype collected by W. T. Neill, August 4, 1950, E. R. Allen-W. T. Neill 14150, not examined by author. Synonymized with D. ocoee by Valentine (1961).
- Desmognathus carolinensis ocoee: Huheey, 1966a:125. New combination.

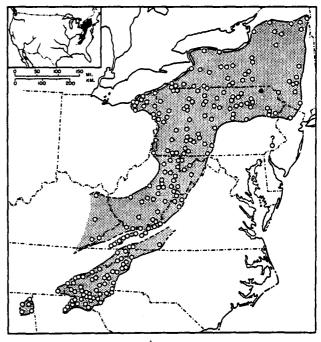
• DIACNOSIS. A semi-terrestrial, round-tailed Desmognathus maturing at snout-vent lengths (SVL) of 30-40 mm depending on locality, in which adult males have pigmented testis lobes and lose vomerine teeth with age.

Characters useful in separating the species from *D. fuscus* are not absolute and must frequently be used in combination. Few can be quantified. They include: the longer, more tapering, and usually keel-less tail; bolder and more variable dorsal coloration; more extreme darkening in adult males; more sinuate jaw margin in males; less stocky build in large adults; general lack of yellow pigment except between the dorsolateral stripes; universal lack of greenish pigment; and more terrestrial habits. In some areas, particularly the north, *D. ochrophaeus* develops a dorsal pattern of two parallel dorsolateral stripes enclosing a mid-dorsal row of dark spots that are frequently chevron-shaped. D. fuscus rarely develops such a pattern.

Juveniles are frequently brightly colored, with dorsal colorations of yellow, orange, and red. They are distinguishable from juvenile D. monticola and D. quadramaculatus in their bolder and more variable dorsal colorations, proportionally smaller heads, keel-less tails, and less stocky morphologies. They usually lack the chestnut larval spots nearly always present in juvenile D. monticola. They are difficult to distinguish from juvenile D. fuscus, but usually have rounder tails and bolder and more variable dorsal patterns. Contrary to Conant's (1958:218) illustrations, juvenile D. ochrophaeus and northern D. fuscus juveniles both frequently lack larval spots.

Larvae are smaller than those of D. monticola and D. quadramaculatus, hatching at 8-10 mm SVL, normally transforming at 10-12 mm, and rarely reaching 15 mm. The larval period is normally 2-8 months in the southern Appalachians (Tilley, 1973b). Larval D. monticola and D. quadramaculatus from southwestern Virginia are larger (Organ, 1961), with D. monticola reaching 20 mm and D. quadramaculatus 44 mm. The larvae resemble transformed juveniles in external morphology more than do larval D. quadramaculatus. Larval D. ochrophaeus closely resemble those of D. fuscus. Larvae of northern D. ochrophaeus do not always lack larval spots (L. P. Orr, pers. comm.), and are thus not separable from larval D. fuscus in that respect, contrary to statements by Bishop (1941, 1947). In some areas larval D. ochrophaeus apparently have fewer gill fimbriae per ramus than D. fuscus larvae (Orr, pers. comm.; Rubenstein, 1969). Bishop and Chrisp (1933) and Eaton (1956) incorrectly state that D. ochrophaeus may transform shortly after hatching. In the southern Appalachians larvae hatched in the fall may occasionally overwinter, while larvae that hatch in the early spring transform in 2-3 months. Organ's (1961) assumption that spring larvae represented fall hatchlings that overwintered appears to have been incorrect. D. fuscus larvae attain larger body sizes than D. ochrophaeus larvae (Rubenstein, 1969, 1971), possibly because they typically overwinter prior to transformation (Wilder, 1913).

• DESCRIPTIONS. ADULTS: Barbour (1953, 1971), Bishop (1941, 1947), Blair, et al. (1968), Cochran and Goin (1970), Cope (1859, description of type; 1869, 1889), Ditmars (1905), Dunn (1916, 1917b, 1926), Eaton (1954, D. perlapsus), Huheey (1966a, 1966b, 1966c), Martof and Rose (1963, color pattern and morphological variation), Neill (1950, D. perlapsus), Nicholls (1949, D. ocoee), Noble (1927a, maxillary teeth and



MAP. The solid circle marks the type-locality; open circles indicate other localities. Solid lines mark well-defined range limits, their absence indicates estimated range limits.

sexual dimorphism; 1931, color pattern variation, maxillary teeth, and sexual dimorphism), Noble and Pope (1929, skull and dentition), Smith (1877), Surface (1913), Tilley (1969, color pattern variation), and Valentine (1961, 1964, D. occoec).

JUVENILES: Bishop (1941, 1947), Bishop and Chrisp (1933), Conant (1958), Dunn (1926), Huheey (1966a), Martof and Rose (1963, color pattern variation), Tilley (1969, color pattern variation). LARVAE: Bishop (1924, 1941, 1947), Bishop and Chrisp (1933), Dunn (1926), Eaton (1956), Martof and Rose (1963, color pattern variation), Noble (1927b, 1931), Rubenstein (1969), Tilley (1969, color pattern variation), Wood and Wood (1955). ECCS, EMERYOS, AND NESTS: Bishop (1941, 1947), Bishop and Chrisp (1933), Dunn (1917a, 1926), Eaton (1954, *D. perlapsus*), Martof and Rose (1963), Noble (1931), Pope (1924), Wood and Wood (1955). SPERMATO-PHORES: Bishop (1941), Organ and Lowenthal (1963). SPERMATOZOA: Noble and Weber (1929). COURTSHIP BE-HAVIOR: Organ (1961). HEDONIC GLANDS: Noble (1929). ELECTROPHORETIC PATTERNS: Shontz (1968), Hinderstein (1971). HAEMATOLOCY: Reynolds and Pickard (1973), Vernberg (1955). GROSS INTERNAL ANATOMY: Wonderly (1963).

Extensive inter- and intrapopulational variation in a number of characters complicates the description of adults and juveniles. The rounded, unkeeled tail is perhaps the most diagnostic morphological character, but even this is subject to geographic variation (Martof and Rose, 1963). Body size undergoes extensive geographic variation (Martof and Rose, 1963), partly as a consequence of variation in age, and hence size, at maturity (Tilley, 1973a).

The color pattern is a complex of several components (Tilley, 1969). Larvae and some juveniles have the row of rounded, unpigmented areas on either side of the midline that are typical of young desmognathines, with four or five pairs between leg insertions. The spots of a given pair may lie alternate or opposite to one another. Larval spots occur in virtually all southern Appalachian larvae but may be poorly defined in Ohio and New York specimens. The spots typically fade with age but traces may persist in adults.

Melanophores congregate lateral to the larval spots, forming dorsolateral stripes. These vary from a straight to an undulating configuration, depending upon the positions relative to the midline of patches of pigment between successive pairs of spots. Straight or slightly undulating stripes are characteristic of northern populations. Blue Ridge populations from southwestern Virginia to the Great Smoky and Great Balsam Mountains are polymorphic, with the incidence of undulating stripes increasing to the south. Populations in the extreme southwestern Blue Ridge Physiographic Province are almost monomorphic for the undulating pattern.

Red or yellow chromatophores occur in many juveniles, particularly between the dorsolateral stripes. In the Great Smokies, Nantahala Mountains, and Highlands Plateau region chromatophores may invade the cheek regions as well. In the Nantahalas occasional specimens have red or yellow legs. The amount and distribution of red and yellow pigment varies both within and between populations. Yellow pigment is most frequent and brightest in females. The bright colorations of many juveniles fade as the animals darken with age. The rate of ontogenetic darkening is highly variable, being most pronounced in males. Old males are typically uniformly dark brown to nearly black, and virtually patternless. The venter typically darkens from pure white in larvae and small juveniles to dark gray in old males.

A melanophore pattern is often present along the midline between the dorsolateral stripes. In the north it often consists of a row of rounded dark spots down the midline, the number of which appears to increase with age. This pattern seldom occurs on a given specimen with undulating dorsolateral stripes, and hence is rare in southern populations.

The larvae typically have distinct, paired larval spots and straight or undulating dorsolateral stripes. Living specimens from southern Blue Ridge populations often have pinkish areas on the cheeks and temporal areas anterior to the gills. These appear to fade before transformation. The gills are usually extremely short and silvery in appearance. The tails of larvae are keeled.

• ILLUSTRATIONS. ADULTS: Angel (1941, skull of adult male and female), Barbour (1971), Bishop (1941, 1947) (the author concurs with Valentine, 1963, that Bishop's fig. 55-1 is a *Desmognathus fuscus*), Cochran and Goin (1970), Conant (1958, see also his illustration of *D. perlapsus*), Cope (1889, head, mouthparts and feet), Ditmars (1905), Dunn (1917a), Fowler (1906), Huheey and Stupka (1967), Jordan (1929), Leviton (1971, mistakenly identified as *Plethodon cinereus*), Martof and Rose (1963), Mertens (1960), Neill (1950, D. perlapsus), Noble (1927a, maxillary tooth, skulls of adults, cross section of palate), Noble (1930, 1931, head of adult with red cheek patch), Noble and Pope (1929, skulls of adults, maxillary and premaxillary bones and teeth), Tilley (1969, dorsal patterns), Valentine (1961, D. occoee), Wake (1966, skull and anterior vertebral column). YOUNG: Bishop (1941), Bishop and Chrisp (1933), Conant (1958), Fowler (1906), Noble (1930). LARVAE: Bishop (1941), Bishop and Chrisp (1933), Tilley (1969). Eccs: Bishop (1941), Bishop and Chrisp (1933), Tilley (1969). Lecs: Bishop (1941), Bishop and Chrisp (1933), Eaton (1954, D. perlapsus), Salthe (1963). SPERMATOPHORES: Bishop (1941), Organ and Lowenthal (1963). ELECTROPHORETIC PATTERNS: Shontz (1968). GROSS INTERNAL ANATOMY: Wonderly (1963).

• DISTRIBUTION. The species as here defined occurs west of the Hudson River, from the Adirondack Mountains through New York State, Pennsylvania, extreme northeastern Ohio, eastern West Virginia, Maryland, and the Allegheny and Shenandoah Mountain sections of Virginia, into the Cumberland Mountains of eastern Kentucky and the southern Blue Ridge Physiographic Province from southwestern Virginia to northeastern Georgia. Disjunct populations occur in the Cumberland Plateau of northeastern Alabama (Valentine, 1961 as *D. occee*; Mount and Folkerts, 1968). It occurs in the Ridge and Valley Physiographic Province only in such high regions as Big Walker and Clinch Mountains in southwestern Virginia. Its distribution in eastern Kentucky is poorly documented.

A record from Columbus, Ohio (U.S.N.M.) is erroneous (Dunn, 1926). Dunn's (1926) records from Sugar Grove, Ohio and Logansport, Indiana were presumably based on *D. fuscus*. Dunn (1926) identified Cox's (1898) specimens from New Brunswick, Canada as *D. fuscus*. An introduced colony, the origin of which is unknown, may occur near Philadelphia, Pennsylvania (C. J. McCoy, pers. comm.).

D. ochrophaeus has the widest altitudinal distribution of any desmognathine, reaching the highest elevations of the eastern United States. At low elevations it inhabits stream margins and seepage areas but individuals, particularly adult males, may move far into adjacent woodlands. Terrestriality increases with elevation, apparently in response to increased humidity at high altitudes (Hairston, 1949).

• Fossil Record. None.

• PERTINENT LITERATURE. Southern Blue Ridge populations were studied by Martof and Rose (1963), who discussed geographic variation, ecology, reproductive patterns, and taxonomic problems in the species. They assigned all populations to a monotypic species, *D. ochrophaeus*, and considered *D. occee* Nicholls a synonym. Tilley (1969) analyzed interand intrapopulational variation in the dorsal pattern in southern Blue Ridge populations. He concurred with Martof and Rose in not recognizing subspecies.

Populations inhabiting wet rockfaces have been sources of controversy. Huheey (1966a) and Mount and Folkerts (1968) followed Martof and Rose (1963) in considering D. ocoee (a name originally applied to a rockface population) a synonym. Valentine (1961, 1964) assigned all low elevation populations of the "ochrophaeus-complex" in the extreme southwestern Blue Ridge Physiographic Province to D. ocoee, which he proposed (1964) might actually constitute a low elevation race of D. carolinensis. He believed the latter form to be distinct from, and in some localities sympatric with, D. ochrophaeus. This elevation of D. o. carolinensis to a full species was contested by Tilley (1969). Huheey and Brandon (1973) and Tilley (1973a, and in prep.) discuss the ecology of rockface populations.

Bishop (1941) thoroughly discussed the life history, reproductive habits, and general ecology of the species in the north. This information is summarized in his 1947 work, with a treatment of southern *D. ochrophaeus*. Some of his information on the larval color pattern and larval period has proved inaccurate (Tilley and Tinkle, 1968; Tilley, 1969 and 1973b). Conant (1958) and Cochran and Coin (1970) give general

accounts of taxa here referred to D. ochrophaeus.

Tilley (1972, 1973a, 1973b) summarized ecological work on the species and provided information on its embryology, brooding behavior, reproductive patterns, and population ecology in the southern Blue Ridge. He compared life history patterns and population structures at different elevations. Fitzpatrick (1973) provided information on the bioenergetics of the female reproductive cycle in northern populations, and concluded that individual females reproduced annually. A similar conclusion was reached by Tilley (1973b). Other in-

formation on the male and female reproductive cycles was provided by Pfingsten (1965, 1966), Collins (1964), Fisher (1964), and Telliard (1964). Gordon, et al. (1962) presented additional ecological information on the species. Organ (1961) presented data on courtship behavior, altitudinal distribution, habitat preferences, reproductive cycles, and population struc-ture of *D. ochrophaeus* in southwestern Virginia. He compared the life history and ecological characteristics of the species with those of other sympatric desmognathines. Tilley (1968) compared body size-fecundity relationships among five desmo-gnathines, including *D. ochrophaeus*. Wood and Wood (1955) discussed nesting habits in the southern Blue Ridge. Hairston (1949) described the vertical distribution and general ecology of D. ochrophaeus in the southern Blue Ridge and commented on taxonomic and evolutionary problems in the species. Bishop and Chrisp (1933) and Bishop (1941) described nesting habits and larvae in New York. Some of their observations were erroneous, as noted above. Pope (1924) described nesting and clutches in the southern Blue Ridge.

Batesian minicry may occur between red-cheeked and red-legged *Plethodon jordani* (the model) and red-cheeked and red-legged D. ochrophaeus (the mimic). The most recent papers are those by Orr (1967, 1968), Huheey (1960, 1966b),

papers are those by Orr (1907, 1900), funcey (1900, 1900), and Huheey and Brandon (1961). D. ochrophaeus and D. fuscus may hybridize along the southeastern escarpment of the Blue Ridge (Bruce, 1965). Martof and Rose (1963), Hairston (1949), King (1939), and Dunn (1926) also commented on the possibility of hybridization between the two forms.

• ETYMOLOGY. The prefix ochro- (Greek) means "yellow" and apparently refers to the yellow to brownish yellow colorations of some individuals, particularly females. The suffix -phaeus (Greek) means "light," perhaps in reference to the bright colorations of some individuals. The vernacular name used here is of the author's choosing.

COMMENT

The nomenclature used here follows Martof and Rose (1963) in recognizing neither D. o. carolinensis nor D. ocoee. In the southern Appalachians and probably in other parts of its range *D. ochrophaeus* is distributed discontinuously, on both a macro- and microgeographic scale. Gene flow between populations, some of which do exhibit distinctive character-istics, may frequently be minimal. The naming of species and subspecies, however, are arbitrary acts under such conditions, and do little to enhance our understanding of either this complex species or the complex phenomena that produced it.

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- STEPHEN G. TILLEY, SMITH COLLECE, NORTHAMPTON, MASSA-CHUSETTS 01060.

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