

AMPHIBIA: CAUDATA: PLETHODONTIDAE

DESMOGNATHUS WRIGHTI

Catalogue of American Amphibians and Reptiles.

Harrison, J.R., III. 2000. *Desmognathus wrighti*.

Desmognathus wrighti King
Pygmy Salamander

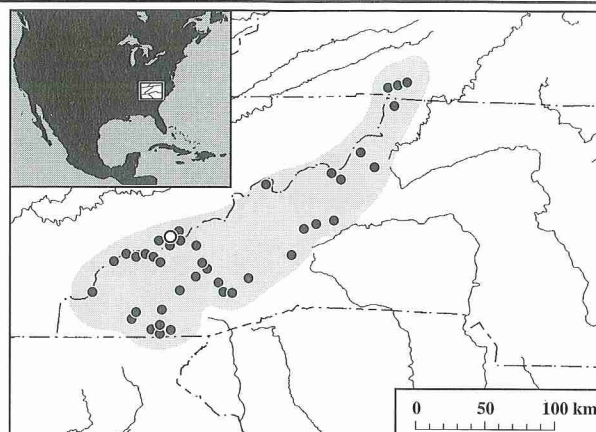
Desmognathus wrighti King 1936:57. Type locality, "... Mount LeConte, Sevier County, Tennessee, Great Smoky Mountains National Park ..." Holotype, National Museum of Natural History (USNM) 101794, adult male (46 mm TL), collected by Willis King (not examined by author); paratypes: USNM 101790–3 (the holotype was erroneously listed in this paratype series), 101795–802, Mt. LeConte; USNM 101803–4, Pecks Corner (Swain Co., NC); USNM 101805–6, Mt. Hardison (Swain Co., NC); USNM 101807–13, Brushy Lead; USNM 101813–4, White Rock, all collected by W. King; Cincinnati Soc. Nat. Hist. 789 (26 spec.), Newfound Gap (Swain Co., NC), collected by W.H. Weller and R. Dury.

• **CONTENT.** No subspecies are recognized, but see **Comment.**

• **DEFINITION.** *Desmognathus wrighti* is a small, moderately slender, round-tailed, terrestrial desmognathine salamander which lacks an aquatic larval stage. Maximum SVL (to anterior corner of vent) is 30 mm in both sexes (Harrison 1963). Most males attain sexual maturity at 17–19 mm SVL, females at 20 mm SVL. The tail is short and averages 13% (adult males) and 16% (adult females) shorter than SVL. Prevomerine teeth are usually retained in adults and average 8.8 (0–18) in males and 10.2 (3–16) in females. The mental hedonic gland cluster of this species, unique among desmognathines, is manifested externally as a large, bifurcate or u-shaped cluster lying within the curve of the lower jaw and extending posteriorly to the jaw hinges (Valentine 1963, Conant 1975, Sever 1976, Conant and Collins 1991). The cluster consists of two more or less discrete groups of five or six convoluted and elongate tubules, one group on each side of the gular area (Harrison 1963, Sever 1976).

The species is distinguished by a broad, bronzy or reddish brown to tan dorsal band, typically with a central herringbone or chevron-like pattern, and usually more reddish brown on the tail. Seventy-nine percent of 234 specimens examined by Harrison (1963) possessed the herringbone pattern; the remaining 21% had dark irregular markings, a row of dots, or lacked dark markings altogether. Dorsal band edges were strongly notched or spotted with remnants of the juvenile paravertebral spots (57%), or were regular (19%), irregular (18%), or obscure (6%). The dorsal band at the base of the tail had regular (44%) or irregular (56%) edges. The bronzy coloration of the dorsal band is produced by deep gold iridophores overlaid by both dark and pale reddish-orange pigment and widely scattered, small, white chromatophores. The venter of the trunk usually is unpigmented, but in most specimens (84%) is invaded to varying degrees by some pigment from the sides. In some specimens, the venter of the trunk is characterized by four separate and deep pale longitudinal gold bands. Much gold pigment is present on and around the heart and on the irises. Dorsal surfaces of head are rugose. The margin of the lower jaw is heavily mottled, contrasting sharply with the usually unpigmented throat (Bishop 1943). Geographical variation in morphometric features and patterns was discussed by Harrison (1963) and Crespi (1996).

Organ (1961b) described recently hatched young. These lack gills, have rounded tails, and differ in pattern from adults primarily by possessing well-defined paravertebral spots and a



MAP. Distribution of *Desmognathus wrighti*; the circle marks the type locality, dots indicate other records.



FIGURE. Adult *Desmognathus wrighti* from Stratton Gap, Graham County, North Carolina (photograph by R. Wayne Van Devender).

concentration of melanophores middorsally. The latter represent the anlagen of the adult herringbone pattern.

• **DIAGNOSIS.** Some individuals of *Desmognathus aeneus* have a middorsal herringbone or chevron-like pattern and are similar in size to *D. wrighti*. *Desmognathus aeneus*, however, typically has a pigmented venter, a tail longer than the SVL, relatively short limbs, smooth skin on the dorsum of the head, an occipital spot or blotch in many individuals, and a small reniform mental hedonic gland cluster (Harrison 1963, 1992). *Desmognathus wrighti* typically has an unpigmented venter, a tail shorter than the SVL, relatively long limbs, rough or rugose skin on the dorsum of the head, no occipital spot or one that is poorly developed, gold pigment on and around the heart and on the venter of the trunk, and a bifurcate or horseshoe-shaped mental hedonic gland cluster. Juveniles or subadults of the *D. ochrophaeus* complex (Tilley and Mahoney 1996), particularly *D. imitator* Dunn, *D. orestes* Tilley and Mahoney, *D. carolinensis* Dunn, and *D. ocoee* Nichols, could also be confounded with *D. wrighti*, as each species has a geographic range that includes populations of *D. wrighti*. However, such specimens typically lack a herringbone or chevron-like dorsal pattern, have a tail longer than the SVL, a pigmented venter, and would lack a mental hedonic gland cluster.

• **DESCRIPTIONS.** King (1936) described the type series of *Desmognathus wrighti* and compared the species with *D. fuscus carolinensis* (= *D. ochrophaeus carolinensis* sensu lato) and *D. f. ochrophaeus* (= *D. ochrophaeus*). Earlier, Weller (1931) provided a brief but accurate description of the species based on

100 specimens from the Great Smoky Mountains which he regarded as a juvenile, "ziczac" form of *D. fuscus carolinensis* (= *D. ocoee* Nichols). Bishop (1943) described adults and commented on habitat, geographic range, and reproduction. Harrison (1963) described and discussed variation in size, body proportions, patterns, egg production, osteology, dentition, and other structural characteristics and compared them with *D. aeneus*. Hinderstein (1969, 1971b) described head musculature and several morphometric features and compared them with those of other desmognathines. Means (1971, 1972) described the morphology of jaw and palatal teeth. Wake (1966) and Caldwell (1977) described osteological characteristics and Robinson (1968) included *D. wrighti* in his studies of plethodontid cranial morphology. Crespi (1996) described and discussed genetic variability and variation in several morphometric characteristics, number of yolk-filled ovarian eggs, number of testicular lobes, and ventral iridophore patterns. Petranks (1998) described both adults and hatchlings.

Brief descriptions of adults and/or statements concerning size were provided by Brimley (1944), Bogert (1954), Oliver (1955), Huheey (1966), Huheey and Stupka (1967), Cochran and Goin (1970), Leviton (1971), Behler and King (1979), Cochran (1982), Smith (1978), Halliday and Verrell (1986), Verrell (1990), Conant (1958, 1975), Conant and Collins (1991, 1998), and Redmond and Scott (1996).

Keys including *Desmognathus wrighti* were provided by Bishop (1943), Powell et al. (1998), Blair (1968), Whitaker (1968), and Ballinger and Lynch (1983). However, those of the last three sources could misidentify some specimens of *D. aeneus* as *D. wrighti*, as they assumed, in error, the absence of herringbone or chevron-like marks in the former species. *Desmognathus wrighti* has been listed in various catalogs and checklists, including those of Schmidt (1953), DePoe et al. (1961), Brame (1967), Gorham (1974), Dowling (1974), Frost (1985), and Banks et al. (1987). Details concerning the type specimen were provided by Cochran (1961).

• **ILLUSTRATIONS.** King (1936), Bishop (1943), Huheey and Stupka (1967), and Petranks (1998) provided black and white photographs of adults. Color photographs of adults were provided by Conant (1958, 1975), Conant and Collins (1991), Conant and Collins (1998), Freytag (1974), Martof et al. (1980), and Petranks (1998). Smith (1978) presented a color drawing. The color photograph of *Desmognathus aeneus* on Plate 94, presented in Behler and King (1979), is a misidentified *D. wrighti*; however, the color photograph of *D. wrighti* on Plate 66 is that species. Bogert (1954) and Conant and Collins (1998) included a line drawing of an adult. Crespi (1996) included photographs of dorsal and ventral pigmentation of specimens from 14 populations throughout the range. Organ (1961b) included black and white photographs of eggs with late embryos, eggs in the process of hatching, and hatchlings, and provided a line drawing of the spermatophore. Conant (1975) and Conant and Collins (1991) provided line drawings of an adult and the mental hedonic gland in comparison with similar illustrations of *D. aeneus*. Hinderstein (1969) illustrated dorsal and ventral views of the head musculature and dorsal, ventral, and lateral views of the skull, and a dorsal view of the head. Means (1974) provided a line drawing of the skull as seen in lateral view and a black and white photograph of the dentary teeth. Valentine (1963a) and Sever (1976) presented line drawings of the mental hedonic gland cluster, and Sever (1976) figured transverse sections. Organ and Lowenthal (1963) included line drawings of the spermatophore. Petranks (1998) included a black-and-white photograph of courting adults with the male depositing a spermatophore. Sever (2000) provided electron-micrographs of the spermatheca.

• **DISTRIBUTION.** *Desmognathus wrighti* is found primarily in isolated populations in high elevation forests of southwestern Virginia, western North Carolina, and eastern Tennessee. Populations are known from elevations ranging from approximately 762–2082 m. The species is characteristic of spruce-fir forests, but populations also occur at lower elevations in mesophytic hardwoods; those found east and south of the present range of spruce and fir may represent post-glacial relicts (Huheey 1966, Tilley and Harrison 1969, Rubin 1971, Bruce 1977) of a former more widespread distribution. Approximately two-thirds of the records shown by Huheey (1966) on a spot distribution map for Great Smoky Mountains National Park are from sites not harboring spruce-fir forest. He suggested that populations in areas of Great Smoky Mountains National Park southwest of Clingman's Dome are either warm-tolerant glacial relicts or perhaps a consequence of rapid recolonization. Tilley and Harrison (1969) and Rubin (1971) reported sympatry between *D. wrighti* and *D. aeneus* at two locations in the Nantahala Mountains of Macon Co., North Carolina. Bruce (1991) reported *D. wrighti* from the upper Nantahala River drainage, North Carolina, at elevations of 1000 m and higher, and sympatry with *D. aeneus* at elevations of 1000–1100 m in the same area. Tilley and Harrison (1969) also provided a spot map showing the distribution of the species in relation to areas supporting spruce-fir forest. Pague (1984) reported *D. wrighti* from Pine Mountain, Grayson Co., Virginia. Mitchell and Reay (1999) listed Virginia records, and provided a spot map showing distribution in that state. Redmond et al. (1990) described general distribution, listed Tennessee counties with records, and provided a spot map showing distribution in Tennessee. Redmond (1991) included *D. wrighti* in his study of Tennessee amphibian biogeography. King (1936, 1939) and Huheey (1966) gave records for Great Smoky Mountains National Park. Other localities were reported by King (1936), Bishop (1943), Hilton (1948), Hoffman and Kleinpeter (1948), and Green (1939). Seehorn (1982) listed the occurrence of *D. wrighti* in National Forests of the southeastern United States, but the inclusion of Cherokee National Forest, Tennessee in the range of the species has not been verified and may be in error. The record of *D. aeneus* from Transylvania Co., North Carolina (Martof and Rose 1963) was based on a misidentified *D. wrighti* (Harrison 1967, 1992). The occurrence of the species in seeps and spring heads in the mountains of Georgia as reported by Wharton (1978) has also not been verified. General statements concerning distribution and/or range maps were provided by Gentry (1955–1956), Leviton (1971), Freytag (1974), Smith (1978), Martof et al. (1980), Frost (1985), Conant (1958, 1975), and Conant and Collins (1991, 1998).

Desmognathus wrighti is a highly terrestrial species that is active under conditions of complete darkness and a saturated atmosphere. Individuals exhibit nearly complete scansorial behavior during their period of activity, climbing to heights of seven feet (= 2.1 m) on living or dead spruces (Hairston 1949). Mathews and Echternacht (1984) stated that on especially damp nights, either from rain or fog, *D. wrighti* may be found on leaves some distance from the ground. Weller (1931) noted that *D. wrighti* (as *D. fuscus carolinensis*) was abundant only under tightly fitting bark of stumps or standing trees at high elevations. King (1936, 1939) stated that the preferred habitat is under small logs and stones in moderately moist areas of spruce-fir forest. One hundred percent of *D. wrighti* observed by Hairston (1949) were in forest habitat with 76% of the individuals more than 200 feet from the nearest stream. Organ (1961a) demonstrated that this species abandons forest habitat in late fall and moves into underground seepage areas for hibernation in winter. In one such hibernaculum, he removed 649 individuals over a two-month period from mid-April to mid-

June. The winter specimens reported by Bruce (1977) from the Cowee Mountains also were found in an apparent hibernaculum, mud and loose gravel in the saturated bank of a seepage area. Hairston (1973) described the horizontal distribution of five desmognathine salamanders in two different mountain areas and postulated that the absence of *D. wrighti* at low elevations is a consequence of potential competition with congeners and lower moisture in forests away from streams. Southern Appalachian Man and the Biosphere (SAMAB) (1996) considered *D. wrighti* a member of a "Species Group 11," faunal and floral elements associated with seeps, springs, and streamside habitats. Inexplicably, however, the species was not included as a member of "Species Group 15," faunal and floral elements of high elevation spruce-fir/northern hardwoods.

• **FOSSIL RECORD.** None.

• **PERTINENT LITERATURE.** Hairston (1949) conducted studies of *Desmognathus wrighti* and other plethodontid salamanders in relation to vertical and horizontal distribution, activity, physical factors influencing distribution, and diet. Bogert (1952) observed relative abundance on White Top Mountain and Mount Rogers, Virginia, and measured substrate temperatures in diurnal shelters occupied by this species. Organ (1961a) included *D. wrighti* in his studies of local distribution, life history, and population dynamics of desmognathine salamanders in Virginia. Huheey and Stupka (1967) commented on predation by *Gyrinophilus* and a "black beetle." Bruce (1972) noted the occurrence of *D. wrighti* as an infrequent species associate of *Gyrinophilus porphyriticus* in the Balsam Mountains of Haywood and Jackson counties, North Carolina. Brandon and Huheey (1975) observed diurnal behavior in all of the desmognathine species they studied except *D. wrighti* and *D. aeneus*. Brodie (1977) reported an antipredator behavior unique among other desmognathines studied; when exposed or touched, *D. wrighti* flips and becomes immobile. Dodd (1990) provided data concerning the influence of temperature and body size on duration of immobility. Hairston (1973, 1980, 1986, 1987) included *D. wrighti* in his studies of interspecific relationships of desmognathine salamanders in relation to abundance, microhabitat segregation, competition, and predation. Bruce (1991) considered *D. wrighti* in his commentary on the evolution of ecological diversification in desmognathine salamanders. Petranks et al. (1993) reported that *D. wrighti* had a 30% frequency of occurrence in 47 sample plots in their study of the effect of timber harvesting on salamanders (but see Ash and Bruce 1994). Singer et al. (1982) reported no significant difference in numbers of *D. wrighti* and four other salamander species between northern hardwoods stands rooted by hogs and stands that were not rooted. However, they did not report that only *D. wrighti* declined significantly as cited by Mathews and Echternacht (1984). Kuken et al. (1994) found that, in a stream contaminated by sulfuric acid and heavy chemicals from the Anakeesta Formation, stream-breeders were almost entirely eliminated, whereas terrestrial breeders, including *D. wrighti*, increased in numbers. Peele (1992) observed behavioral interactions between *D. wrighti*, *D. ochrophaeus*, and *D. aeneus*. Bruce (1996) included *D. wrighti* in his study of interspecific variation in age at first reproduction, fecundity, and body size in multispecies assemblages of desmognathine salamanders.

Brooks (1948), Organ (1961b), Houck (1980), and Verrell (1999) described courtship behavior. Brock and Verrell (1994), Verrell (1997), and Verrell and Mabry (2000) presented information concerning the courtship pattern. Houck and Sever (1994) discussed the relationship of mental glands to reproduction and behavior, including failure of the *D. wrighti* mental gland, while pulling and snapping, to deliver courtship phero-

mones. However, Sever (1976) indicated that *D. wrighti* is novel in that mental gland pores deliver secretions at the base of the elongated mandibular teeth. Promislow (1987) noted similarities between the courtship of *D. wrighti* and *D. aeneus*, including a "biting phase" not known to occur in other desmognathines. Verrell (1994), however, noted that a "bite-and-seize" courtship behavior pattern, observed consistently in *D. wrighti* and *D. aeneus*, was also observed in *D. imitator*, but not consistently and with differences. Houck and Verrell (1993) included *D. wrighti* in their review of courtship behavior in plethodontid salamanders. Valentine (1963) and Harrison (1963) briefly described the mental hedonic gland cluster, but Sever (1976) described this structure in detail and compared it with that of other plethodontids. Sever (1983, 1991, 1994a) included *D. wrighti* in his studies of cloacal anatomy and the phylogeny of salamander cloacae. Sever and Trauth (1990) described the cloacal anatomy of females and noted that, unlike other desmognathines, both *D. wrighti* and *D. aeneus* lack cloacal glands other than spermathecae. Sever (1994b) studied regionalization of secretory activity in the spermatheca and commented on the phylogeny of sperm storage. Sever and Hamlett (1998) studied the alignment of sperm in the spermatheca. Wortham et al. (1977) described the morphology of spermatozoa and stated that the spermatozoa of *D. wrighti* were the third longest among those of seven species of desmognathine salamanders examined, and differ from those of *D. aeneus* in all spermatozoan dimensions. Houck et al. (1985) reported *D. wrighti* as one of several plethodontids capable of multiple inseminations. King (1936) reported a female with oviducal eggs and females with enlarged ovarian eggs in September. Organ (1961b) provided information on a nest site, egg masses and attending females, the hatching process, hatchlings, courtship, and the spermatophores. Organ and Loewenthal (1963) mentioned size and appearance of the spermatophores. Valentine (1963b) compared the morphology of hatchling *D. aeneus chermocki* to those of *D. wrighti*.

Salthe (1969) noted that *Desmognathus wrighti* has direct development, but the smallest ovum size of his reproductive Mode III. Wake and Marks (1993) mentioned the species in their review of studies of development in plethodontid salamanders. Collazo and Marks (1994) included for comparison one *D. wrighti* egg cluster in their study of the ancestral plethodontid developmental pattern. Rose (1995) examined four embryos and found that this species has apparently lost the 4th ceratobranchial. Collazo (1996) included *D. wrighti* in his study of evolutionary correlations between early development and life history in plethodontid salamanders and teleostean fishes. Nussbaum (1985) listed the species as one with parental care (embryo guarding) in a terrestrial nest site. However, known nest sites were located in an underground seepage area (Organ 1961a, 1961b). Tilley and Bernardo (1993) included *D. wrighti* in their review of studies of plethodontid life histories.

Uzzell (1961) observed that 3 of 11 adult *Desmognathus wrighti* had some calcification in basibranchial 1. Brame (1962) and Dyrkacz (1981) reported an albino specimen from Great Smoky Mountains National Park. Hinderstein (1969, 1971b) included this species in studies of the desmognathine jaw apparatus and head musculature. Edwards (1976) included *D. wrighti* in a study of spinal nerves and their bearing on salamander phylogeny. Lopez and Brodie (1977) included the species in a study of costal groove function. Wake et al. (1987) noted the presence of a much reduced lateral line system in *D. wrighti* and *D. aeneus*. Caldwell (1980) included *D. wrighti* in a study of lens morphology as an identification tool for desmognathine salamanders; this species and *D. aeneus* have the lowest number of radii per lens quadrant. Halley et al. (1986), Sessions and Larson (1987), and Licht and Lowcock (1991) included *D. wrighti* in their studies of genome size in salamanders. Villolobos et al.

(1988) noted the presence of nucleated erythrocytes in *D. wrighti*. Rubenstein (1971) suggested that cranial osteology provided no evidence for paedomorphism in this species or in *D. aeneus*.

• **REMARKS.** The standardized common name for *Desmognathus wrighti* is "Pygmy Salamander" (Conant et al. 1956; Collins et al. 1978, 1982; Collins 1990). Brimley (1944), however, used the common name "Wright's Desmognath."

The SSAR Montetary Value of Amphibians Subcommittee (1989) assigned a value of \$1.00 per specimen of *Desmognathus wrighti*.

LeGrand and Hall (1995) placed *Desmognathus wrighti* in category W5 of North Carolina's "Watch List," species with increasing amounts of threats to their habitats. In Tennessee, *D. wrighti* is regarded as a species in need of management (Tennessee Wildlife Resources Agency 1994) and has been assigned a rank of S2, rare and imperiled within the state (Withers 1996). Pague and Mitchell (1987) reviewed the status of *D. wrighti* in Virginia and concluded that it should be considered rare in Virginia. Mitchell (1991) and Pague (1991) listed *D. wrighti* as a species of special concern.

• **ETYMOLOGY.** The specific epithet is a patronym honoring George M. Wright, a former Chief of the Wildlife Division, National Park Service.

• **COMMENT.** *Desmognathus wrighti* is currently regarded as a monotypic species. Brown and Bishop (1947) suggested that it has close affinities with *D. ochrophaeus* and *D. aeneus*. Neill (1950) stated that *D. wrighti* and *D. aeneus* are probably but subspecifically distinct. Dean (1959) derived *D. wrighti* successively from an "*ochrophaeus*" and a "pygmy" archetype based on his studies of amino acid chromatograms. Hairston (1949, 1987) and Organ (1961a) viewed *D. wrighti* as the terminal desmognathine species in an ecological and evolutionary progression toward complete terrestriality. Folkerts (1968) attributed the evolution of *D. wrighti* to derivation from an *ochrophaeus*-like stock through miniaturization with subsequent removal to higher elevations. Tilley (1968) included this species in his analysis of size-fecundity relationships and their evolutionary implications in five desmognathine salamanders. Hinderstein (1969, 1971a) placed (provisionally) *D. wrighti* and *D. aeneus* in his species Group III based on lactate dehydrogenase electrophoresis. Caldwell (1977) concluded, from studies of desmognathine cranial osteology, that *D. wrighti* is closely related to *D. aeneus*, but has a unique skull. He also stated that *D. wrighti* appeared more advanced than *D. aeneus*, and has diverged considerably from that species. Sweet (1980) included *D. wrighti* in his study of allometry, life history, and evolution of desmognathine salamanders. Promislow (1987) mentioned (as pers. comm.) preliminary electrophoretic studies of Steve Tilley showing that *D. wrighti* is significantly differentiated from *D. aeneus* and other desmognathines. Bruce (1991) hypothesized that *D. wrighti* and *D. aeneus* have derived life histories, evolved in the same environment as that of the aquatic desmognathines, but exhibited opposite trends, leading to direct development and miniaturization. Wake (1992) included *D. wrighti* as one of several species he considers as "miniaturized plethodontids." Titus and Larson (1996) found that *D. wrighti* is the sister taxon to all other desmognathines based on their analysis of mt-DNA sequences and 13 morphological and reproductive characters. They suggested that the species' small size, terrestriality, and direct development are ancestral rather than derived characters. Crespi (1996) found large genetic distances between two geographically separate clusters of populations, suggesting that *D. wrighti* as currently recognized is not monotypic, but instead a complex of two different allopatric species.

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