

**Catalogue of American Amphibians and
Reptiles 925**

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Desmognathus monticola.

***Desmognathus monticola* Dunn
Seal Salamander**

Salamandra phoca Matthes 1855:273. *Lapsus*.
See **Comments**.

Desmognathus monticola Dunn 1916:73.
Type locality, "Elk Lodge Lake, near Brevard, [Transylvania County,] North Carolina; altitude about 3000 feet." Holotype, National Museum of Natural History (USNM) 38313, an adult male, collected 13 July 1908 by R. Tipping and E. Tipping (not examined by authors).

Desmognathus monticola Dunn 1918b:463.

Incorrect attribution. See **Comments**.

Salamandra phoca: Dunn 1923:39.

Desmognathus phoca: Dunn 1926:73.

Desmognathus fuscus fuscus: Netting 1933a:105. Incorrect attribution. See **Comments**.

Desmognathus phoca: Netting 1935:43. Incorrect attribution. See **Comments**.

Desmognathus phoca: Hibbard 1936:279. Incorrect attribution. See **Comments**.

Desmognathus phoca: Scharlinski 1939:57. Incorrect attribution. See **Comments**.

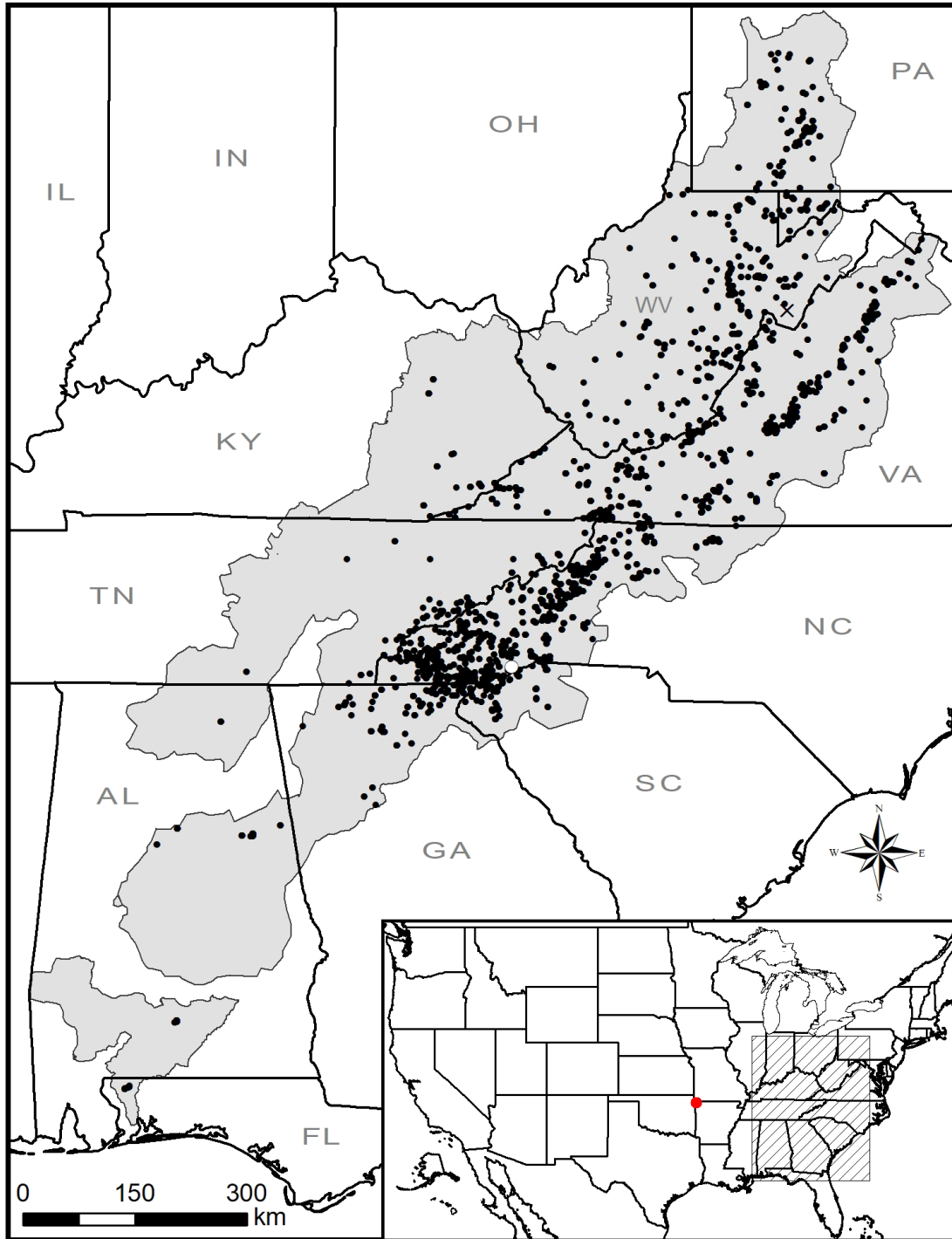
Desmognathus phoca: Yoder 1940:91. Incorrect attribution. See **Comments**.

Desmognathus monticola: Grobman 1945:39.

Desmognathus monticola jeffersoni: Hoffman 1951:250. Type locality, "Saddle Hollow on Jarman's Mountain, 2 miles west of Crozet, Albemarle County, Virginia (elevation 1600 feet)." Holotype, USNM 126891, an adult, collected 11 March 1945



FIGURE 1. An adult *Desmognathus monticola* from Macon County, North Carolina. The blunt snout and bulging eyes that characterize the head give the salamander a seal-like appearance. Photo by Todd Pierson.



MAP. Geographic distribution of *Desmognathus monticola* in the eastern United States. Gray shading indicates the range with a periphery defined by watershed boundaries. The white circle marks the type locality, the "x" marks the two closely adjacent fossil localities, and the black dots represent voucher specimens in major museum collections (n = 9921). Coordinates associated with specimens were obtained from iDigBio (idigbio.org; accessed 30 June 2017) and VertNet (vertnet.org; accessed 12 December 2017), and then verified using county-level distribution maps in state and regional publications (see Distribution and Comments sections). Note the isolated population in the western panhandle of Florida. A red dot in the inset map marks an introduced population in the Ozark Plateau of Arkansas.

by R. L. Hoffman (not examined by authors).

Desmognathus monticola monticola: Hoffman 1951:251.

Desmognathus monticolus: Spight 1967:128. *Lapsus*.

Desmognathus monticola: Hulse et al. 2001:81. Incorrect attribution. See **Comments**.

Desmognathus monticola: Rissler and Taylor 2003:201. Incorrect attribution. See **Comments**.

Desmognathus monticola: Graziano and Reid 2006:6. Incorrect attribution. See **Comments**.

Desmognathus monticola: Beamer and Lamb 2008:147. Incorrect attribution. See **Comments**.

Desmognathus (Desmognathus) monticola: Dubois and Raffaëlli 2012:144.

CONTENT. No subspecies are currently recognized, however, two subspecies were described (see **Nomenclatural History**).

DESCRIPTION. Ova are nonpigmented and deposited in clusters of 13–40. Egg suspension cords are relatively long and their attachment points are often visible. Four epi-branchial placodes are associated with the embryonic pharyngeal arches. Hatchling larvae range from 11–20 mm total length (TL), lack balancers, and have narrow, cylindrical, pointed digits (four on forelimbs, five on rear limbs). Mandibular grooves bisect the lower lip anteriorly, and the tail fin originates at the tail-body junction. Gill rami of larvae are relatively short and mound-like with 16–17 filiform fimbriae bilaterally. The medium brown dorsum has four to five pairs of prominent, red dorsolateral spots between the limb in-



FIGURE 2. A juvenile *Desmognathus monticola* from Indiana County, Pennsylvania. The dorsum of a typical juvenile has four or five pairs of orange, reddish-orange, or chestnut-colored spots bordered by darker pigments. A pale line extends from the eye to the angle of the jaw, but this characteristic is often obscured by dark pigments in older individuals. Photo by Kurt Regester.

sertions. The underside of the tail is diffusely blotched. Larvae have keratinized toe tips and metamorphose at 35–50 mm TL. In young juveniles, the four or five pairs of dorsal spots between the limb insertions are orange, reddish-orange, or chestnut-colored, and the venter is whitish or pale. Dorsal spots are invaded by darker pigment, and the ventral surface becomes increasingly gray with age.

The head of both adult and juvenile salamanders is proportionally large relative to body size. The head is characterized by a blunt snout, bulging eyes, and mottling with small brown and black spots on the dorsal surface. A pale line extends from the eye to the angle of the jaw. A tubercle in the anterior angle of the eye and a gular fold are present. The rear limbs are proportionally longer and more robust than the forelimbs. The relative lengths of the forelimb digits are $I < IV < II < III$; relative lengths of the rear limb digits are $I < II < V < IV < III$. The distal regions of the digits have keratinized friction pads that give a darkened appearance to the tips of the toes. The trunk of the body has 14 costal grooves. Two intercostal folds between the adpressed limbs are typical for young individuals, whereas three intercostal folds are typical for adults. The proximal portion of the tail is round. The distal two-thirds of the tail are laterally compressed and distinctly keeled.

Dorsal and ventral colorations are clearly demarcated. The venter has uniformly spaced melanophores, appears pale, and lacks conspicuous mottling. A line of small, irregularly shaped white spots is often present on the lower sides of the body between the fore and rear limbs. The dorsum is light brown or grayish in background color and may have reticulated patterning. Dark brown or black mottling and worm-like markings are typically present; in most individuals, these markings extend to the dorsolateral surfaces of the body and dorsal surface of the tail. In the Blue Ridge Mountains physiographic province, dark dorsal markings may be reduced to scattered, round spots. Patterns of pigmentation

are obscured as the background color of the dorsum becomes darker with age. Mottling and color patterns are highly variable among individuals, and are markedly reduced or absent in many populations. Albino specimens have been reported (Brame 1962; Houtcooper 1979, 1981).

Desmognathus monticola is a moderately long and heavy-bodied salamander (45–80 mm snout–vent length [SVL], 75–150 mm TL). The maximum size of adult males commonly exceeds that of females. Adult males can be distinguished from females by the presence of enlarged premaxillary teeth, papillose cloacal lips, a slightly more flexuous outline of the jaw, and an inconspicuous mental gland. The testes are unpigmented. Vomerine teeth are not lost by males following sexual maturity. The vomerine teeth form two short, slightly arched series that approximate each other along the median line. The parasphenoid teeth, which occur in long, narrow series, are well separated but confluent anteriorly.

DIAGNOSIS. In contrast to *Desmognathus monticola*, eggs deposited by *Desmognathus folkertsi*, *Desmognathus marmoratus*, and *Desmognathus quadramaculatus* have short suspension cords and they appear tightly attached to the substrate. Published sources lack sufficient information for the positive identification of eggs from those of sympatric congeners. The identification of an attending parent can serve for field identification. Information on species-specific distributions and microhabitat preferences will generally facilitate diagnoses of all life stages.

Larval *Desmognathus monticola* have keratinized toe tips and four or five dorsolateral spots are present on the dorsum. Larval life stages of *Desmognathus abditus*, *Desmognathus carolinensis*, *Desmognathus imitator*, *Desmognathus ochrophaeus*, *Desmognathus ocoee*, and *Desmognathus orestes* do not have keratinized toe tips; the dorsum of those species may be uniformly reddish to brown,

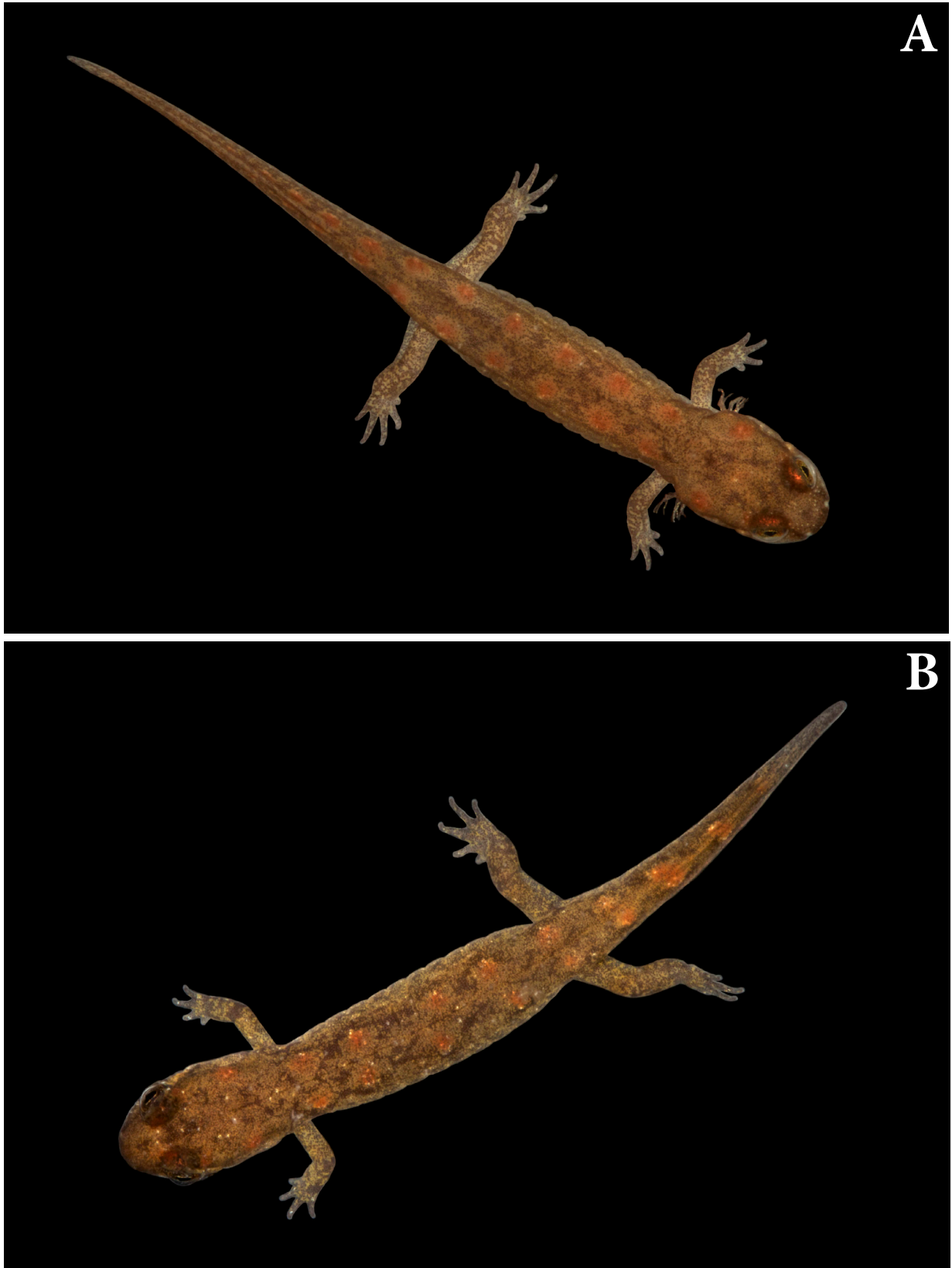


FIGURE 3. Larval and recently metamorphosed *Desmognathus monticola* from Oconee County, South Carolina. (A) The dorsum of a typical larva has four or five pairs of prominent dorsolateral spots between the limb insertions. Larvae possess relatively short gill rami and have cylindrical, pointed digits with keratinized toe tips. (B) The spots of a recently metamorphosed individual are typically bordered by dark pigments. Photos by Todd Pierson.

patterned with 2–7 dorsolateral spots, or patterned with dorsolateral spots and a lateral stripe. Larvae of several congeners typically have a greater number of dorsolateral spots, including *Desmognathus auriculatus* (7–9), *Desmognathus conanti* and *Desmognathus fuscus* (5–13), *Desmognathus folkertsi* and *Desmognathus quadramaculatus* (6–8), and *Desmognathus welteri* (5–8). Additional characteristics can be used to diagnose larvae of *Desmognathus monticola* from those of sympatric congeners. *Desmognathus monticola* does not have black stripes along the lateral margins of the dorsolateral spots (present in *Desmognathus conanti* and *Desmognathus fuscus*) or white spots associated with the lateral line pores (present in *Desmognathus folkertsi* and *Desmognathus quadramaculatus*). *Desmognathus monticola* has fewer costal grooves (14) than *Desmognathus santeetlah* (16), and a less prominent white line from the eye to angle of the jaw. Unlike the wide head of *Desmognathus monticola* that appears rounded in dorsal view, the relatively narrow head of *Desmognathus marmoratus* appears strongly pointed. Further, the gills of *Desmognathus monticola* are colored similarly to its brown body whereas the pale gills of *Desmognathus marmoratus* contrast markedly with its darker body color. The gills of *Desmognathus monticola* possess 16–17 gill fimbriae per side, compared to a greater number of gill fimbriae in *Desmognathus welteri* (17–27) and *Desmognathus auriculatus* (22–40). In contrast to the medium brown body color and prominent red-orange spots on the dorsum of larval *Desmognathus monticola*, the body of *Desmognathus welteri* is uniformly green to brown and the rows of dorsolateral dots are faint; the body of *Desmognathus auriculatus* is darkly pigmented and the dorsolateral spots are pale.

Adult *Desmognathus monticola* are relatively large (7.5–15 cm TL) and have keeled tails. Adults of several sympatric congeners are generally smaller (≤ 10 cm TL) and have

tails that are round or oval in cross section for their entire length (*Desmognathus aeneus*, *Desmognathus abditus*, *Desmognathus carolinensis*, *Desmognathus imitator*, *Desmognathus ochrophaeus*, *Desmognathus ocoee*, *Desmognathus orestes*, *Desmognathus organi*, and *Desmognathus wrighti*). Among congeners with keeled tails, *Desmognathus monticola* is characterized by internal nasal openings that are circular. The head is not distinctly flattened, possessing a gradual slope starting at the eyes. The venter is uniformly colored white to light gray, and gray-black friction pads cover the tips of the digits. *Desmognathus marmoratus* has slit-like internal nasal openings, a distinctly flattened head (slope starting behind the eyes), and a dark gray to black venter. *Desmognathus quadramaculatus* and *Desmognathus folkertsi* also have darkly colored toe tips. However, they can be diagnosed by their black bellies and two rows of light, distinctly round spots along the lower lateral surface between the limbs. The tips of the digits in *Desmognathus auriculatus*, *Desmognathus conanti*, *Desmognathus fuscus*, and *Desmognathus santeetlah* lack friction pads and thus appear white or light gray; the ventral surfaces of those species range from light gray to gray-brown to black. *Desmognathus welteri* lacks bold markings on the dorsum and a distinct demarcation between the dorsal and ventral colorations. The venter of *Desmognathus welteri* lacks uniformity, being slightly mottled in juveniles and heavily mottled with brown in older individuals. The proximal third of the tail is evenly rounded in *Desmognathus monticola* whereas the base of the tail in *Desmognathus welteri* is laterally compressed.

PHYLOGENETIC RELATIONSHIPS. Most *Desmognathus*, including *Desmognathus monticola*, have an aquatic larval stage. However, they are nested in a clade of direct-developing species indicating a major life-history reversal from direct development to an



FIGURE 4. An adult *Desmognathus monticola* from Johnson County, Tennessee with eggs. The rear limbs are proportionally longer and more robust than the forelimbs. The proximal portion of the tail is round; the distal two-thirds of the tail are laterally compressed and distinctly keeled. Photo by Scott Bolick.

aquatic larval stage (Chippindale et al. 2004). *Phaeognathus* is the sister taxon to *Desmognathus*, and Pygmy salamanders (*Desmognathus wrighti* and *Desmognathus organi*) are sister to the clade including all other members of *Desmognathus*. At least three sister taxa to *Desmognathus monticola* have been proposed based on mitochondrial DNA, nuclear DNA, morphological, and reproductive character data: *Desmognathus apalachicola* (Titus and Larson 1996), *Desmognathus carolinensis* (Pyron and Wiens 2011; Rissler and Taylor 2003), and *Desmognathus ocoee* (Beamer and Lamb 2008; Kozak et al. 2005; Martin et al. 2016; Shepard et al. 2016).

Populations assigned to *Desmognathus monticola* typically form a well-supported clade and have relatively low genetic variation across much of their distribution. Populations within the Appalachian Highlands and Al-

legheeny Plateau range are relatively uniform in haplotype diversity and represent a lineage associated with a northward post-Pleistocene range expansion from the southern highlands of the Appalachian Mountains (Beamer and Lamb 2008; Kozak et al. 2005; Rissler and Taylor 2003). Several southern populations occur in historical refugia, where greater than 50% of haplotype diversity is restricted to less than 3% of the current distribution (Bonett et al. 2007). Haplotypes from an introduced population in Arkansas are identical to those from Lumpkin, Towns, Union, and White counties in northeastern Georgia (Bonett et al. 2007).

PUBLISHED DESCRIPTIONS. Descriptions were provided by Anonymous (1987), Ashton and Ashton (1988), Barbour (1971), Bartlett (1989), Bartlett and Bartlett (1999),

Beane et al. (2010), Behler and King (1979, 1985, 1988), Bishop (1943, 1947, 1962, 1967, 1969, 1994), Camp (2008), Camp and Tilley (2005), Catlin (1984, 1992), Conant (1958, 1975), Conant and Collins (1991a, 1991b, 1998), Dodd (2004), Dunn (1916, 1917a, 1917b, 1918a, 1926, 1972), Folkerts (1986), Freytag (1960, 1961, 1967), N. Green and Pauley (1987), Houtcooper (1979), Huheey and Stupka (1967), Hulse et al. (2001), Klingelhöffer (1956), Martof et al. (1980), Matsui (1993), Means (1978, 1992), J. Mitchell and Gibbons (2010), Mount (1975, 1996), Mount et al. (1984), Murray (2018), Nerz (2011), Petranka (1998), Powell et al. (2016), Raffaëlli (2007, 2013), Tilley and Huheey (2001), Valentine (1963, 1967), Wallays (2006) and Wyckoff and Niemiller (2011). Descriptions of eggs and larvae were provided by Altig and McDiarmid (2015).

ILLUSTRATIONS. Various life stages of *Desmognathus monticola* have been photographed or illustrated: **eggs** (Petranka 1998), **larvae** (Altig and McDiarmid 2015; Ashton and Ashton 1988; Camp 2008; Dodd 2003; J. Mitchell and Gibbons 2010; Noble 1931, 1954; Petranka 1998; Wyckoff and Niemiller 2011), **juveniles** (Conant 1958, 1975; Conant and Collins 1991a, 1991b, 1998; Powell et al. 2016), **adults in black-and-white** (Freytag 1967; Harrison 1950a, 1950b; Hoffman 1951; Krysko et al. 2011; Mansueti 1947; Means 1978, 1992; Mount 1975, 1996; Nerz 2011; Obst et al. 1984, 1988; Petranka 1998), and **adults in color** (AmphibiaWeb 2019; Ashton and Ashton 1988; Barbour 1971; Bartlett and Bartlett 1999, 2006; Beane et al. 2010; W. Brown et al. 2003; Camp 2008; Cassie 1999;

Coborn n. d., 1996; H. Collins 1959, 1981; Dodd 2004; Folkerts 1986; D. Green et al. 2013; N. Green and Pauley 1987; Hennessy 2016; Herrmann 2000, 2001; Hulse et al. 2001; J. Mitchell 1977a; J. Mitchell and Gibbons 2010; J. Mitchell et al. 2006; Pauley 2004; Petranka 1998; Pingleton and Holbrook 2019; Powell et al. 2016; Rimpp 1985; Shaffer 1991, 1995; Shupe 2018; H. Smith 1978; Staniszevski 1995; Wyckoff and Niemiller 2011). Additional relevant photographs documented **habitat** (King 1939) and **predation** (Bernardo and Yoke 2006; Lawhorn et al. 2017).

Photographs of several cellular and anatomical characteristics have been published: **femur histology** (Laurin et al. 2009), **mental gland histology** (Sever 1976), **nasal gland morphology** (Dawley 2017), **nuclear materials** (Hally et al. 1986), **spermatozoa morphology** (Wortham et al. 1982), **toe morphology and histology** (Caldwell and Trauth 1979), and **tooth morphology** (Matson et al. 2010; Means 1974).

Species characteristics have been illustrated in line drawings of the **adult dorsal pattern** (Allyn 1952, 1956, 1961, 1977; N. Green 1969), feeding (Lombard and Wake 1977; Pough et al. 1998, 2016); **skull** (Caldwell 1977; Means 1974; Rubenstein 1971), **spermatophore** (Noble and Weber 1929; Organ and Lowenthal 1963), **tail cross section** (Powell et al. 1998, 2012, 2019), and **teeth** (Caldwell 1977; Caldwell and Trauth 1979; Noble 1927).

DISTRIBUTION. *Desmognathus monticola* has a broad geographic range through the central and southern Appalachian Mountains of North America. Most populations occur

FIGURE 5 (facing page). Variation in coloration and pattern in metamorphosed *Desmognathus monticola*: (A) Graham County, North Carolina, (B) Macon County, North Carolina, (C) Macon County, North Carolina, (D) Caldwell County, North Carolina, (E), Indiana County, Pennsylvania, (F) Graham County, North Carolina, (G) Indiana County, Pennsylvania, and (H) Oconee County, South Carolina. The dorsal pigmentation pattern of the typical adult is increasingly obscured with age by a dark background coloration (G–H). Photos by Carter Ricks (A, B), Todd Pierson (C, D, H), Chris Bortz (E), Stephen Tilley (F), and Edwin Patterson (G).



at elevations between ~400–1400 m, but as high as 1700 m. The continuous portion of the range extends from western Pennsylvania southward to West Virginia, western Maryland and western Virginia, eastern Kentucky and eastern Tennessee, western North Carolina and northwestern South Carolina, northern and central Alabama, and northern Georgia, USA. Disjunct populations occur on the coastal plain of southern Alabama and the westernmost region (Escambia County) of the panhandle of Florida, USA. An introduced population occurs on the Ozark Plateau of Arkansas, USA (Bonett et al. 2007), where salamanders were most likely relocated for use as fish bait.

Distribution maps were provided by Ashton (1978), Barbour (1971), Bishop (1943, 1947, 1962, 1967, 1969, 1994), Caldwell (1977), Camp (2008), Camp and Tilley (2005), Conant (1958, 1975), Conant and Collins (1991a, 1991b, 1998), Dunn (1917b, 1926, 1972), Freytag (1974, 1984), D. Green et al. (2013), Grobman (1945), Hoffman (1951), J. Mitchell and Gibbons (2010), Petranka (1998), Powell et al. (2016), H. Smith (1978), and Stevenson (1976). **Regional maps** were provided by Beane et al. (2010), Camp (2008), Folkerts (1986) Franz (1972), N. Green and Pauley (1987), Harris (1969, 1975), Huheey (1966), Hulse et al. (2001), McCoy (1982), Means (1978, 1992), J. Mitchell (1977a), J. Mitchell and Gibbons (2010), J. Mitchell and Reay (1999), Shaffer (1991, 1995), Tobey (1985), Williamson and Moulis (1979), and Wyckoff and Niemiller (2011). A map of records in the Great Smoky Mountain National Park, Tennessee was given by Huheey (1966).

Desmognathus monticola inhabits mesic hardwood forests. Habitats are characterized by seeps and low order streams providing cool, well-aerated water and abundant cover. Metamorphosed individuals are found under woody debris and stones located outside the main flow of water, and typically below headwaters of seeps. Adults use larger cover

objects than juveniles. Small individuals are frequently found in the interstitial spaces of streambed substrates and among layers of leaf litter. Areas adjacent to seeps and streams are also used by salamanders; these include streamside burrows, crevices on the faces of moist cliffs, and forest leaf litter. During and following periods of precipitation, individuals have been observed 1–2 m above ground, positioned upon the trunks of trees.

FOSSIL RECORD. Fossils dated to the Pleistocene Epoch have been reported from two caves in Pendleton County, West Virginia (Holman 1995, 2006). A single vertebra from Hamilton Cave was described and associated with the Irvingtonian North American Land Mammal Age (NALMA) (Holman and Grady 1989). Two fossils of 13 and 5 vertebrae were described from New Trout Cave and associated with the Rancholabrean NALMA (Holman and Grady 1987). The convex or flattened posterior end of the vertebral neural arch was used for species-level identification (Holman 2006).

PERTINENT LITERATURE. Published references to the species are listed by topic: **acidification** (Little et al. 1991; J. Mitchell 1999; Roudebush 1988, 1989), **adult habitat** (Bickert 1969; Camp 1997a; Hairston 1949; Kleeberger 1985; Krzysik 1979; Organ 1961; Tilley 1973, 1980), **aggression** (Camp 2003; Jackson and Cupp 1997; Keen and Sharp 1982, 1984; Nelson 1979; Southerland 1986a), **albinism** (Brame 1962), **antipredator behavior** (Brodie 1978; Dodd and Brodie 1976; Fauth 1996; Hensel and Brodie 1976; Howard and Brodie 1973), **bait trade** (Cogger et al. 2002, 2004; Freytag 1974, 1984; Jensen and Waters 1999, 2000; Martof 1953), **behavior** (Forester 1978; Gordon et al. 1962; Mabry and Verrell 2004; Mathis et al. 1995; Rissler et al. 2004; Shupe 2018; Soler 1950), **biochemical genetics** (Beamer 2015; Beamer and Lamb 2008; Bernardo et al. 2007; Bonett et al. 2007; Casey

2002a; Chippindale et al. 2004; Goin and Goin 1971; Integrated Taxonomic Information System 2017; Kozak 2005; Kozak et al. 2005; Larson et al. 2003; Martin 2015; NCBI 2017; Pyron and Wiens 2011; Rissler 2000; Rissler and Taylor 2003; Rissler et al. 2004; Rovito 2009; Tilley 1997, 2016; Tilley et al. 2008a; Titus and Larson 1996), **biogeography** (Redmond 1991), **biomass** (Crawford and Peterman 2013; Hairston 1987; Woodall and Wallace 1972), **blood** (Davic and Gallati 1979; Reynolds and Pickard 1973; Vernberg 1955; Villolobos et al. 1968), **body size** (Beachy and Bruce 1999; Bruce 1987; Davic 1983), **body temperature** (Brattstrom 1963), **breeding season** (Organ 1961; Tilley 1968, 1973, 1977), **cell size** (Roth et al. 1994), **chemical cues** (Brown and Martof 1966; Forester et al. 2000; Jacobs and Taylor 1992; Kats and Dill 1998; Moberly 2012; Roudebush and Taylor 1986a, 1987b; Southerland 1986a; Steffen 2015), **citation for original description** (Beltz 1995), **climate change** (Bernardo and Spotila 2006; Bernardo et al. 2007; Dodd 1997; Grant et al. 2010; Grover 2000; Hamed 2014; Hoffacker et al. 2018; Keitzer and Goforth 2013; Markle and Kozak 2018; Milanovich et al. 2015), **cloacal anatomy** (Sever 1994a; Sever and Trauth 1989, 1990), **clutch attendance** (Bannikov 1969; Bruce 1996; Camp 1997a; Nussbaum 1985, 1987, 2003; Organ 1961; Pope 1924), **clutch size** (Bruce 1990b, 1996; Camp 1997a; Folkerts 1968; Organ 1961; Pope 1924), **common and scientific name checklists** (Banks et al. 1987; J. Collins 1990, 1997; J. Collins and Taggart 2002, 2009; J. Collins et al. 1978, 1982; Comité sur les Français Standardisés 2012; Conant et al. 1956a, 1956b; Crother et al. 2001; Fouquette and Dubois 2014; Freytag 1974, 1984; Highton et al. 2001, 2017; Hutchins et al. 2003; Schmidt 1953, 1954; Stejneger and Barbour 1917, 1923, 1933, 1939, 1943; Tilley et al. 2008b, 2012), **communities** (Beachy 1994; Bishop 1926; Bruce 1972, 1985, 1986, 2011; Dunn 1924; Hairston 1980a, 1987; Jaeger and Walls 1989; Martof and Rose 1962; Pough et al. 1998; Resetarits 1991; Schwartz 1954, 1957; Sever et al. 1976; Southerland 1985; Spohn and Sattler 1990), **competition** (Brandon and Huheey 1971; Hairston 1981; Hoffacker et al. 2018; Kleeberger 1983, 1984), **conservation** (Bailey et al. 2006; Millsap et al. 1990), **costal grooves** (Highton 1957), **critical thermal maxima** (Hutchison 1961; Layne 1984; Layne and Claussen 1987; Markle and Kozak 2018; Sealander and Adolph 1966; Werber and Benton 1967), **density** (Bruce 1995; Kleeberger 1984), **diel activity** (Brandon and Huheey 1975; Gordon et al. 1962; Hairston 1949, 1986; Hall and Taylor 1988; Holland and Taylor 1989; Keen 1982; Keen and Reed 1984a, 1984b; 1985a, 1985b, 1985c; Lynnette and Andreadis 2000; Shealy 1975; Sievert and Andreadis 2002), **diet and foraging** (Bernardo 2002; Brandon 1965; Brandon and Huheey 1971; W. Brown et al. 2003; Camp 1997b; Donovan 1972; Duncan 1970; Felix and Pauley 2006; Franz 1966; Gorsuch and Owen 2014; Hairston 1949, 1986; Huheey 1966; Kleeberger 1984, 1985; Krzysik 1979; Kuzmin 1992; Pough et al. 1998, 2001, 2004, 2016; Shealy 1975), **dispersal** (Bruce 1986; Grant et al. 2010), **distribution** (Adams et al. 1996; Ashton and Ashton 1988; Ballinger and Lynch 1983; Bartlett and Bartlett 1999; Bishop 1924, 1925, 1926, 1928; Blair et al. 1957, 1968; Breder and Breder 1923; Chamberlain 1928; H. Collins 1959; Cooper 1948, 1960a, 1960b, 1961, 1965; Duellman and Sweet 1999; Dury and Williams 1933; Franz 1972; Gentry 1955; N. Green 1969; Harris 1969, 1975; Hoffman 1945; Hoffman and Kleinpeter 1948; Huheey 1966; Jackson 1944; Jopson 1984; King 1939; Manis et al. 2005; Martof and Rose 1962; McCauley and East 1940; McClure 1931; Means and Longden 1970; Mainz 1975; Meshaka et al. 2008; J. Mitchell and Reay 1999; Mount 1975, 1996; Neill 1941, 1954; Netting 1932c; Nicholls 1950; Patterson and Regester 2016; Penney 1952; Pickens 1927; Pope 1928; Redmond 1980; Rose and Dobie

1963; Sever 1984; Thompson 1982; Thurow 1957; Tilley and Harrison 1969; Tobey 1985; Welter and Carr 1939; Williamson and Moulis 1979, 1994b; Wilson and Friddle 1950; Zell 2017), **eggs** (Altig and McDiarmid 2015; Brady 1924; Bruce 1989a, 1989b, 1990a, 1996; Camp 1997a; Dodd 2003; Folkerts 1968; Nussbaum 1987, 2003; Organ 1961; Pope 1924), **electrophoresis** (Hinderstein 1969, 1971b; Shontz 1968), **evolution** (Camp et al. 2000; Collazo 1990; Eastman 2010; Morescalchi 1975; Noble 1927; Sever et al. 2016; Shepard et al. 2016; Tipton-Jones and Pyles 1994; Wake 1964, 1966; White et al. 2000), **field guides** (Ballinger and Lynch 1983; Bartlett and Bartlett 1999, 2006; Behler and King 1979, 1985, 1988; Bishop 1943, 1947, 1962, 1967, 1969, 1994; Cassie 1999; Cochran and Goin 1970; Conant 1958, 1975; Conant and Collins 1991a, 1991b, 1998; Hipes et al. 2001; Pauley 2004, 2013; Powell et al. 2016; H. Smith 1978; Thompson 1982), **genome** (Bachmann 1970; Hally et al. 1985, 1986; Larson 1984; Morescalchi 1975; NCBI 2017; Sessions and Larson 1987), **general ecology** (AmphibiaWeb 2019; Arnold 2000; Barbour 1953; Bond 2007; Brandon 1966; Brown 1992; Cochran 1961a, 1968; Cogger et al. 2002, 2004; H. Collins 1959; Crockett 2001; Dodd 2003; Duellman and Trueb 1986, 1994; Gibbons and Buhlmann 2001; D. Green et al. 2013; N. Green 1937; Hairston 1973; Leviton 1972; Mattison 2005; McCoy 1982; Rimpp 1985; Schneider 2010; Svancara 2010; Tilley 1973; Vitt and Caldwell 2009, 2014; Wallace et al. 1992; Wells 2007; Zug 1993; Zug et al. 2001), **growth rate** (Bruce 1989a, 2016a, 2016b; Castanet et al. 1996; Hally et al. 1985), **gut fungus** (Tills 1977), **habitat** (Bailey et al. 2006; Bruce 1987; H. Collins 1981; Cooper 1960b, 1961; Eaton 1954; Ford et al. 2002b; Grant et al. 2005; Grover 1996; Jackson 1944; Means 2000; Metts et al. 2001; J. Mitchell et al. 2006; Newman 1955; Noble and Evans 1932; Petranka and Smith 2005; Resetarits 1997; Sattler and Gibson 2018), **habitat change** (Bourne 2015; Crawford 2007; Dodd 1997; Gingerich 2009; Gordon et al. 1962; L. Green 2006; Hamilton 2002; S. Jones 2010; Kong 2006; Matthews et al. 2010; McDonald 2001; Roudebush 1988, 1989; Southerland and Stranko 2008; Walz 2002; Ward 2005; Watkins-Colwell and Leenders 2006; Whiteleather 2001; Wood and Williams 2013a), **habitat selection** (Hairston 1987; Keen 1985), **home range** (Hardin et al. 1969; Kleeberger 1984, 1985; MacGregor 1982b), **integument** (Houck and Sever 1994; McMahan and Pav 1982; Means and Karlin 1989), **interspecific interactions** (Bruce 2008; Carr and Taylor 1983, 1985; Davic 1979; Fauth 1998; Grover 2000; Hairston 1983, 1986; Juterbock 1977a; Keen 1982, 1985; Keen and Sharp 1984; Kleeberger 1983, 1984; Mathis et al. 1995; Organ 1961; Roudebush and Taylor 1986b, 1987a; Southerland 1984, 1986a, 1986b, 1986c; Tilley 1973; White et al. 2000), **interspecific spacing** (Fauth et al. 1992; Folkerts 1968; Grover 2000; Hairston 1949; Karlin and Guttman 1979; Keen 1982; Keen and Sharp 1984; Krzysik 1979; Organ 1961; Shealy 1968, 1975; Southerland 1986a), **intraspecific spacing** (Anonymous 1989; Camp and Lee 1996; Colley et al. 1989; Hairston 1986; Keen and Colley 1987; Krzysik and Miller 1979; Southerland 1986a, 1986b, 1986c), **introduced populations** (Bonett et al. 2007; C. Bush et al. 2017; Connior et al. 2013), **inventories** (Anonymous 1981, 1987, 1998; Buhlmann 1987; F. Bush 1959; Colwell 1983; Dodd 2003; Frantz 1992; Jung et al. 2000, 2005; Neff 2017; Netting and Wilson 1940; Rosenberg 1978; Sattler and Gibson 2018; Simpson 2013; Tuberville et al. 2005; Windsor 1931, 1932), **juvenile habitat** (Anonymous 1989; Brandon and Huheey 1971; Colley et al. 1989; Folkerts 1968; Hairston 1986; Keen and Colley 1987; Krzysik and Miller 1979; Shealy 1975), **keys to adults** (Ashton 1978; Barbour 1971; Blair 1957, 1968; Brimley 1926, 1944; Chermock 1952; Dunn 1917b, 1918a, 1926, 1972; Feuer 1967; N. Green 1951, 1969; MacGregor

1982b; Martof 1956; Netting 1935; Powell et al. 1998, 2012, 2019; Stevenson 1976; Thompson 1982), **keys to larvae** (Altig and Ireland 1984; Altig and McDiarmid 2015; Ireland 1981), **key to skull** (Caldwell 1977), **land use** (Ash and Bruce 1994; Brannon and Purvis 2008; Crawford and Semlitsch 2007, 2008; Ford et al. 2002a; Knapp et al. 2003; Mackey et al. 2014; Matthews et al. 2010; Moseley et al. 2008; W. Peterman 2008; Peterman et al. 2011; Petranka and Smith 2005; Petranka et al. 1993; Price et al. 2016, 2018; Stranko et al. 2010; Surasinghe 2013; Surasinghe and Baldwin 2015; Ward et al. 2008; Williams 2003; Williams et al. 2017; Wood and Williams 2013b), **larvae** (Altig and McDiarmid 2015; Eaton 1956), **larval behavior** (Orr and Maple 1978), **larval development** (Bruce 1989b, 1990b, 1995, 2019; Bruce and Hairston 1990; Bruce and Hally 1986; Dodd 2004; Folkerts 1968; Juterbock 1984; Organ 1961; Rubenstein 1969, 1971), **life history evolution** (Arnold 2000; Arnold et al. 2017; Bonett and Blair 2017; Bruce 1989b, 1996, 2005, 2007, 2009, 2010, 2013, 2019; Bruce and Hairston 1990; Bruce and Hally 1986; Chippindale et al. 2004; Duellman 2007; Hairston 1973; Houtcooper 1981; MacGregor 1982a; Stebbins and Cohen 1995; Tilley 1980; Tilley and Bernardo 1993), **locomotion** (Edwards 1976), **longevity** (Bowler 1977; Bruce 1990a; Bruce and Hairston 1990; Bruce et al. 2000, 2002; Castanet et al. 1996; Snider and Bowler 1992), **marking** (Kinkead et al. 2006; S. Mitchell et al. 2017; Perry et al. 2011), **monitoring** (Dodd et al. 2001; Grover 2006; Welsh and Droege 2001), **morphology** (Caldwell and Trauth 1979; Dawley 2017; Dunn 1924; Fowler and Dunn 1917; Highton 1961; Hinderstein 1971a; Means 1972, 1974; Pingleton and Holbrook 2019; Rehorek et al. 2013; Roth and Walkowiak 2015; Sever 1974, 1983; Wake et al. 1988), **museum collections** (Cochran 1961b; Dunn 1918b; N. Green 1949; Hoffman and Mitchell 1994; [Wiesenberg] 1976; Williamson and Moulis 1994a), **nomenclature** (Brame 1972; Dubois and Raffaelli 2012; Dunn 1916, 1923; Grobman 1945; Sokolov 1988; Zhao et al. 1993, 1998), **numeric codes** (Brame et al. 1978), **nutrient cycling** (Drumheller 1979; Keitzer and Goforth 2013; Milanovich et al. 2015; Stiffler 1993, 2005; Woodall 1972), **oocyte counts** (Bruce 1995, 1996; Bruce and Hairston 1990; Tilley 1968), **oophagy** (Camp 1997a), **osteology** (Caldwell 1977; Castanet et al. 2003; Juterbock 1977b, 1978a; Laurin et al. 2004, 2009; Wake 1964, 1966), **pathogens** (Davidson and Chambers 2011; Hossack et al. 2010; Keitzer et al. 2011; McAlpine 1996; Rothermel et al. 2008; Spaulding et al. 2018; Timpe et al. 2008; Vazquez and Rothermel 2007; Vazquez et al. 2009), **parasites** (Baker 1987; Baker et al. 1987; Cheng 1958; Dunbar and Moore 1979; Dyer and Brandon 1973; Goater 2000; Goater et al. 1987; Jones 1987; Joy et al. 1993; Rankin 1937a, 1937b, 1938; Sellers et al. 1981), **phylogeography** (Bernardo et al. 2007; Bonett et al. 2007; Casey 2002a, 2002b; Mabry and Varrrell 1997; Martin 2015; Martin et al. 2016; Spight 1967), **physiology** (Beckenbach 1975; Bernardo et al. 2007; Brown et al. 1979; Lanza 1959; Spotila 1972; Vernberg 1955; Whitford and Hutchison 1965; Wittle 1983), **popular accounts** (Allyn 1952, 1956, 1961, 1977; Anonymous 1976b; N. Green 1943; Mansueti 1947; J. Mitchell 1977a; Morris 1945, 1957, 1974; Netting 1933b), **population sampling** (Bailey et al. 2004a; Graeter et al. 2013; Grover 2006; Hyde and Simons 2001; Jaeger et al. 2016; Mackey et al. 2010; Marsh 2009; Pauley and Little 1998; Rubio 1968), **population trends** (Dixon and Pechmann 2005; Hairston 1996; Hairston and Wiley 1993; Tipton-Jones and Pyles 1994), **predation** (Bernardo and Yoke 2006; Bruce 1979; Hairston 1980b, 1986; Jaeger et al. 1998; Peterman 2007; Resetarits 1991; Tilley 1968), **regulations on collection** (Bartlett 1986), **reproduction** (Arnold 1972, 1977; Brady 1924; Bruce 1989b, 1990b, 1995, 1996, 2018; Bruce and Hairston 1990; Duncan 1970; Organ 1961; Pope 1924; Tilley 1968;

Tilley and Tinkle 1968), **seasonal activity** (Shealy 1975), **sexual behavior** (Arnold 1972; Arnold et al. 2017; Brock and Verrell 1994; Keen and Reed 1985a; Mabry 2004; Mabry and Verrell 2003; Noble 1931, 1954; Noble and Brady 1930; Organ 1961; Pough et al. 2001, 2004; Verrell 1999; Verrell and Mabry 2000), **sexual dimorphism** (Bruce 1993; Castanet et al. 1996, Noble 1929, 1931, 1954), **sexual maturity** (Bruce 1989b, 1990b, 1995; Bruce et al. 2000, 2002; Castanet et al. 1996; Juterbock 1978b; Means and Longden 1970; Organ 1961), **spermatheca** (Sever 1994b), **spermatophore** (Noble and Weber 1929; Organ and Lowenthal 1963), **spermatozoa** (Barker and Baker 1970; Goin and Goin 1962; Scheltinga and Jamieson 2003; Sever 2000; Sever and Hamlett 1998; Wortham et al. 1977), **state and provincial publications** (Anonymous 1976a, 2017; Camp et al. n.d.; Hoffman 1983, 1985; Hoffman and Kleinpeter 1948; Hutchison 1956; J. Mitchell 1981; Moriarty and Bauer 2000), **state and regional checklists and bibliographies** (Arment 2005; Bailey et al. 2004b; Barbour 1950, 1957; Beltz 1989; Brimley 1926, 1939, 1944; Burger 1958a, 1958b, 1959; Chambers 2006; DePoe et al. 1961; Driver 1942; Dunn 1920; Echternacht 1980; Echternacht and Harris 1993; Enge and Dodd 1986, 1992; Fergus 2000, 2003; Garriock et al. 1996; Garton et al. 1993; Gentry 1955; N. Green 1936, 1937, 1948, 1954, 1961, 1963, 1964; N. Green and Brant 1966; N. Green and Dowler 1966; Hayslett 1992; Johnson 1970; Lovich 1997; MacGregor 1974, 1982b; McCoy 1986, 1989a, 1989b, 1992; Meshaka et al. 2012; J. Mitchell 1977b, 1981; J. Mitchell and Pague 1984; Moler 1988, 1990, 1991, 1999; Montanucci 2006; Neill 1949; Netting 1931, 1932a, 1932b, 1933a, 1934a, 1934b, 1936a, 1936b, 1939a, 1939b, 1946a, 1946b, 1947, 1949, 1950; Netting and Orton 1950; Netting and Richmond n.d., 1955, 1970, 1974; Penney 1952; Pinder and Greenlee 1999; Rappole 2007; Redmond and

Scott 1996; Redmond et al. 1990; Richmond and Boggess 1941; Richmond and McCoy 1965; Roble and Hobson 1995; Rubenstein 1968; Sattler 1995; Scott and Redmond 2002; A. Smith 1945; Tilley et al. 2000; Virginia Herpetological Society 1968; Witt 1993; Wolf 1981; Young 1993), **subspecies** (Hoffman 1951), **survivorship** (Bruce 1990a, 1995; Dullman and Trueb 1986, 1994; Organ 1961; Porter 1972; Tilley 1968), **systematics** (Caldwell and Folkerts 1976; Hess 2016; Hess and Townsend 2017), **tail autonomy** (Wake and Dresner 1967), **taxonomic references** (BoldSystems 2019; Frank and Ramus 1995; Frost 1985, 2017; Frost et al. 2006; Harding 1983; Integrated Taxonomic Information System 2017; NCBI 2017), **territories** (Keen and Reed 1984a, 1984b, 1985a, 1985b; Keen and Sharp 1984), **toxicology** (Raimondo et al. 2003), **vision** (Caldwell 1980, Roth et al. 1998), and **worldwide checklists** (Brame 1967; Gorham 1974; D. Mitchell 2017).

ETYMOLOGY. *Desmognathus* is derived from the Greek words *desmos*, δεσμός, ('ligament') and *gnathos*, γνάθος, ('jaw'). The generic name is descriptive of the large atlanto-mandibular ligaments that are manifest, characteristic bilateral protuberances over the adult mandibular joint. The specific epithet *monticola* is a Latin word meaning "mountain-dwelling" and refers to the general geographic range of the species.

NOMENCLATURAL HISTORY. *Desmognathus monticola* was the first species described by zoologist Emmett R. Dunn and appears in his research between 1916 and 1920. Dunn (1923) later recognized that Matthes (1885) had named a similar salamander *Salamandra phoca* and suggested the name *Desmognathus phoca*. Authors used *Desmognathus phoca* until 1943. Grobman (1945:p. 40) clarified the identity, distribution, and nomenclature of the species; he considered

“*Salamandra phoca* Matthes a synonym of *Desmognathus fuscus fuscus* (Rafinesque)” and “*Desmognathus monticola* Dunn as the valid name for the salamander currently recognized under the name *Desmognathus phoca* (Matthes)”. Several authors continued to use *Desmognathus phoca* in subsequent articles (Cheng 1958; Nicholls 1950; Penney 1952; Vernberg 1955).

Additional English names and scientific names included in literature are **Appalachian Seal Salamander** (*Desmognathus monticola monticola*: Barbour 1971; Behler and King 1979, 1985, 1988; Brame et al. 1978; Burger 1958a; Chermock 1952; J. Collins et al. 1978, 1982; Conant 1975; Conant et al. 1956a, 1956b; Cooper 1960a, 1965; DePoe et al. 1961; Franz 1966; N. Green 1969; N. Green and Dowler 1966; Harris 1969, 1975; Hutchison 1961; McCoy 1982, 1986, 1992; Organ 1961; Organ and Lowenthal 1963; Rubenstein 1969; Seehorn 1982; Shaffer 1991, 1995; Virginia Herpetological Society 1968; Williamson and Moulis 1979; and *Desmognathus monticola*: Gingerich 2009; Joy et al. 1993; Kong 2006; Ward 2005; Ward et al. 2008), **Blue Ridge Seal Salamander** (*Desmognathus monticola jeffersoni*: Schmidt 1953), **Mountain Desmognath** (*Desmognathus phoca*: Brimley 1926), **Seal Salamander** (*Desmognathus monticola monticola*: Barbour 1957; Martof 1956; D. Mitchell 2017; Moler 1988; Schmidt 1953; Wrobel 2004), **Virginia Seal Salamander** (*Desmognathus monticola jeffersoni*: Behler and King 1979, 1985, 1988; Brame et al. 1978; Burger 1958a; J. Collins et al. 1978, 1982; Conant 1975; Conant et al. 1956a, 1956b; Harris 1969, 1975; Seehorn 1982; Virginia Herpetological Society 1968), and **Wood Puppy** (*Desmognathus monticola*: Breder and Breder 1923).

REMARKS. The illustration of *Desmognathus phoca* (= *monticola*) used by Bishop (1943, 1947, 1962, 1967, 1969, 1994) “is of

a typically colored specimen of [*Desmognathus*] *welteri*, and is not [*Desmognathus*] *monticola*” (Juterbock 1984).

COMMENTS. Invalid distribution records included those associated with *Desmognathus conanti* in Monroe County, Alabama (Beamer and Lamb 2008; Rissler and Taylor 2003), *Desmognathus fuscus* in Blair and Clearfield counties, Pennsylvania (Hulse et al. 2001; Netting 1933a, 1935; Yoder 1940), and *Desmognathus fuscus* in Adams County, Ohio (Graziano and Reid 2006; Matson et al. 2010). A specimen from Edmonson County, Kentucky (MCZ [Museum of Comparative Zoology] 2230) was noted by Dunn (1918b) likely in error. The same specimen was later included in a list of salamanders examined by Dunn (1926, 1972), along with reference to the type specimen of *Desmognathus phoca* (= *Desmognathus fuscus*) from Taylor’s Creek (Hamilton County, Ohio) near Newport, Kentucky (Matthes 1855). When Grobman (1945) clarified the identity of *Desmognathus monticola*, he noted a second invalid record from Edmonson County, Kentucky (Hibbard 1936) and rejected an additional record from Norfolk County, Virginia (Scharlinski 1939).

Desmognathus monticola is relatively abundant throughout most of its range. However, this species is adversely affected by factors associated with the degradation of lotic systems and adjacent terrestrial habitats. Factors that have been examined in this context include decreased water quality, increased sedimentation, edge and road effects, mountaintop removal mining, and valley filling (Price et al. 2016, 2018; Ward et al. 2008). Terrestrial habitat quality is adversely impacted by clear-cut, even-aged, and partial cut timber harvests in riparian zones and forest stands (Ash and Bruce 1994; Moseley et al. 2008; Petranka et al. 1993; Surasinghe and Baldwin 2015). For example, terrestrial habitat use by salamanders decreased

following a riparian timber harvest; further, relative abundance of salamanders remained depressed in even-aged forest stands for up to 40 years (Crawford and Semlitsch 2008; Peterman et al. 2011). Management plans require an overall stream buffer of at least 100 m to retain essential habitat for terrestrial life stages using riparian zones (Crawford and Semlitsch 2007).

Desmognathus monticola is found in the salamander bait trade. Sixty-seven percent of 'spring lizards' sold in northern Georgia bait shops were *Desmognathus monticola* (Jensen and Waters 1999, 2000). The relocation of these salamanders to uninhabited areas has resulted in at least one introduced population in Arkansas (Bonett et al. 2007). Surveillance efforts and detailed studies on the ecopathology of fungal (*Batrachochytrium dendrobatidis*, *Batrachochytrium salamandrivorans*) and viral pathogens (*Ranavirus*) are needed. *Batrachochytrium dendrobatidis* was not detected in populations in Georgia, North Carolina, and Tennessee (Keitzer et al. 2011; Rothermel et al. 2008; Timpe et al. 2008), and prevalence in the central Appalachians of Maryland and Virginia was relatively low (Kozak et al. 2005). Salamanders experimentally infected with *Batrachochytrium dendrobatidis* exhibited histological signs of disease but no mortality occurred and few clinical signs of disease were observed (Vasquez et al. 2009).

Species-level responses to climate change have been examined in the context of several characteristics of amphibians, including variation in physiological tolerance, interspecific competition, population size, habitat preference, and range size (Bernardo and Spotila 2006; Bernardo et al. 2007; Dodd 1997; Grant et al. 2010; Grover 2000; Hamed 2014; Hoffacker et al. 2018; Markle and Kozak 2018). *Desmognathus monticola* is a broadly distributed, eurythermal generalist strongly associated with lotic systems. The species is not physiologically constrained to a relative-

ly narrow range of environmental temperatures, so it is among amphibians least likely to be impacted by effects of climate change (Bernardo et al. 2007). Larval life stages of salamanders are a large standing stock of nitrogen, phosphorus, and calcium in headwater Appalachian streams, where they excrete limiting nutrients in stream nutrient cycles (Keitzer and Goforth 2013; Milanovich et al. 2015). Desmognathine salamanders such as *Desmognathus monticola* are dominant vertebrate consumers in most headwater streams and are an important component of lotic systems and adjacent habitats.

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