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Scarpetta, S. G. 2019. *Aneides hardii*.

***Aneides hardii* (Taylor)
Sacramento Mountains Salamander**

Plethodon hardii Taylor 1941:77. Type-locality, "Sacramento Mountains at Cloudcroft (9,000 ft. [2745 m]), [Otero County], New Mexico." Holotype, male, originally designated E. H. Taylor-H. M. Smith Mexican collection (EHT-HMS) 23656, now designated Field Museum of Natural History 100103 (Marx 1976; Wake 1965), collected by Dilbert Elmo Hardy, 29 June 1940. Type specimen not examined by author.

Aneides hardii: Lowe 1950:95.

Aneides hardyi: Schmidt 1953:51. Erroneously attributed to Lowe 1950.

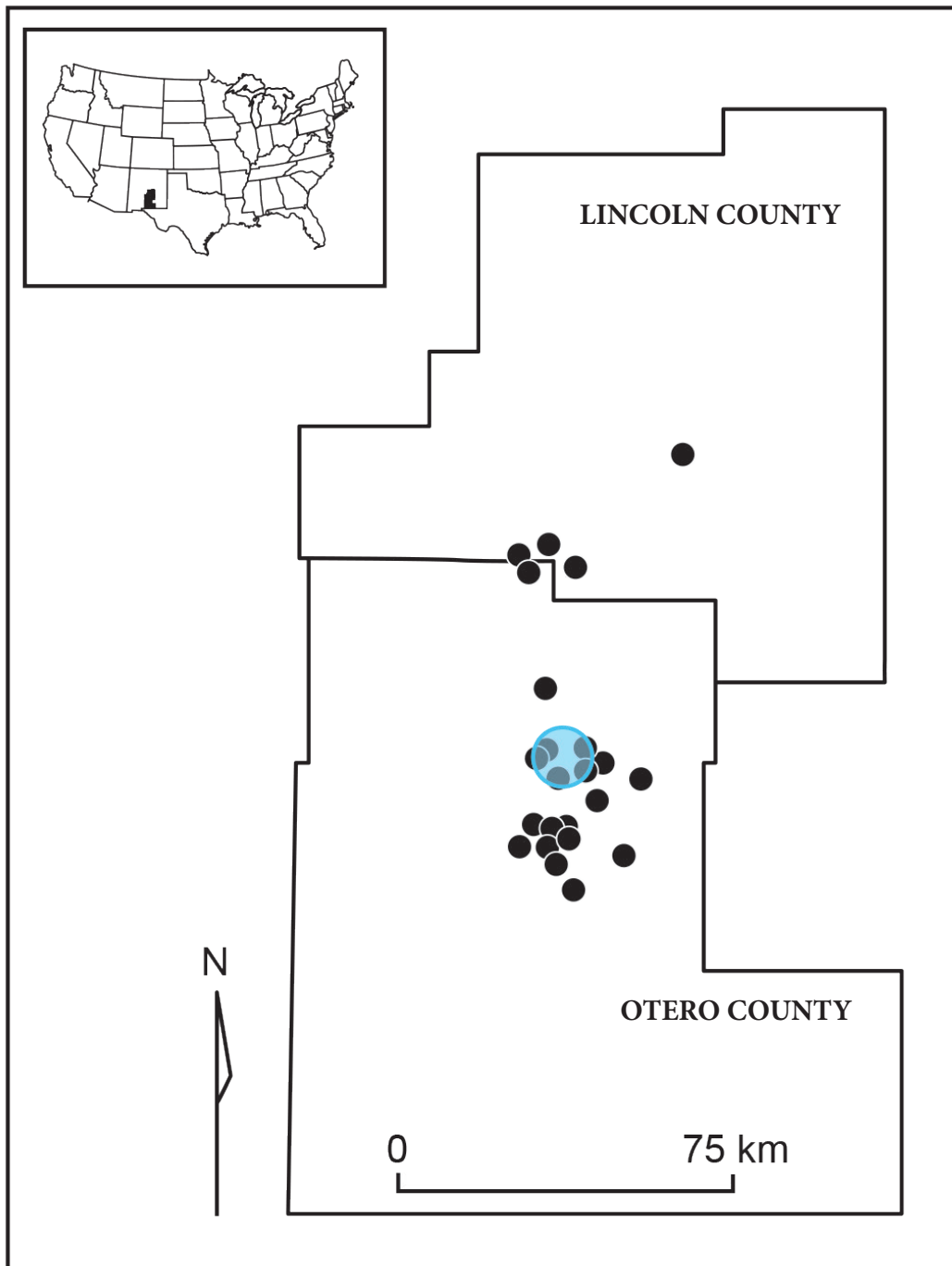
CONTENT. No subspecies have been described.

DESCRIPTION. Dorsally, both adults and juveniles are blackish brown to brown and

are usually mottled with a variable greenish-gray to bronze color, often with gold flecks. The largest adults may lack mottling (Wake 1965). Juveniles may have a brownish or bronze dorsal stripe. Adult snout-vent length (SVL) is 40–58 mm (Wake 1965) and is sexually dimorphic (mean male SVL 48.4 mm, mean female SVL 44.5 mm; Degenhardt et al. 1996, [2005]; Staub 1984). Hatchling SVL is 11–13 mm (Weigmann et al. 1980). Tail length is generally slightly less than the SVL (Wake 1965). Total length for all animals is 25.5–100.7 mm (Findley 1959; Stebbins 2003). Both the trunk and tail are round in shape. There are 14–15 costal grooves, with a range of 2–4.5 intercostal folds between adpressed limbs. Limbs and digits are short, although the limbs were originally described as "well developed" (Taylor 1941; p. 78). There are four digits at the end of each forelimb and five digits at the end of each hindlimb, and the tips of the toes are slightly rounded (Stebbins and McGinnis 2018). The temporal region of the head is slightly enlarged by the jaw musculature, especially in males. The vomerine teeth extend laterally beyond the lateral margins of the internal nares. Maxil-



FIGURE 1. Adult *Aneides hardii* found east of Cloudcroft, Lincoln County, New Mexico. Photograph by the author.



MAP. Distribution of *Aneides hardii*. Black dots represent individual records across Lincoln and Otero counties, New Mexico; transparent blue circle represents an approximation of the type locality: “Sacramento Mountains at Cloudcroft (9,000 ft.), New Mexico.” Distribution compiled from records published by Degenhardt et al. (1996, [2005]) and from VertNet (2019).

lary teeth are short, conical, and numerous (Wake 1965). Males have 14–22 maxillary teeth (mean 19); females have 28–36 maxillary teeth (mean 31). The tooth row extends posterior to or slightly beyond the anterior

edge of the eyeball. All species of *Aneides* lack lateral-line sense organs, although those organs are present in some plethodontid salamanders (Hilton 1947).

DIAGNOSIS. *Aneides hardii* is the only known plethodontid salamander from the Sacramento Mountains. The nearest plethodontid, *Plethodon neomexicanus*, occurs in the Jemez Mountains of New Mexico approximately 400 km (250 mi) north of the Sacramento Mountains. *Plethodon neomexicanus* is distinguished morphologically from *Aneides hardii* by having 18–20 costal grooves and a range of 7.5–8.5 intercostal folds between the toe tips of adpressed limbs (Degenhardt et al. 1996, [2005]). The only other New Mexican salamander, *Ambystoma mavortium*, is potentially sympatric with *Aneides hardii*, but is not known from higher elevations in the Capitan, Sacramento, or White mountains. In other parts of its range (including the states of Colorado, USA, and Chihuahua, Mexico) *Ambystoma mavortium* has been found at sites over 3000 m in elevation, but those populations often are pedomorphic (Nafis 2018a; Petirs 2002). *Ambystoma mavortium* can be easily distinguished from *Aneides hardii* by its large size (adult SVL 76–165 mm), barred dorsal pattern, aquatic larvae, broad head, and lack of a nasolabial groove.

PHYLOGENETIC RELATIONSHIPS. *Aneides hardii* is allied with other taxa of the genus *Aneides*. *Aneides hardii* was recovered as the sister taxon to *Aneides flavipunctatus* in some phylogenetic analyses of molecular data (Macey 2005; Mueller 2005; Mueller et al. 2004), although those studies included only those two species of *Aneides*. Other analyses of molecular data, including analyses of immunological data, recovered a sister taxa relationship between *Aneides hardii* and the entire western clade of *Aneides*, including *Aneides ferreus*, *Aneides flavipunctatus*, *Aneides lugubris*, and *Aneides vagrans* (Baum and Larson 1991; Larson et al. 1981; Pyron and Wiens 2011; Zheng et al. 2011). In phylogenetic analyses of molecular data *Aneides* was variably recovered as sister to *Hydromantes* (Mueller 2005; Zheng et al. 2011), *Ensatina* (Chippindale et al. 2004), the clade composed



FIGURE 2. Dorsal color variation in adult *Aneides hardii* at a single locality: adjacent to U. S. Hwy 82 east of Cloudcroft, Lincoln County, New Mexico. Photographs by the author.

of *Desmognathus*, *Phaeognathus*, *Hydromantes*, and *Speleomantes* (Frost et al. 2006), the clade composed of *Desmognathus* and *Phaeognathus* (Zheng et al. 2011), or the clade composed of *Desmognathus*, *Phaeognathus*, and *Karsenia* (Pyron and Wiens 2011). Systematic analyses of morphological data recovered a sister relationship between *Aneides* and *Plethodon* (Wake 1964, 1966).



FIGURE 3. Forest habitat for adult *Aneides hardii* pictured in Figures 1 and 2: along U. S. Hwy 82 east of Cloudcroft, Lincoln County, New Mexico. Photograph by the author.

PUBLISHED DESCRIPTIONS. In addition to the original description by Taylor (1941), detailed descriptions were provided by Degenhardt et al. (1996, [2005]), Frost (2019), Hammerson (2004), Raffaelli (2007, 2013), Ramotnik (2005, 2018), Stebbins (1951, 1954, 1962, 1966, 1985a, 1985b, 2003), Stebbins and McGinnis (2018), Wake (1965), and Wikipedia contributors (2018).

ILLUSTRATIONS. **Color photographs** were provided by Behler and King (1979, 1985, 1988), CalPhotos contributors (2012), Degenhardt et al. (1996, [2005]), Gin (2004), iNaturalist (2019), Nafis (2018b), Ramotnik (2005, 2018), Schaaf (2010), Stebbins (2003), Stebbins and McGinnis (2018), and Wikipedia contributors (2018). **Black-and-white photographs** were provided by Petranka (1998), Ramotnik (1997a, 1997b), and Ramotnik and Scott (1988). **Color illustrations**

were published by Stebbins (1966). **Black-and-white illustrations** were provided by Freytag (1968, 1974, 1984). Black-and-white illustrations of individual skeletal elements were published by Min et al. (2005) and Wake (1963, 1966). A black-and-white illustration of the musculature of *Aneides hardii* was provided by Hilton (1952).

DISTRIBUTION. Three isolated populations are known from the Capitan, Sacramento, and White mountains of south-central New Mexico in Lincoln and Otero counties. *Aneides hardii* is found at elevations greater than 2400 m. In forested mesic areas composed primarily of Douglas fir and Engelmann spruce, these salamanders can be encountered under and within logs, moist litter, and other debris. Above the tree line, the species is associated with rockslides and mats of moss and lichen. The range is discontinuous and limited to pockets of suitable habitat, where the salamander can be locally abundant. Geographic range was previously documented by Degenhardt et al. (1996, [2005]), Findley (1959), Freytag (1968, 1974, 1984), Gin (2004), Green et al. (2013), Hammerson (2004), iNaturalist (2019), Meents (1987), New Mexico Department of Game and Fish (2006b), Petranka (1998), Pope and Highton (1980), Pratt (1963), Ramotnik (1997b, 2005, 2018), Ramotnik and Scott (1988), Salas et al. (2017), Schaaf (2010), Schad et al. (1959), Scott and Ramotnik (1989a), Scott et al. (1987), Stebbins (1966, 1985a, 1985b, 2003), Stebbins and McGinnis (2018), Tanner (1978), Wake (1965), and Williamson et al. (1994).

FOSSIL RECORD. None (Brame 1967; Holman 2006).

PERTINENT LITERATURE. Relevant citations are listed by topic: **behavior** (Crump 1995; Liemnec-Tyburczy and Sapp 2017; Mathis et al. 1995; Staub 1993; Wells 2007), **biogeography** (Blair 1958; Degenhardt et

al. 1996, [2005]; Hubbard 1977; Lowe 1950; Macey 2005; Martin 1961; Pope and Highton 1980; Ramotnik 2005, 2018; Rimpp 1985; Tanner 1978), **capture** (Haan and Desmond 2004, 2005; Scott and Ramotnik 1989b), **conservation and threats** (Anonymous 1987; Bean 2016; Biota Information System of New Mexico [BISON-M] 1999; Borg 2001; Fitzgerald et al. 2004; Grialou et al. 2000; Haan and Desmond 2004; Haan et al. 2007; Hammerson 2004; Hubbard et al. 1979; Kaufmann et al. 1998; Mitchell 2017; New Mexico Department of Game and Fish 1988, [1993], 1996, 1998, 2000a, 2000b, 2005, 2006a, 2006b, 2008a, 2008b, 2010, 2012, 2014, 2016a, 2016b; Painter et al. 2017; Petranka 1998; Ramotnik 1997b, 1997c, 2005, 2007a, 2007b, [2007c]; Ramotnik and Scott 1988; Ramotnik et al. 2004; Salas et al. 2017; Scott and Ramotnik 1988, 1989a, 1989b, 1990; Scott et al. 1987; Staub 1986, U. S. Department of the Interior, Bureau of Land Management 1985; U. S. Fish and Wildlife Service [no date], 1985, 1989, 1991, 1994, [the species was anomalously omitted from U. S. Fish and Wildlife Service 1998]; U. S. Forest Service 1998a, 1998b, 2003, 2005, 2011; White and Ramotnik [2008a], 2008b; WildEarth Guardians 2008; Wyman 2003), **diet** (Ramotnik 2005, 2018; Sapp 2002; Scott 1990; Scott and Ramotnik 1989b), **ecology and natural history, including habitat** (Bean 2016; Degenhardt et al. 1974; Haan et al. 2007; Hammerson 2004; Johnston and Schad 1959, 2010; Jones et al. 2016; Meents 1987; Moir and Smith 1970; New Mexico Department of Game and Fish 1988, [1993], 1996, 1998, 2000a, 2000b, 2005, 2006a, 2008a, 2008b, 2010, 2012, 2014, 2016a; Petranka 1998; Ramotnik 2005, 2018; Ramotnik and Scott 1988; Sapp 2002; Scott 1990; Scott and Ramotnik 1989a, 1992; Scott et al. 1987; Weigmann et al. 1980; Wells 2007; Welsh and Droege 2001; Williams 1976, 1978; Williams and Degenhardt 1974; Williamson et al. 1994), **genetics** (Chong and Mueller 2017; Fonseca et al. 2006; Green and Sessions 2007; King 1991; Larson and Wilson 1989; Macgre-

gor and Jones 1977; Mizuno and Macgregor 1974; Osborne et al. 2017; Pope and Highton 1980; Sessions and Wiktorowski 2000), **history of collectors** (Beolens et al. 2013; Lovich et al. 2012), **osteology** (Schaaf 2010; Wake 1963, 1964, 1966), **phylogenetic and systematic relationships** (Baum and Larson 1991; Chipindale et al. 2004; Frost et al. 2006; Larson 1984; Larson et al. 1981, 2003; Lowe 1950; Macey 2005; Mahoney 2001; Mueller 2005; Mueller and Boore 2005; Mueller et al. 2004; Plötner et al. 2007; Pyron and Wiens 2011; Reilly et al. 2015; Schaaf 2010; Sessions and Kezer 1987; Vieites et al. 2011; Wake 1963, 1964, 1966; Wiens and Morrill 2011; Zheng et al. 2011), **physiology** (Carey 1988; Hilton 1947, 1952; Whitford 1967, 1968), **predation on** (Painter et al. 1999), **reproduction** (Bruce 2000; Degenhardt et al. 1974; Johnston and Schad 1959, 2010; Petranka 1998; Ramotnik 2005, 2018; Sapp 2002; Schwartz 1955; Williams 1973, 1976, 1978; Williams and Degenhardt 1974; Williamson et al. 1994), **taxonomy and nomenclature** (Collins 1990, 1997; Collins and Taggart 2002, 2009; Collins et al. 1978, 1982; Comité sur les Noms Français Standardisés 2012; Committee on Standard English and Scientific Names 2008, 2012, 2017; Conant et al. 1956a, 1956b; Crother et al. 2001; Frank and Ramus 1995; Frost 1985; Mitchell 2017; Painter 2002; Sokolov 1988; Stuart and Painter 2005; Wrobel 2004; Zhao et al. 1993, 1998).

The species is treated in the following field guides, general works, and handbooks (some of which may contain brief descriptions and illustrations): Anonymous (2002), Arment (2005), Bartlett and Bartlett (2009, 2013), Behler and King (1979, 1985, 1988), Bishop (1943, 1947, 1962, 1967, 1969, 1994), Cassie (1999), Eley et al. (1985), Gin (2004), Hubbard et al. (1979), New Mexico Department of Game and Fish (1988, [1993]), Smith (1978), Stebbins (1951, 1954, 1962, 1966, 1985a, 1985b, 2003), and Stebbins and McGinnis (2018). The species also appears in bibliographies, checklists, faunal lists, and

keys including those by Beltz (1995), Glaw et al. (1998, 2000a, 2000b), Gorham (1974), Hutchins et al. (2003), Painter (2002), Painter et al. (2017), Powell et al. (1998, 2012, 2019), Slavens (1982), Stejneger and Barbour (1943), and Stuart (2002, 2005).

REMARKS. *Aneides hardii* is a species of concern due to its limited range and vulnerability to habitat loss. The species is listed as threatened by the New Mexico Department of Game and Fish (2016a) but is not currently listed by the U. S. Fish and Wildlife Service (no date) and is listed as ‘Least Concern’ by CITES (Hammerson 2004). The species is notable for its local abundance in appropriate habitat and apparent resilience to anthropogenic threats (Ramotnik 2005, 2018; Scott and Ramotnik 1992). Intense logging during the last century appears to have had no long-term effect on salamander populations, nor have occasional fires (Ramotnik 2005, 2018; Ramotnik et al. 2004). The geographic distribution of *Aneides hardii* appears to be stable (Ramotnik 1997b). However, intensive logging in combination with slash removal and burning may decrease or eliminate populations of *Aneides hardii* (Ramotnik and Scott 1988). Additionally, although milder fires have little effect on local salamander populations, severe burns cause salamanders to leave the area or retreat deep underground, and surface habitats after a severe fire are not suitable for habitation by salamanders for at least five years after the fire (Ramotnik 2005, [2007c]). Future stability of the species is difficult to predict, and intensive, long-term studies of the effects of logging, fires, and other anthropogenic threats on *Aneides hardii* are needed (Ramotnik 1997b; Ramotnik and Scott 1988).

Aneides hardii and *Plethodon neomexicanus* are the only native plethodontid salamanders in New Mexico and the only native plethodontid species found between the westernmost populations of *Eurycea* in cen-

tral Texas (Devitt et al. 2019), the single species of *Isthmura* found in central Chihuahua and Sonora (Lemos Espinal and Smith 2007; Rorabaugh and Lemos-Espinal 2016; Rovito et al. 2015), and the various plethodontid taxa found in the Sierra Nevada Mountains in central California (Stebbins 2003; Stebbins and McGinnis 2018). Studies of genetic variation showed that the three populations of *Aneides hardii*, each occupying a different mountain range, last shared a common ancestor during the Pleistocene (Pope and Highton 1980). The three populations have significant differences in their mean snout–vent length and mean snout–vent length relative to mean tail length, but the range of values overlap extensively among populations such that individuals from each population could not be separated from one another (Schad et al. 1959). The skeletal morphology of the Capitan Mountains population and the Sacramento Mountains population is identical (Wake 1965). The divergence between the western clade of *Aneides* (*Aneides ferreus*, *Aneides flavipunctatus*, *Aneides lugubris*, and *Aneides vagrans*) and *Aneides hardii* was estimated to have occurred around 25 Ma during the late Oligocene (Zheng et al. 2011) or circa 20 Ma during the early to middle Miocene (Larson and Wilson 1989; Larson et al. 1981).

ETYMOLOGY. This species is named for its original collector, Dilbert Elmo Hardy (see Beolens et al. 2013; Brame et al. 1978; Taylor 1941).

ADDITIONAL VERNACULAR NAMES. “Sacramento Mountains Sediena” was used by Mitchell (2017); “Sediena” is “*Aneides*” spelled backwards, which appears to be the derivation of that common name. “Salamandre des montagnes de Sacramento,” the French equivalent of the English vernacular name, was provided by Comité sur les Noms Français Standardisés (2012). The German name “Neumexikanischer Baumsalamander”

was provided by Sokolov (1988). The English vernacular name is often listed as “Sacramento Mountain Salamander” (e.g., Degenhardt et al. 1996; Ramotnik 2005, 2018; Wake 1965); however, I have followed the name provided by the most recent publications from the Society for the Study of Amphibians and Reptiles (SSAR), “Sacramento Mountains Salamander” (Committee on Standard English and Scientific Names 2017; SSAR North American Species Names Database 2019).

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