Zootaxa 4838 (2): 221–247
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4838.2.4
http://zoobank.org/urn:lsid:zoobank.org:pub:FD35BBCC-D29D-419A-ACB1-1F563A7D3B8A

The herpetological legacy of Jacob Green and the nomenclature of some North American lizards and salamanders

R. ALEXANDER PYRON[1,2] & DAVID A. BEAMER[3]
[1]*Department of Biological Sciences, The George Washington University, 2023 G St. NW, Washington, DC, 20052, USA.*
rpyron@colubroid.org; *https://orcid.org/0000-0003-2524-1794*
[2]*Division of Amphibians and Reptiles, Department of Vertebrate Zoology, National Museum of Natural History Smithsonian Institution, Washington, DC, 20560, USA.*
[3]*Department of Natural Sciences, Nash Community College, Rocky Mount, NC, 27804, USA.*
dbeamer@nashcc.edu; *https://orcid.org/0000-0003-0796-274X*

Abstract

Jacob Green was born in 1790 to a prominent New Jersey family of scholars and theologians. He taught at the College of New Jersey (now Princeton University) from 1818 to 1822 before co-founding Jefferson Medical College (now Thomas Jefferson University) in 1825, where he taught Chemistry until his death in 1841. Between 1818 and 1831, he published a series of nine papers on lizards, salamanders, and snakes, authoring the original description of several well-known species of salamanders from the eastern United States. Many of his names are ambiguous; some have been adjudicated by the ICZN, while others are currently treated as *nomina dubia.* Here, we review all of Green's publications, report on newly re-discovered or re-interpreted material from several major natural history collections, and resolve most if not all remaining issues through a series of taxonomic actions. In particular, we first designate a neotype for *Salamandra nigra* Green, 1818. We then place *S. sinciput-albida* Green, 1818 and *S. frontalis* Gray *in* Cuvier, 1831 in synonymy with *S. scutata* Temminck *in* Temminck & Schlegel, 1838 and invoke Reversal of Precedence under Article 23.9 to designate them *nomina oblita.* We also designate a lectotype for *S. bislineata* Green, 1818. Finally, we resurrect the name *S. fusca* Green, 1818 as the valid name for the species *Desmognathus fuscus,* assuming priority over *Triturus fuscus* Rafinesque, 1820, designating *S. fusca* Laurenti, 1768 a *nomen oblitum,* and placing *S. nigra* Green, 1818 in synonymy. While Green's herpetological legacy is not as expansive as that of some of his successors such as Holbrook, he is nonetheless a foundational early worker in salamanders, having described some of the most-studied species in the world.

Key words: Taxonomy, *Lacerta, Salamandra,* Titian Ramsay Peale, Philadelphia

Introduction

Jacob Green was born in Philadelphia on the 26th of July 1790 (Adler *et al.* 2007), and smallpox in infancy left him functionally blind in his right eye (Green *in* Gayley 1858). His early interests included chemistry, electricity, and natural history (botany in particular), and he received his Bachelor of Arts from the University of Pennsylvania in 1807 (Smith 1923). He then embarked on a variety of practices in law, medicine, and the natural sciences, and was awarded honorary degrees from Rutgers (1812), Princeton (1815), and Yale (1827; see Bennett 1949).

His grandfather, the elder Jacob Green (1722–1790), had served as acting president of Princeton (then the College of New Jersey) during the 1758–1759 term, and his father Ashbel Green (1762–1848) became its eighth president in 1812. In the fall of 1818, the younger Jacob Green was appointed Professor of Chemistry, Experimental Philosophy, and Natural History at Princeton under his father's leadership. Just prior to assuming this post, Jacob communicated a major work on the lizards and salamanders of the northeastern USA to the Academy of Natural Sciences of Philadelphia (ANSP), read on the 12th of May and published in September (Green 1818). He later published a short note on a collection of subfossil rattlesnake skeletons from a cave near Princeton (Green 1821).

Both Ashbel and Jacob Green left Princeton in 1822 due to significant differences of opinion with the trustees and student body. In 1825, Jacob co-founded Jefferson Medical College in Philadelphia (now Thomas Jefferson

Accepted by M. Vences: 3 Aug. 2020; published: 26 Aug. 2020

University) with several colleagues, a new medical campus of Jefferson College (now Washington & Jefferson College) in Canonsburg (Bennett 1949). He assumed a post as Professor of Chemistry, which he held until his death in 1841. He published seven additional notes, descriptions, and letters regarding lizard and salamander taxonomy from 1825 to 1831 (Green 1825a,b, 1827a,b, 1830, 1831; Peale & Green 1830). From April to November 1828, he toured England, France, and Switzerland, visiting several major museums and meeting European scientific luminaries such as John Dalton (father of atomic theory) and Michael Faraday (father of electromagnetism), in addition to the biological dignitaries Gray, Cuvier, and Lamarck (see Smith 1923).

While a letter to Cuvier (Green 1830) indicated a desire to contribute a lengthy monograph on salamanders, Green's health began to fail rapidly in his 40's, and he died of heart failure on the 1st of February 1841 at the age of 50. His herpetological legacy of nine brief publications is somewhat underappreciated compared to later American workers in the field such as Holbrook, Baird, or Stejneger. While his contributions were few in number and pages, he nevertheless authored the original description of several common salamander species in the eastern USA, exerting a strong early influence on herpetology there and abroad.

In his publications, Green offered accounts for species then in the lizard genera *Agama, Lacerta,* and *Scincus* and the salamander genera *Proteus* and *Salamandra*. Some of these he was describing for the first time; for others he was simply providing updated accounts or noting varieties of previously described taxa. A few of the salamander names have been considered *nomina dubia* by later authors (see Crother *et al.* 2003). However, some of these ambiguous names are associated with widely studied species such as *Desmognathus fuscus*, and it is thus imperative that their allocation be resolved to promote taxonomic stability. This task requires a full understanding of Green's knowledge of salamanders, so we consider all of his names here. A revised understanding of extant material from his collections aids in this effort; we surveyed the material in the Academy of Natural Sciences of Drexel University (formerly the ANSP) and the National Museum of Natural History (NMNH), and made several notable discoveries. Below, we are able to allocate nomina to taxa, and in many cases assign extant type material, for all of Green's names. This resolves much of the lingering confusion regarding the nomenclature of some eastern USA salamanders.

Green's Collections

Green amassed a large personal collection of amphibians and reptiles, parts of which are putatively still extant at the ANSP (see Malnate 1971), the NMNH (United States National Museum [USNM] series), and possibly the British Museum of Natural History (BMNH), and the Muséum national d'histoire naturelle (MNHN; see below). Most if not all of the specimens at the ANSP currently associated with Green were donated on 7 January 1851, 9 years after Green's death, by his friend Franklin Bache (Anonymous 1852; Leidy 1852). Bache (1792–1864) was the great-grandson of Benjamin Franklin and Recording Secretary of the ANSP from 1819–1821 (Anonymous 1877; Wood 1865). The specimens Bache donated are generally catalogued with labels such as "Dr. Bache, Green Coll." or similar, and are thus to be considered as "types by association" (Bell 1996), as they generally cannot be linked definitively to Green's original descriptions.

In addition to the ANSP material, Cope (1868) states that USNM 3968, the "alleged holotype" of *Salamandra jeffersoniana* Green, 1827a, was received from "Dr. F. Bache," and Yarrow (1882) states that it was collected by "Dr. J. Green." Cope (1870, 1889) later stated that USNM 4743 (now missing) were Green's types for *Salamandra cirrigera* Green, 1831, received from "Dr. F. Bache." Finally, Yarrow (1882) states that USNM 3738 are the "alc. types" of *Spelerpes bilineata* Green, 1818, from "Dr. J. Green." This suggests that the NMNH material referable to Green also likely originated from a donation from Bache after Green's death.

Thus, it is important to note at the outset that many specimens currently associated with Green's names cannot be linked directly to his original descriptions. Many of Green's specimens at the ANSP and NMNH are apparently from Bache's donation of Green's specimens, and their "type" status seems to come only from later workers such as Cope. Cataloging at the ANSP did not begin until the 1890's (N. Gilmore, *pers. comm.*). Malnate (1971) states that Fowler made note of any specimens known to him to be types, and this card catalog was later expanded by Dunn. From this, we receive most of our modern allocation of accessioned ANSP material to Green's names, but it is unclear at present on what evidence Fowler or Dunn based some of these associations. Smith & Taylor (1950) and Bell (1996) noted some apparent mix-ups of Green's material that may have occurred during his lifetime, in the intervening period after his death prior to Bache's donation, or at the Academy some time before the initial cataloging.

In summary, few if any extant records exist to provide a definitive link between many specimens currently considered types and the original descriptions. In some cases, we are able to provide character-based evidence based on examination with reference to the diagnosis. In other cases, we continue to accept existing designations as accurate; doing so seems to be the most prudent course of action so as not to disturb taxonomic stability. If the need arises, these specimens could simply be designated as neotypes in the future or disregarded if more persuasive material is discovered. Some putative types seem to have been extant in the past but later lost, while other names do not appear to have ever been linked to particular specimens.

Green's descriptions of amphibians and reptiles

As noted above, Green's vision was impaired from infancy, which may have affected some of his descriptions and diagnoses as discussed below. Additionally, his earliest works displayed a relative inexperience with amphibian biology, alternating between unqualified rejection or uncritical reliance on authorities such as Daudin, introducing a few lapses that were quickly corrected by others such as Say (1818) and Harlan (1827a). In contrast, Green's later work became increasingly rigorous and easier to interpret in a modern context. Listed and discussed here in chronological and bibliographic order, Green gave descriptions or accounts of the following specific nomina. We then give the modern common and Latin name in parentheses; some of these are novelties or at odds with prevailing synonymy and are thus discussed at length.

Green's first and most extensive taxonomic paper (Green 1818) contains descriptions or accounts of 16 different lizards and salamanders. Green begins with a discussion of "Order II. Saurian Reptiles. *Genus* Lacerta." by stating that "Daudin has subdivided this genus into seven sections, but as I think this mode leads to uncertainty in arranging the animals, I have not adopted it." Indeed, Daudin (1802a:89) had divided his "Quatrième genre. Lézard, *lacerta*" into seven "sections" or informal species groups by geography and gross morphology, including many New World teiids among others. For one of these, *Lacerta quinquelineata* Daudin, 1802a, Green (1818) provided an account as:

Lacerta quinquelineata Daudin 1802a (var.)

The "Striped L[izard]." (Five-Lined Skink; *Plestiodon fasciatus*); no type specimen designated; no type locality given. Green describes this variety as "Whole length between five and six inches; *tail* longer than the body, tapering, cylindrical, slender, and pointed; *ear hole* oval; *scales* above and beneath oval; *back* dark chesnut-brown, marked with five longitudinal light blue lines, the central one commences at the snout, which is pointed, divides between the eyes, unites again over the throat, and continues to the end of the tail; *beneath* whitish, and streaked; *feet* five-toed, clawed." Given this description and Green's residence and field work primarily in the vicinity of Princeton, it seems noncontroversial to conclude that he is describing *Lacerta fasciata* Linnaeus, 1758.

However, Green states in his introduction that he is referring to Daudin's *Lacerta* in its seven sections, of which *L. quinquelineata* Daudin, 1802a:243 is actually a teiid ("Sixième section. Lézards dracénoides"). Daudin (1802a:243) clearly intends his name as a new species, giving a description in Latin. In comparison, he references Sloane (1725)'s pre-Linnaean "*Lacerta major, cinereus, maculatus,"* now known as *Pholidoscelis dorsalis* (Gray, 1838) from Jamaica. Finally, Daudin states (translated): *"I do not know exactly in which part of the earth this singular species of saurian lives; however I believe it from Jamaica, because I found, in Sloane's work on the natural history of this island, the description and a fairly correct figure of a lizard which I suspect to be similar, or who belongs at least to the same section."* The name *L. quinquelineata* Daudin, 1802a is a junior primary homonym of *L. quinquelineata* Linnaeus, 1766, and is a *nomen oblitum,* apparently never having been associated with a specimen in the MNHN, nor referenced by later authors as a synonym for *P. dorsalis* (see Brygoo 1989).

While the name *"Lacerta quinquelineata"* was preoccupied by *L. quinquelineata* Linnaeus, 1766, rules of homonymy were not in place in 1802, and Daudin (1802b:272) later gave an account of the "Five-Lined Skink" (*"Le scinque a cinq raies"*) which he calls *Scincus quinquelineatus,* citing *L. quinquelineata* Linnaeus, 1766 for the original description. Say (1818) noted this discrepancy, pointing out that Green's name and description applied to Daudin's *S. quinquelineatus,* not his *L. quinquelineata.* Green notes that his species differs from the "nominal race" only in the color of the dorsal stripes (white in his variety, yellow in Carolina), apparently in reference to Linnaeus' skink rather than Daudin's teiid. Subsequently, Fitzinger (1843) designated *L. quinquelineata* Linnaeus, 1766 as the

type species of *Plestiodon* Duméril & Bibron, 1839. We note that while *L. quinquelineata* Linnaeus, 1766 has been treated as a junior subjective synonym of *L. fasciata* Linnaeus, 1758 (e.g., Daudin 1802b; Green 1818; Say 1818), this is merely convention, and it may instead represent *Scincus laticeps* Schneider, 1801 or *Eumeces inexpectatus* Taylor, 1932, all of which occur in "Carolina" (see Smith 2005).

Lacerta hyacinthina Green, 1818

The "Indigo L[izard]." (Eastern Fence Lizard; *Sceloporus undulatus*); no type specimen designated; no type locality given. Stejneger & Barbour (1943) stated that the type locality was "probably the vicinity of Princeton, New Jersey." Malnate (1971) stated that the syntypes were "ANSP 8345–46, 8348; New Jersey; Jacob Green (?)." As noted above and discussed by Bell (1996), we believe this to be a reliance on early notes from Fowler or Dunn, hence Malnate's question mark. The series ANSP 8345–8348 is from the 1851 Bache donation of the Green collection and was thus interpreted by Dunn to represent the types of *L. hyacinthina* Green, 1818 and *L. fasciata* Green, 1818 (see below). However, Bell (1996) noted that ANSP 8348 is actually an *S. graciosus* Baird & Girard, 1852, and that no documentary evidence tied these specimens to Green's descriptions. Therefore, Bell (1996) rejected the type status of ANSP 8345–46 & 8348, and designated ANSP 35082 as the neotype, from "Crossley Preserve, western Berkeley Township, Ocean County, New Jersey, 4.76 mi (7.05 km) directly west of the Garden State Parkway bridge over Toms River at Toms River, New Jersey." Say (1818) noted that this species had already been described as *Stellio undulatus* Bosc & Daudin *in* Latreille & Sonnini, 1801. The name subsequently enjoyed a long modern tenure as a valid subspecies of *Sceloporus undulatus*, from Smith (1948) until Leaché & Reeder (2002; see Bell *et al*. 2003).

Lacerta fasciata Green, 1818

The "Banded L[izard]." (Eastern Fence Lizard; *Sceloporus undulatus*); no type specimen designated; no type locality given. Malnate (1971) states that ANSP 8347 is the holotype from New Jersey, with collector "Jacob Green (?)." As noted above, there is some question as to whether or not the series ANSP 8345–8348 actually represents primary types for any of Green's names. However, we find no reason to reject the type status of ANSP 8347 at present, as it is indeed a female that matches Green's description (see Smith 1938). To preserve stability, we continue to accept existing designations of Green's putative "types by association" unless otherwise specified. Based on the description and specimen, this name is clearly a junior subjective synonym of *Stellio undulatus* Bosc & Daudin *in* Latreille & Sonnini, 1801 as noted by Say (1818) and confirmed by Smith (1938). It is also a junior primary homonym of *Lacerta fasciata* Linnaeus, 1758 (see Bell *et al.* 2003; Smith 1948) and thus permanently unavailable under Article 57.2 of the ICZN (Anonymous 1999).

Green (1818) subsequently offers accounts and descriptions of species in "Order III. Batracian reptiles. *Second family.* Tailed batracians. *Genus* Salamandra." The first of these is:

Salamandra maculata Green, 1818

The "Brown-spotted Salamander" (Red Salamander; *Pseudotriton ruber*); no type specimen designated; no type locality given. Green (1818) describes this species as "Length four or five inches; *tail* about as long as the body, tapering, slightly compressed, and pointed; *back* whitish, sprinkled with irregular, reddish-brown spots; *beneath* white; anterior *feet* four-toed, posterior feet five-toed," seemingly referring to a light-colored or faded specimen of *Pseudotriton.* Despite the similarity in name and assumptions by some subsequent authors (e.g., Gray *in* Cuvier 1831), this name was apparently erected by Green to refer to specimens of the Red Salamander, *P. ruber* (Sonnini de Manoncourt & Latreille, 1801), and not the Spotted Salamander, *Ambystoma maculatum* (Shaw, 1802). Green knew the Spotted Salamander as *Salamandra subviolacea* Barton, 1804, giving accounts in Green (1825a; 1827a).

Indeed, Cope (1869) states that *Salamandra rubriventris* Green, 1818, *S. maculata* Green, 1818, and *S. subfusca* Green, 1818 are all junior subjective synonyms of *S. rubra* Sonnini de Manoncourt & Latreille, 1801, though he instead attributes this name to "Daud., Hist. Rept. viii, 227, pl. 97, f. 2," and not Sonnini de Manoncourt & Latreille (1801). The reason for this confusion is unclear, given Daudin (1803:227)'s clear reference to "Latreille, Hist. nat. des reptiles, in-18, additions, tom. IV, p. 305." Cope (1869) further suggests that the oddly whitish coloration of Green's specimen was likely due to bleaching in preservative. Thus, it is clear that *Salamandra maculata* Green,

1818 is a junior subjective synonym of *S. rubra* Sonnini de Manoncourt & Latreille, 1801, and not *Lacerta maculata* Shaw, 1802. This synonymy was noted by several later authors, including Dunn (1926), and Martof (1975).

Green (1818) applied two other names to populations of *Pseudotriton: "rubriventris"* and *"subfusca"* (see below), apparently confused by the degree of color-pattern polymorphism and ontogenetic darkening in this species, and perhaps also observing specimens of *P. montanus* Baird, 1850 along with *P. ruber.* Some of these populations (*"rubriventris"*) he considered conspecific ("varieties") with *Salamandra rubriventris* Daudin, 1803 (a junior synonym of *Triton alpestris* Laurenti, 1768 [*Ichthyosaura alpestris*]), while he cautiously considered *"maculata"* and *"subfusca"* to be distinct species. Indeed, he later stated in a letter to Cuvier (Green 1830) that "The S. Rubra of Daudin, which appears to have been the first of these animals described, comes very near to my S. Rubriventris. Var. Whether the S. Maculata be a distinct species, is yet doubtful. These three, in certain stages of growth, and especially when preserved in alcohol, require minute attention to distinguish from each other."

However, Green apparently makes a curious error of attribution and citation between 1818 and 1830. It seems obvious from the context that Green intends to compare his specimens with the Red Salamander (*Pseudotriton ruber*), and not the Alpine Newt (*Ichthyosaura alpestris*), with which the Red Salamander could hardly be confused. Say (1818) pointed out this discrepancy. Correspondingly, Daudin (1803:227, Pl. XCVII, Fig. 2) gave an account and illustration of *Salamandra rubra* Sonnini de Manoncourt & Latreille, 1801, directly citing those authors. However, Green (1818) explicitly describes his *S. rubriventris* as a variety of *S. rubriventris* Daudin, 1803*,* citing "vol. 8, p. 239, pl. 98, fig. 1," which clearly describes and illustrates an Alpine Newt. Why Green (1818) cites Daudin (1803)'s description of *S. rubriventris* from page 239 rather than his account of *S. rubra* on page 227 as seemingly intended is unclear. By 1830, it seems that Green had recognized his mistake regarding Daudin's *S. rubriventris* and refers correctly to Daudin's *S. rubra.*

Salamandra fasciata Green, 1818

The "Banded S[alamander]." (Marbled Salamander; *Ambystoma opacum*); syntypes putatively ANSP 1420–1423 (*fide* Malnate 1971); type locality not given, restricted to "vicinity of Princeton, New Jersey" by Schmidt (1953) without justification. The syntypes are extant in the ANSP collection; Malnate (1971) lists them as originating from "New Jersey; Dr. Bache." Thus, these are among the putative types-by-association for which little direct evidence links them to this description. Assuming we continue to treat ANSP 1420–1423 as the syntypes, their "original" type locality of "New Jersey" would retain precedence over Schmidt (1953)'s unjustified restriction. The description states "Length between four and five inches; *tail* about as long as the body, oval, tapering, and pointed; *snout* rounded; *back* brown, marked with transverse, irregular blue bands; upper part of the *tail* brown, marked with light yellow spots; *beneath* ash colour; anterior *feet* four-toed, posterior five-toed." This description and a brief examination of the putative syntypes confirms the identity of this taxon as the Marbled Salamander, and it was designated as a junior subjective synonym of *Salamandra opaca* Gravenhorst, 1807 by Baird (1850).

Salamandra subfusca Green, 1818

The "Olive-brown S[alamander]." (Red Salamander; *Pseudotriton ruber*); no type specimen designated; no type locality given. Green describes this species as "Length six inches; *tail* rather shorter than the body, tapering, slightly compressed, and pointed; *snout* rather oval; *back* of an olive-brown hue, marked with dark spots; *beneath* yellowish, and spotted; anterior *feet* four-toed, posterior five-toed." Based on this description, this species was designated a junior subjective synonym of *Salamandra rubra* Sonnini de Manoncourt & Latreille, 1801 by Baird (1850), and later treated as such by Cope (1869), Dunn (1926), and Martof (1975). The description clearly refers to an age-darkened specimen, which are common in many populations (Petranka 1998; Powell *et al.* 2016). Green notes that he has two apparent varieties of this taxon, one with more distinctive spots than the other; he attributes this difference to ontogenetic variation. It is also possible that he obtained *P. montanus* Baird, 1850 from southern New Jersey. He also compares the coloration to the "common Water Newt of New England," showing that he was familiar with the adult form of *Triturus (Diemictylus) viridescens* Rafinesque, 1820 (*Notophthalmus viridescens*).

Salamandra longicauda Green, 1818

The "Long-tailed S[alamander]." (Long-Tailed Salamander; *Eurycea longicauda*); no type specimen designated; type locality "in marshy places, in the state of New-jersey." Dunn (1926) stated that the types were not known to exist; multiple specimens were clearly examined as a range of lengths is given. A search of the collections at the

ANSP did not yield any further material that could be confidently associated with this description. As the definition of this taxon is not in dispute, a neotype designation is not warranted (Article 75.1). We suggest that the watercolor plate Mss.B.P.31.15d.149b in the Titian Ramsay Peale Sketches collection at the American Philosophical Society in Philadelphia dated 1 May 1819 may represent one of Green's original specimens (Fig. 1). The two were close friends (Smith 1923), and the original description of *Ambystoma tigrinum* (Green, 1825a) was based on a live pet of Peale's and his illustration thereof (see below).

FIGURE 1. A watercolor painting of *Salamandra longicauda* Green, 1818 by Titian Peale, dated 1819 (Mss.B.P31.15d.149b). This may represent one of Green's original specimens. The margin notes in pencil (cropped from the original) read "4 ¾ inches long," "Pitts[g] [Pittsburg?] May 1st 1819," and "n° 4." Courtesy of the American Philosophical Society.

Salamandra nigra Green, 1818

The "Black S[alamander]." (Northern Dusky Salamander; *Desmognathus fuscus*); no type specimen designated; no type locality given. Green describes this species as "Length about four inches; *tail* of the length of the body, tapering, oval, and pointed; *snout* oval; *eyes* black, prominent, and approximate; *back* blackish; *sides* sprinkled with small white spots; *beneath* whitish; anterior *feet* four-toed, posterior feet five-toed." Green further notes "this differs from Daudin's *La S. noire* [*Salamandra atra* Laurenti, 1768], that being uniformly black." Given the description and Green's residence and fieldwork in Pennsylvania and New Jersey, it is clear that this name was intended to represent populations of what are now known as *Desmognathus fuscus* (Rafinesque, 1820); Northern Dusky Salamanders from the northeastern United States. Indeed, most early authors used it this way, such as Harlan (1827a), de Kay (1842), and Hallowell (1856, 1858), along with the names *Salamandra intermixta* Green, 1825b and *S. picta* Harlan, 1825 (see below) for various populations of what are now known to be the same species (Dunn 1917).

However, Holbrook (1842)'s account of *"Triton niger.*–Green.*"* expanded Green's name to refer in part to southern Appalachian populations of large, heavy-bodied, black-bellied salamanders that are now known as *Desmognathus quadramaculatus* (Holbrook, 1840), populations which Dunn (1917) notes represent a species that Green likely never saw. Holbrook states he has seen this species in "Carolina and Georgia;" these are presumably MCZ 183 from "Charleston, S.C." and ANSP 14001 from "Penn." which were "presented" to those museums by Holbrook and are the oldest-known specimens of what is now known as *D. quadramaculatus* (see Dunn 1926). Having examined them, they are both of the southern montane form now referred to as *D. quadramaculatus* (Petranka 1998; Powell *et al.* 2016); the catalog localities at MCZ and ANSP are thus presumably in error. The former was likely the port from which Holbrook shipped the specimen, while the latter was recorded in the ANSP ledger by Fowler in the late 19th or early 20th century, likely based on only Holbrook (1842)'s account.

The bottle of MCZ 183 contains a handwritten note from Barbour stating that it was "probably given by Holbrook to Louis Agassiz." The ANSP specimen (14001) was reported as missing by Adler (1976) citing communication from E. Malnate (ANSP; see Malnate 1971), although it is currently extant in the collection in remarkably poor condition. One of these two specimens is presumably the one illustrated on Pl. 27 of Holbrook (1842). Holbrook additionally states that he received specimens from Louisiana; these were likely either *Desmognathus conanti* Rossman, 1958 or *D. valentinei* Means, Lamb, and Bernardo, 2017 (see Beamer & Lamb 2020). He also placed *Salamandra intermixta* Green, 1825b and *S. picta* Harlan, 1825 in synonymy with *Triton niger.* Though Holbrook likely conceived of this species as representing primarily northeastern "dusky" salamanders, the (perhaps inadvertent)

inclusion and illustration of large, heavy-bodied, black-bellied specimens from the southern Appalachians and description of the range as "the Atlantic States from lat. 43° to the Gulf of Mexico" expanded his concept of *T. niger* to include what are now known as *D. fuscus* and *D. quadramaculatus* from the Appalachians and Piedmont, as well as *D. conanti* or *D. valentinei* from the Coastal Plain.

Following Holbrook (1842), the name *"nigra"* was frequently applied to large, heavy-bodied, black-bellied specimens of *Desmognathus* from the southern Appalachians (see Valentine 1974), starting with Baird (1850). Baird mentions examining a single specimen of "D. niger" in the ANSP which he speculated might have been Green's holotype, but we agree with Dunn (1917) that this was Holbrook's specimen ANSP 14001. Cope (1869) mentions examining the same specimen, which he identifies as *"D. niger,"* and considers it distinct from *D. fuscus*. The catalog entry for ANSP 14001 identifies it as "*Desmognathus niger*." Finally, Hallowell (1858) referred to a specimen of *D. auriculatus* (Holbrook, 1838) from Holbrook in the ANSP, which we also think was very likely ANSP 14001, it being the only Holbrook specimen present at the ANSP that is not clearly referable to what is now known as *D. fuscus*.

Stejneger (1903) then re-described *Desmognathus quadramaculatus* (Holbrook, 1840) based on a series (USNM 30891–30902) from Grandfather Mountain, at or near the type locality of *Leurognathus marmoratus* Moore, 1899. From this, we receive the modern conception of the taxon (*sensu* Valentine 1974) as a large, heavy-bodied, black-bellied species from the southern Appalachians. Interestingly, Stejneger (1903) also continued to recognize *"D. nigra,"* although he did not cite a taxonomic authority, and he did not describe his conception of that taxon. Very few authors after 1903 continued to recognize or use the name *D. nigra,* most still in reference to "black-bellied" rather than "dusky" salamanders (e.g., Brimley 1907; Brimley & Sherman 1908; Stone 1906). Despite having priority and being the available, valid name for the taxon now known as *D. fuscus*, the name *Salamandra nigra* Green, 1818 subsequently fell into disuse, and was considered to be a *nomen dubium* by Crother *et al*. (2003).

FIGURE 2. A specimen (ANSP 900) of *Triturus fuscus* Rafinesque, 1820 from "Dr. Bache, Green coll.," locality "near Phila.," here designated as the neotype of *Salamandra nigra* Green, 1818. This name is thus a senior subjective synonym of *Triturus fuscus* Rafinesque, 1820.

However, at least some of Green's original material is extant. Two collections in the ANSP catalogued as *"D. fuscus"* originate from "Dr. Bache, Green Coll." These are ANSP 900–912 ("near Phila.") and 955–979 ("Penns."). Having examined them, they are all apparently *fuscus,* likely from Pennsylvania as recorded. These are likely those referenced by Hallowell (1858) as among the 40 specimens of *"Desmognathus niger"* present in the collections of the Academy "presented by Dr. Bache, (Green collection,)." Similarly, while Harlan (1827a) does not mention specimens of *Salamandra bislineata* Green, 1818, *S. sinciput-albida* Green, 1818, *S. erythronota* Green, 1818, or *S. fusca* Green, 1818 in the cabinet of the Academy, he does mention them for *S. cinerea* Green, 1818 and *S. nigra* Green, 1818. We suggest that no other species from the vicinity of Princeton or Philadelphia could fit Green's description. To remove any potential ambiguity, we thus designate ANSP 900 (Fig. 2), a specimen of *Triturus fuscus* Rafinesque, 1820 from "Dr. Bache, Green coll.," locality "near Phila.," as the neotype of *S. nigra* Green, 1818. The name *S. nigra* Green, 1818 would thus assume priority over *T. fuscus* Rafinesque, 1820 as noted by previous authors (see Frost 2002), were it not for action we take here to validate the name *S. fusca* Green, 1818 for this species (see below).

Salamandra bislineata Green, 1818

The "Two-lined S[alamander]." (Northern Two-Lined Salamander; *Eurycea bislineata*); type specimens not originally designated but stated to be ANSP 695–698 by Fowler & Dunn (1917); type locality not originally stated but restricted to "New Jersey (probably Princeton?)" by Fowler (1907). Dunn (1926) stated there were no types in existence and probably never were any, but the basis of this statement is unclear. Yarrow (1882) listed USNM 3738 (two specimens) from "West'n Pennsylvania" collected by "Dr. J. Green" as the "Alc. type." Cope (1889) repeated that USNM 3738 from "western Pennsylvania" were the types, but also stated that Green's types were probably from New Jersey. The designation of USNM 3738 as the types was followed by Stejneger and Barbour (1917, 1933), but not by Cochran (1961) in her list of USNM type material.

FIGURE 3. A poorly preserved specimen (USNM 3738) that we are nevertheless comfortable in assigning to *Salamandra bislineata* Green, 1818. Referred to by Cope (1889) as the "alcoholic type" from "Western Pennsylvania" collected by "Dr. J. Green," which was followed by Stejneger and Barbour (1917, 1933), but not by Cochran (1961) in her list of USNM type material. Based on Green's collections in western Pennsylvania primarily occurring after 1826, we do not consider this part of the original type series.

Examination of USNM 3738 and the NMNH catalog reveals a single small *Eurycea bislineata* in extremely poor, nearly unrecognizable condition (Fig. 3), putatively collected by Green in 1818 with the locality "western Pennsylvania." However, the accounts in Green (1818) all appear to be based on material collected by Green around Princeton and Philadelphia. We can find no reference to any collection by Green in western Pennsylvania until 1826 when he began to visit Jefferson College in Canonsburg, where he gave summer lectures after 1828 (Bennett 1949) and later described several species (Green 1827a). Thus, while USNM 3738 may be a Green specimen, we suggest it is not part of the original type series for *Salamandra bislineata* Green, 1818. Below (see accounts for *S. erythronota, S. cinerea,* and *S. fusca*), we report on the discovery of an additional specimen from the ANSP Green collection that bears heavily on interpretation of the type material and locality.

Salamandra sinciput-albida Green, 1818

The "White-nosed S[alamander]." (Four-Toed Salamander; *Hemidactylium scutatum*); no type specimen designated; type locality "found in Newjersey." Green describes this species as "Length about three inches; *tail* shorter than the body, thick, tapering, and pointed; *snout* oval, white above; *eyes* protuberant; *back* dirty ferruginous; *beneath* yellowish; anterior *feet* four-toed, posterior five-toed." Regarded by Dunn (1926) as a senior subjective synonym of *Tritrurus fuscus* Rafinesque, 1820, but without a clear explanation for preferring the younger name. Considered to be a *nomen dubium* by Crother *et al*. (2003).

In contrast to Dunn (1926)'s assertion, it seems exceptionally unlikely that *Salamandra sinciput-albida* Green, 1818 was intended to refer to *Triturus fuscus* Rafinesque, 1820. Green (1818) notes that it was "…said to inhabit shallow waters," where the verb "said" suggests that Green himself never saw a live example, or at least never collected one in the wild. The small size; short, thick tail; reddish-brown back; and white patch on the snout immediately call to mind *Hemidactylium scutatum* (Temminck *in* Temminck & Schlegel, 1838). Indeed, we suggest that no other New Jersey species could fit this description. The only objection to this is Green's statement of a yellowish venter rather than white, and his note of five toes on the rear foot rather than the four toes the species is known for.

The former could be explained if he never saw a live specimen, only receiving preserved specimens that had been discolored, as Cope (1869) suggested for *S. maculata* Green, 1818. While adult newts (*Notophthalmus viridescens*) often have yellowish venters, Green (1818)'s account of *S. subfusca* Green, 1818 shows he was already familiar with this species, and the size, tail, and dorsal coloration further reject this possibility. We also reiterate that Green's vision was impaired, and that his descriptions of color pattern do not match modern understandings for many species. For instance, he describes *Salamandra fasciata* Green, 1818 (*Ambystoma opacum*) as being "brown" with "blue bands," while living specimens of this species are generally jet black with white, grey, or silver bands (Petranka 1998; Powell *et al.* 2016). With regard to the number of toes, he may have miscounted or received a mutated specimen, and both inaccuracies could be explained if he only received secondhand reports. Harlan (1827a) placed *S. sinciput-albida* Green, 1818 with the "land salamanders" provisionally on the form of the tail and did not note any specimens in the Academy. This further supports the idea that neither Green nor Harlan had actually collected or observed this taxon themselves.

Accordingly, we remove *Salamandra sinciput-albida* Green, 1818 from the synonymy of *Triturus fuscus* Rafinesque, 1820, and place it in synonymy with *S. scutata* Temminck *in* Temminck & Schlegel, 1838. We note that the holotype (RMNH 2301) of *S. scutata* Temminck *in* Temminck & Schlegel, 1838, is from "Nashville, Tenn." (see Hoogmoed 1978). Given the much later date and distant geographic origin of this specimen and the lack of any *Hemidactylium* specimens in the ANSP collection referable to Green, we refrain from designating a neotype for *S. sinciput-albida* Green, 1818.

Ordinarily, this action would require application of the Principle of Priority under Article 23.1, with *Hemidactylium sinciput-albida* (Green, 1818) replacing *Hemidactylium scutatum* (Temminck *in* Temminck & Schlegel, 1838) as the senior-most available, valid name for this species. However, this would disrupt prevailing usage, and we thus invoke Reversal of Precedence under Article 23.9 to avoid this. Literature searches through Web of Knowledge and Google Scholar reveal no usage of the name *Salamandra sinciput-albida* Green, 1818 as a valid name after 1899 (23.9.1.1), while the period from 1969 to 2019 records at least 1,180 usages (23.9.1.2) of *Hemidactylium scutatum* (Temminck *in* Temminck & Schlegel, 1838).

We thus regard the more senior name *Salamandra sinciput-albida* Green, 1818 as a *nomen oblitum,* and the junior objective synonym *S. scutata* Temminck *in* Temminck & Schlegel, 1838 as a *nomen protectum.* The name

S. frontalis Gray *in* Cuvier, 1831 was erected as a replacement name for *S. sinciput-albida* Green, 1818, and we thus remove it from the synonymy of *Triturus fuscus* Rafinesque, 1820 and place it in the synonymy of *S. scutata* Temminck *in* Temminck & Schlegel, 1838. We again invoke Reversal of Precedence under Article 23.9 to consider *S. frontalis* Gray *in* Cuvier, 1831 a *nomen oblitum,* as it does not ever appear to have been used as a valid name outside of its original publication. Recent molecular analyses reveal the presence of multiple clades within *Hemidactylium scutatum* (see Herman & Bouzat 2016), with specimens from Tennessee and New Jersey representing different lineages. Thus, *S. sinciput-albida* Green, 1818 would still be an available name for a northeastern species of *Hemidactylium* if one were to be described in the future (see Ohler & Dubois 2018). In this case, a neotype from New Jersey would likely be warranted.

Salamandra rubriventris Daudin, 1803 (var.)

The "Red S[alamander]." (Red Salamander; *Pseudotriton ruber*); no type specimen designated, type locality "in the neighbourhood of Princeton, in shallow streams." Green (1818) describes this species as "Length between six and seven inches; *tail* shorter than the body, slightly tapering, compressed, and pointed; *skin* slimy; *back* blackish, with brown spots; *sides* red; *beneath* red; *eyes* protuberant; *snout* rounded; anterior *feet* four-toed, posterior five-toed." This was regarded as a new name *S. rubriventris* Green, 1818 by later authors (Holbrook 1842; de Kay 1842), and thus a junior subjective synonym of *S. rubra* Sonnini de Manoncourt & Latreille, 1801, and a junior primary homonym of *S. rubriventris* Daudin, 1803, which is a junior subjective synonym of *Triton alpestris* Laurenti, 1768.

However, Green (1818:353) states that: "This I think is only a variety of *La S. ventre orangé* of Daudin, a description and figure of which he has given in his vol. 8, p. 239, pl. 98, fig. 4" and refers to it again as "*Salamandra rubriventris,* var." on the same page. Thus, he did not regard his *"rubriventris"* as a new species, only a variety, and was simply applying the name *S. rubriventris* Daudin, 1803 to a population of what is now known as *Pseudotriton ruber*. Therefore, there is no name *S. rubriventris* Green, 1818. However, as noted above and by Say (1818), it seems that he intended to compare his specimens to Daudin (1803:227)'s account of *S. rubra* Sonnini de Manoncourt & Latreille, 1801, not that of Daudin (1803:239)'s description of *S. rubriventris*. The explanation for this lapsus is unclear.

Green (1818) then introduces a new division, the "Land Salamanders." These include:

Salamandra erythronota Rafinesque, 1818a (the "Red-backed S[alamander].")
and
Salamandra cinerea Green, 1818 (the "Dapple S[alamander].")

Rafinesque (1818a) described the Red-Backed Salamander (*Plethodon cinereus*) as *Salamandra erythronota* Rafinesque, 1818a in March 1818, several months before Green (1818)'s paper was read. Green (1818) himself stated that he was applying "Mr. Rafinesque's name" to red-backed populations from "Newyork" and "Newjersey." He then describes *S. cinerea* Green, 1818 for the lead-backed form from "Newjersey." Neither Rafinesque (1818a) nor Green (1818) explicitly designated any type specimens. In his letter to Cuvier, Green (1830) stated: "The S. cinerea is almost always found associated with the S. erythronota, and though very different from it in colour, I am disposed to think it merely a variety of that species." A long period of taxonomic confusion and nomenclatural instability followed (see Goodwin 1960; Highton 1960; Reed 1960), wherein attribution and allocation of the names *"erythronota"* and *"cinerea"* varied significantly from author to author and publication to publication.

This culminated in Dunn (1926) using *Salamandra cinerea* Green, 1818 for the red-backed salamander and recognizing the lead-backed form as a color morph, establishing a long-term trend thereafter despite the clear priority (and more straightforward logical applicability) of the name *S. erythronota* Rafinesque, 1818a for the species. To preserve prevailing usage, later authors successfully petitioned for suppression of *S. erythronota* Rafinesque, 1818a (Anonymous 1963a; Highton 1961). This established *S. cinerea* Green, 1818 as the available, valid name for the Red-Backed Salamander. Fowler (1907) and Fowler and Dunn (1917) listed Green's series ANSP 1227–38 from "New Jersey" as the syntypes. Highton (1962) restricted this to 1232–34 & 37 (the lead-backed specimens), from which he designated 1232 as the lectotype, rendering the remaining specimens paralectotypes.

We note again that these specimens originated from "Dr. Bache, Green Collection," as per Fowler's handwritten entry in the ANSP catalog, and thus don't bear a direct link to Green (1818)'s original description. Fowler (1907)

revised the type locality to "near Princeton?" and Schmidt (1953) to "vicinity of Princeton." However, Highton (1962)'s lectotype designation reverted the type locality back to the "New Jersey" of the ANSP catalog, originally "Newjersey" in Green (1818). These specimens and the jar containing them (and others) are also relevant to several of Green (1818)'s other names, including *S. bislineata* and *S. fusca* (see below).

Salamandra glutinosa Green, 1818

The "Glutinous S[alamander]." (Northern Slimy Salamander; *Plethodon glutinosus*); no type specimen designated; no type locality given. Green (1818) describes this species as "Length six inches; *tail* nearly twice as long as the body, tapering, and pointed, near the end slightly compressed; *snout* obtuse; *eyes* prominent and dark brown; *back* blackish, marked with white spots, composed of small dots; *beneath* black; anterior *feet* four-toed, posterior five-toed." He further notes "Found under stones, in elevated situations. A glutinous fluid exudes from the pores of the skin; this fact is only uncommon as to the quantity." This description clearly refers to the Northern Slimy Salamander and could apply to no other northeastern USA species. Given the exceptional diversity in this complex (Highton *et al.* 1989) and the potential ambiguity of the type locality and thus allocation of this name, a neotype designation may be warranted in the future. However, we were unable to locate any contemporary material with a connection to this taxon, and thus refrain at present. Dunn (1926) stated that the type locality was "obviously Princeton, New Jersey," but this is not indicated in Green (1818)'s description. An expanded account and figure (Fig. 4) of a "variety" of this species from Chartier's Creek, Washington County, Pennsylvania was given by Green (1827a, unnumb. [third] Pl.).

FIGURE 4. Green (1827a)'s figure (third unnumbered plate) of a "variety" of *Salamandra glutinosa* Green, 1818, from Washington County, Pennsylvania, drawn by W. Mason and engraved by P.E. Hamm.

Salamandra fusca Green, 1818

The "Brown S[alamander]." (Northern Dusky Salamander; *Desmognathus fuscus*); no type specimen designated; no type locality given. Green (1818) describes this species as "Length about three inches; *tail* length of the body, tapering and slightly compressed; *snout* obtuse; *eyes* not remarkably prominent; *back* uniformly of a yellowish brown colour; *beneath* white, with a line, on each side, of black spots; *throat* spotted with black; anterior *feet* four-toed, posterior five-toed." Most authors have agreed that this represents the "dusky" salamander (*D. fuscus*) of the northeastern USA (see Dunn 1917). However, the name *Salamandra fusca* Green, 1818 is a junior primary homonym of *S. fusca* Laurenti, 1768, which was designated as a junior subjective synonym of *S. atra* Laurenti, 1768 by Merrem (1820), and *S. fusca* Green, 1818 is thus permanently unavailable barring Reversal of Precedence.

Accordingly, the names *Salamandra nigra* Green, 1818, *S. intermixta* Green, 1825b, and *S. picta* Harlan, 1825 were variously applied to northeastern "dusky" salamanders until Holbrook (1842). Baird (1850) then applied the name *S. nigra* to the "black-bellied" salamanders and resurrected the name *Triturus fuscus* Rafinesque, 1820 for the "dusky" salamanders, with *S. intermixta* Green, 1825b, *S. picta* Harlan, 1825, and *S. quadramaculata* Holbrook, 1840 in synonymy. Rafinesque's name was later placed on the Official List of Specific Names in Zoology (Anonymous 1956). Rafinesque (1820) had also described a species clearly referable to "*fuscus"* as *T. nebulosus* Rafinesque, 1820 from "near New York, at Harlem and Long Island." The name *"fuscus"* was selected over *"nebulosus"* by Baird (1850) acting as the First Reviser (Article 24.2.1), who declared *"nebulosus"* a *nomen dubium*. Populations in Harlem have been genetically identified as conspecific with the remaining populations in the northeastern

USA by Munshi-South *et al*. (2013), confirming their subjective synonymy. No specimens have been associated with either Green or Rafinesque's names historically.

However, relevant material may be present in the putative type-series of *Salamandra cinerea* Green, 1818. Dunn (1926) stated that such a series did not exist, but Fowler (1907) and Fowler and Dunn (1917) identified Green's series ANSP 1227–38 from "New Jersey" in the ANSP as the syntypes. Highton (1962) formally restricted the syntypes to 1232–1234 & 1237, these being the lead-backed specimens in the jar, to differentiate the type series from the red-backed *S. cinerea* Rafinesque, 1818a. He further designated 1232 as the lectotype, rendering 1233, 1234, and 1237 paralectotypes. Of the remaining 8 specimens, 5 are red-backed *Plethodon cinereus*: 1227, 1230, 1231, 1235, and 1236. He states that 1229 "is in such poor condition I cannot identify it." However, upon examination it seems to be a small, likely red-backed *P. cinereus* in acceptable condition (Fig. 5), with what appear to be 19 visible costal grooves. Of the two remaining specimens in the series, we concur with Highton that 1238 is clearly a large *Eurycea bislineata*, and that 1228 seems to be a larval or transforming *Desmognathus fuscus*.

FIGURE 5. A poorly preserved specimen (ANSP 1229) that we are nevertheless comfortable in assigning to *Plethodon cinereus* (Green, 1818). Fowler (1907) and Fowler and Dunn (1917) had considered the series ANSP 1227–38 from "Dr. Bache, Green Collection," locality "New Jersey" as the syntypes of *Salamandra cinerea* Green, 1818, but Highton (1962) restricted this to 1232–34 & 37, designating 1232 as the lectotype, rendering the remaining specimens paralectotypes. Thus, this specimen no longer has any name-bearing function.

The *Eurycea bislineata* ANSP 1238 (Fig. 6) bears a faded parchment tag that appears to read (at least in part) "Green Coll." Fowler and Dunn (1917) considered ANSP 695–698 as syntypes of *Salamandra bislineata* Green, 1818; it seems prudent that 1238 be considered a syntype, as well, given that it is labeled as originating from the Green collection and is physically associated with the other Green types. We hereby designate ANSP 1238 as the lectotype of *S. bislineata* Green, 1818, rendering ANSP 695–698 paralectotypes. As noted above, we do not consider USNM 3738 to be part of the type series for this species.

The putative *Desmognathus fuscus* ANSP 1228 (Fig. 7a, b) is quite interesting. It agrees with the original description of *Salamandra fusca* Green, 1818 in several crucial respects, including an SVL of approximately 1.5 inches, obtuse snout without prominent eyes, and a uniformly brown dorsum and white venter. The specimen is poorly preserved, so it is difficult to tell if the line of black spots on either side of the venter and the black spotting of the throat mentioned in the description were once present and have faded in preservative. The specimen appears to have 14 costal grooves and hindlimbs much stouter than the forelimbs, key characteristics of *Desmognathus* (Petranka 1998; Powell *et al*. 2016).

Most crucially, Green (1818) mentions accidentally severing the tail of the single specimen he encountered. He states "Note. I know not whether this is a land or water animal; it was found under a rail in a moist place, some distance from a stream. The tail, which was accidentally separated from the body, preserved a vibratory motion for some time. This motion of the tail, when amputated, is I believe common to all Salamanders, and indeed to most reptiles." The specimen ANSP 1228 is also missing its tail, and an examination of the stump seems to indicate an injury in life, as the musculature has begun to contract around the break as seen in living organisms having undergone caudal amputation or autotomy, rather than a ragged or jagged edge as typically observed when a specimen is fractured after preservation. There are several pieces of tail in the jar, but they all appear to correspond to the other specimens of *Plethodon.* Thus, we regard ANSP 1228 as the likely holotype of *Salamandra fusca* Green, 1818. A single jar in the Academy of Natural Sciences of Drexel University is now recognized to contain the type specimens of three of the most well-known amphibian species in the world: *Desmognathus fuscus, Eurycea bislineata,* and *P. cinereus.*

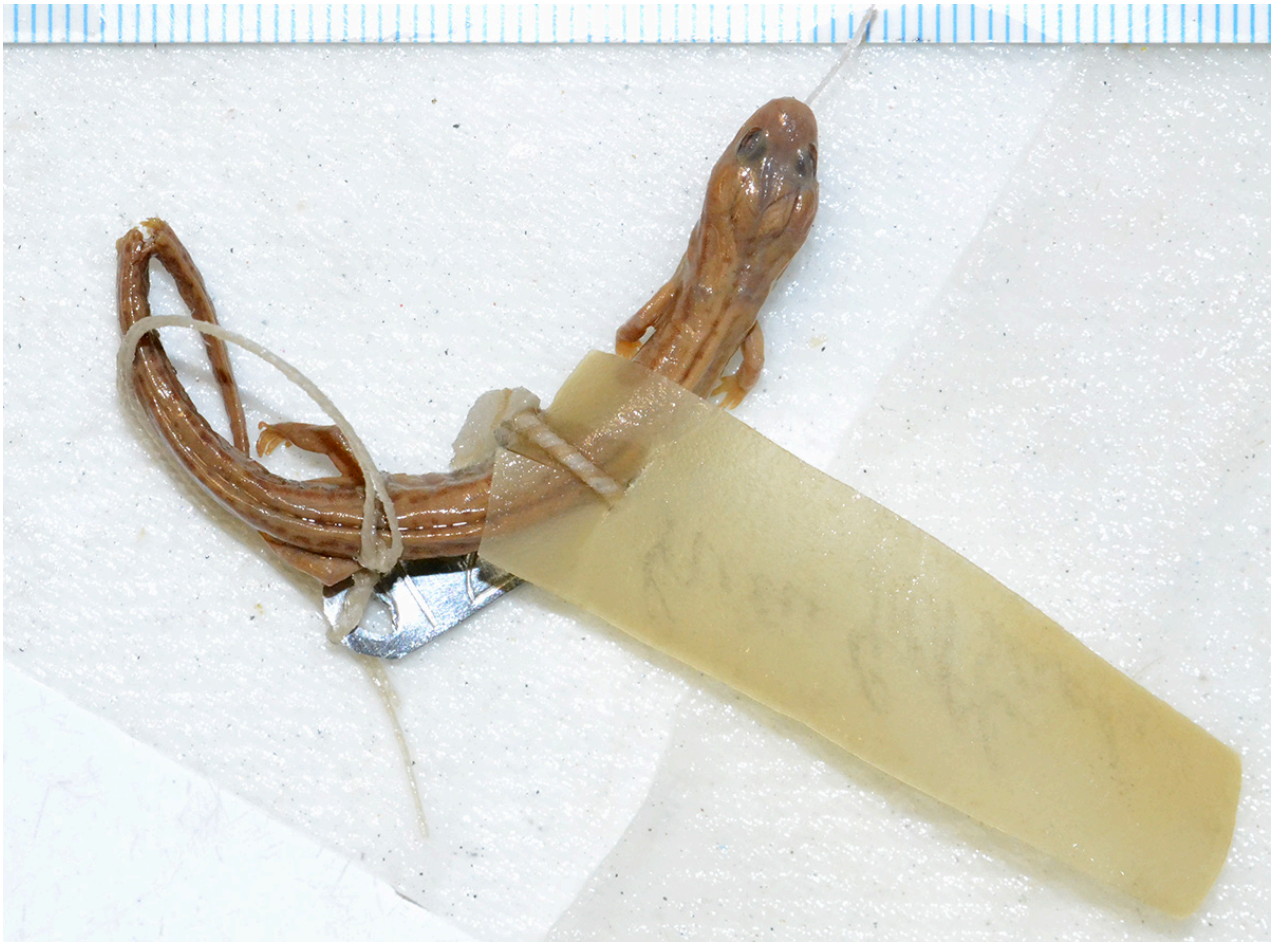

FIGURE 6. Newly designated lectotype (ANSP 1238) of *Salamandra bislineata* Green, 1818. Recorded in the ANSP catalogue as *"P. cinereus"* from "New Jersey" originating with "Dr. Bache, Green Collection." Fowler and Dunn (1917) considered ANSP 695–698 the syntypes, which we here designate as paralectotypes.

However, this does not change the fact that *Salamandra fusca* Green, 1818 is a junior primary homonym of *S. fusca* Laurenti 1768, and thus remains unavailable. Based on the action we have taken above to reinstate the availability, validity, and subjective synonymy of *S. nigra* Green, 1818 over *Triturus fuscus* Rafinesque, 1820, that species would, barring further action, now necessarily be referred to as *Desmognathus niger* (Green, 1818). Indeed, such an action was taken by Frost (2002) in version 2.21 of Amphibian Species of the World. This led Crother *et al*. (2003) to declare *S. nigra* Green, 1818 a *nomen dubium* and reinstate *T. fuscus* Rafinesque, 1820 to maintain prevailing usage. However, that action is untenable based both on our neotype designation for *S. nigra* Green, 1818, and the long usage of that name to refer to both dusky *and* black-bellied populations of *Desmognathus* (e.g., Baird 1850; Hallowell 1856; Harlan 1827a).

Instead, we will again invoke Reversal of Precedence under Article 23.9 to maintain prevailing usage of the

name *Desmognathus fuscus*. We state that, to our knowledge, *Salamandra fusca* Laurenti 1768 has not been used as a valid name after 1899 (23.9.1.1). Accordingly, the name *"D. fuscus"* has been used in at least 1,900 separate publications since 1969 according to searches of Web of Knowledge and Google Scholar. The vast majority of these publications do not cite a taxonomic reference. We do concede that Dunn (1926) and Anonymous (1956) cemented the author as Rafinesque in the minds of most workers, and that at least 100 studies since 1969 attribute the name to him. However, the name *"fuscus"* was attributed to Green by Mount (1975), Smith and Kohler (1977), Brandon and Huheey (1979), Dyer *et al*. (1980), Morris *et al*. (1983), Holman and Grady (1989), Klein (1989), Buhlmann (2001), Simon *et al*. (2002), Gibson *et al*. (2004), McAllister and Bursey (2004), Southerland *et al*. (2004), Cassell and Jones (2005), Garriock and Reynolds (2005), Lanza *et al*. (2004), Means *in* Lannoo (2005), Miller *et al*. (2005), McAllister *et al*. (2006), Raffaëlli (2007), Byrne *et al*. (2008), Schausberger and Hoffman (2008), Grant *et al*. (2009), Stranko *et al*. (2010), Huntsman *et al*. (2011), Price *et al*. (2012), Meshaka and Layne (2015), and Williams (2015).

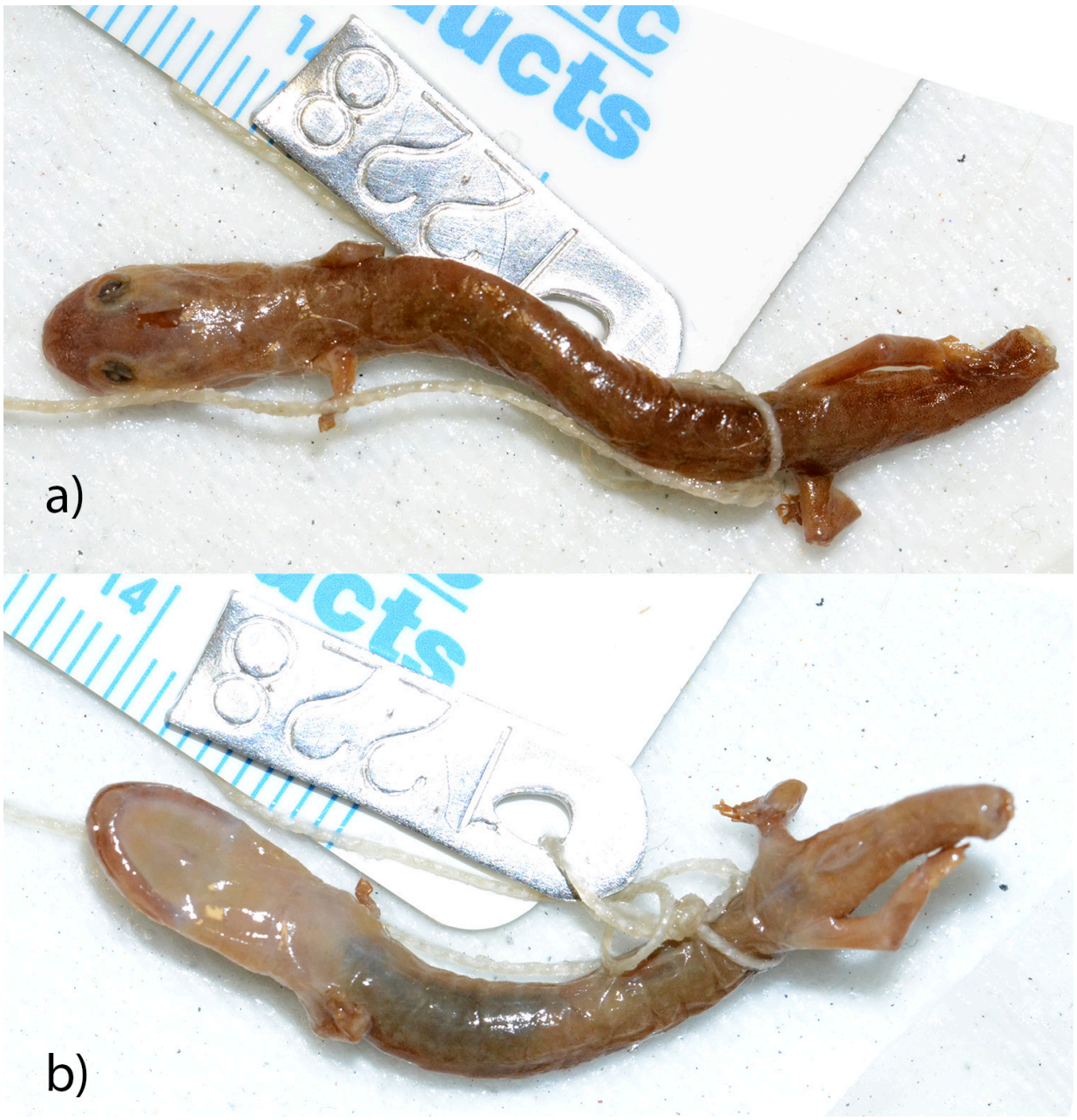

FIGURE 7. Newly recognized holotype (ANSP 1228) of *Salamandra fusca* Green, 1818 in dorsal (a) and ventral (b) view. Recorded in the ANSP catalogue as *"P. cinereus"* from "New Jersey" originating with "Dr. Bache, Green Collection." No specimens have been associated with this name historically. In particular, we note 14 apparent costal grooves, hind limbs more robust than forelimbs, and apparently partially healed broken tail, linking it to Green (1818)'s description. Primary type of *Desmognathus fuscus* (Green, 1818).

Article 23.9.1.2 requires use of the junior name in at least 25 works by 10 authors in the preceding 50 years, spanning at least 10 years. For the specific epithet *"fuscus"* generally, this has clearly been met. For *Salamandra fusca* Green, 1818 specifically, we record the aforementioned 27 usages by more than 10 authors from 1975 to 2015, satisfying the Article in the narrower sense for that name as well. Thus, under Article 23.9.2, we state that *S. fusca* Green, 1818 is a valid *nomen protectum,* and that *S. fusca* Laurenti 1768 is an invalid *nomen oblitum.* This cements Green (1818) as the correct taxonomic authority for the species currently known as *Desmognathus fuscus* (Green, 1818). We note that future taxonomic revisions may restrict the concept of this species, which corresponds to the "*fuscus* B" lineage of recent molecular analyses (Beamer & Lamb 2020; Kozak *et al*. 2005; Pyron *et al*. 2020).

Proteus neocaesariensis Green, 1818

The "Newjersey Proteus" (Tiger Salamander; *Ambystoma tigrinum*); type specimen not designated; type locality implied as "New Jersey" by the common name and restricted to "vicinity of Princeton" by Schmidt (1953) without justification. Gray (1850) notes that there are nine larval specimens of this species in the collection of the British Museum, of "different ages" from "N. America, "presente[d] by Jacob Green, M.D." Green visited London in 1828 and met with Gray at the BMNH (Smith 1923). Thus, it seems likely that these specimens were presented at that time. They may thus represent some of the original types from Green's personal collection. However, there is little apparent evidence on which to confirm or deny this, such as illustrations or notes on identifying characteristics of particular specimens.

Green (1818) describes this species as "Length between four and five inches; *tail* as long as the body, tapering and forming a fin; *snout* obtuse; *tongue* short, round, adhering to the lower jaw, and having a cartilaginous edge; *branchiae* persistent; *eyes* very small; *nostrils* invisible; *back* dirty white, with small dots, margined with a narrow red line, commencing at the fore shoulder, and terminating at the posterior legs; *beneath* whitish; posterior *feet* five-toed, anterior four-toed." Green also states "This is the only species known in America. There are but three yet described in the books, the *P. anguinus, P. Mexicanus, and P. tetradactylus.*" These are *P. anguinus* Laurenti, 1768, *Gyrinus mexicanus* Shaw & Nodder, 1798 (*Ambystoma mexicanum,* as *"P. Mexicanus"*), and *Sirena maculosa* Rafinesque, 1818b (*Necturus maculosus,* as *"P. tetradactylus,"* a Latinization of *Proteé tétradactyle* Lacépède, 1807, a *nomen oblitum*), showing his familiarity with these species as then known. Thus, it is clear that Green regarded his species as a proteid, of which he also considered the neotenic axolotl (an ambystomatid) a member.

However, Say (1818) noted that this species was likely the same as *Siren operculata* Palisot de Beauvois, 1799. Both names were later placed on the Official Index of Rejected and Invalid Species Names in Zoology (Anonymous 1963b,c) along with *Axolotus philadelphicus* Jarocki, 1822 after petitioning by later authors (Smith & Tihen 1961), in favor of the name *Salamandra tigrina* Green, 1825a (see below). We found no ANSP material related to this species, or any reason to disagree with previous authors in treating this name as an earlier, now suppressed senior synonym for the species now known as *Ambystoma tigrinum.* Interestingly, Green (1827a) persisted in recognizing this species as distinct from his own *Am. tigrinum*.

Green finally describes another specimen: "I have another animal which resembles the Proteus, inasmuch as it is furnished with a fin tail, and gills, but I will not be positive that it is a new species. If it is only the larva of a species of Salamander, it must belong to a much larger species of that genus than I have yet seen in this neighbourhood; the following is a description of it: Length about three inches; *tail* as long as the body, tapering, and in the form of a fin; *snout* oval; *eyes* very small; *nostrils* invisible; *neck* with gills; *back* black and white, confusedly mixed; *beneath* whitish; anterior *feet* four-toed, posterior five-toed, toes cloven to the base." Say (1818) later suggested that this might be the young of *Salamandra subviolacea* Barton, 1804 (*Ambystoma maculatum*), but this seems unlikely given that larval Spotted Salamanders do not generally reach a length of 3 inches (Petranka 1998; Powell *et al*. 2016).

As an addendum, we note that Green states "this is the only species known in America" before listing *Proteé tétradactyle* Lacépède, 1807, a *nomen oblitum* for *Sirena maculosa* Rafinesque, 1818b, which is obviously widespread in the eastern USA. Lacépède (1807) was unsure of the origin of the MNHN specimen he examined, which he states had been brought to Bordeaux from an unknown country and given to M. Rodrigues, a very zealous naturalist, who procured it for the museum. As noted by Waite (1907), *Necturus* were commonly believed to be larval *Cryptobranchus* in Green's time. This is evident in Say (1818)'s reply to Green (1818), wherein he states that the animal described by Schneider (1799) from Lake Champlain (a mudpuppy) was probably the young of *Salamandra alleganiensis* Sonnini de Manoncourt & Latreille, 1801. Similarly, Barton (1807) described a composite of *Cryptobranchus* and *Necturus* and proposed giving it the names *S. horrida, S. maxima,* or *S. gigantea.* The description of

Sirena maculosa Rafinesque, 1818b did not appear until November 1818, after the September publication of Green (1818). Thus, Green would have been unaware of *Necturus maculosus* as a distinct USA species in May 1818, when his paper was first read.

Salamandra tigrina Green, 1825a

No common name given; (Tiger Salamander; *Ambystoma tigrinum*); type specimen described as a living individual, part of the personal collection of noted American artist and naturalist Titian Peale; type locality "near Moore's town in New Jersey." The disposition of this specimen is unknown; it may still be extant among the various collections of Peale's artifacts in Baltimore and Philadelphia. Green notes that Peale "has made a very accurate drawing of the *S. tigrina.*" We believe this to be the sketch Mss.B.P.31.15d.150b in pencil in the Titian Ramsay Peale Sketches collection at the American Philosophical Society in Philadelphia, dated 1819 (Fig. 8). Yarrow (1882) listed USNM 3970 as a type, in reference to a paratype of *S. lurida* Sager, 1839, which was designated a junior subjective synonym of *S. tigrina* Green, 1825a by Cope (1868). Thus, the suggestions by Yarrow (1882) and Fouquette and Dubois (2014) that USNM 3970 is a paratype of *S. tigrina* Green, 1825a are in error.

FIGURE 8. A pencil sketch we suggest is of *Salamandra tigrina* Green, 1825a by Titian Peale, dated 1819 (Mss.B.P31.15d.150b). This may represent the holotype, which was a living pet of Peale's, and of which Green 1825a notes Peale "has made a very accurate drawing." Courtesy of the American Philosophical Society.

Salamandra intermixta Green, 1825b

No common name given; (Northern Dusky Salamander; *Desmognathus fuscus*); no type specimen designated; type locality given as "common in the neighbourhood of this city [Philadelphia]. It is also found in the southern states." This was restricted to "Jefferson College, Pennsylvania" by Schmidt (1953) without justification. The description is given as "*Length* five or six inches: *tail* rather longer than the body, tapering, slightly compressed and pointed: *snout* oval and a little truncated: *eyes* dark, protuberant and approximate: *teeth* small and numerous: *back* brownish, with dark undulating marks, or interrupted stripes, seen most distinctly when the animal is in the water: *sides, underpart* of the *body* and *legs,* sprinkled with umber, clear white, and yellowish white dots, pretty equally intermixed, which, when the animal is in a favourable light, have somewhat the appearance of prismatic drops of dew, in some specimens may be seen a row of small white points along the sides. When the animal is old, the speckled appearance on the under part of the body is obliterated. The posterior legs are proportionably longer than the others: *fore feet* four-toed: *hind feet* five-toed." This description matches quite closely the appearance of *D. fuscus* from the northeastern USA. Given the specificity of the description and the locality, a neotype designation is unwarranted. An expanded account was given by Green (1827a), noting the exceptional variation in what is now known as *D. fuscus* (Green, 1818).

This species was designated a junior subjective synonym of *Salamandra nigra* Green, 1818 by Holbrook (1842), and of *Triturus fuscus* Rafinesque, 1820 by Baird (1850). Why Green felt that these new populations were distinct from the previous species described by himself and Rafinesque is unclear. Curiously, Harlan (1827b) suggested that *S. intermixta* Green, 1825b was a junior synonym of *S. picta* Harlan (1825), citing it as *S. intermixta* Green, 1827a. However, Green (1827b) replied that Green (1827a) was simply providing an account of *S. intermixta* Green (1825b), which was published in August of 1825, while Harlan (1825) was published in December. Thus, *S. picta* Harlan, 1825 is actually a junior subjective synonym of *S. intermixta* Green, 1825b. Green (1827b) notes that "in

two cabinets at least, besides my own, the specimens of these animals were labelled with that name." Thus, while at least two other museums (presumably the ANSP and Maclurian Lyceum; see below) had contemporaneous specimens of Green's species, he still retained his personal collection which presumably included his "types," if he held such a notion as "type" specimens (see below).

Salamandra porphyritica Green, 1827a

The "Porphyritic Salamander" (Spring Salamander; *Gyrinophilus porphyriticus*); numerous type specimens referenced in the description in "Cabinet of the Maclurian Lyceum–my collection," the one figured in Green (1827a, Pl. 2) is presumably the holotype; type locality given as "French creek, near Meadville, Crawford county, Pa." The Maclurian Lyceum was a "rival" museum to the ANSP from 1827–1829 (Baatz 1988), but we can find no reference to the current disposition of these collections. Brandon (1966) was similarly unable to locate them and thus designated MCZ 35778 as the neotype, from "a small spring-fed stream (flowing directly into French Creek) at Liberty and Linden streets, Meadville, Crawford Co., Pa." The diagnostic *canthus rostralis* is evident in the drawing (Fig. 9) and confirms the identity of this species. The original holotype may still be extant; see below.

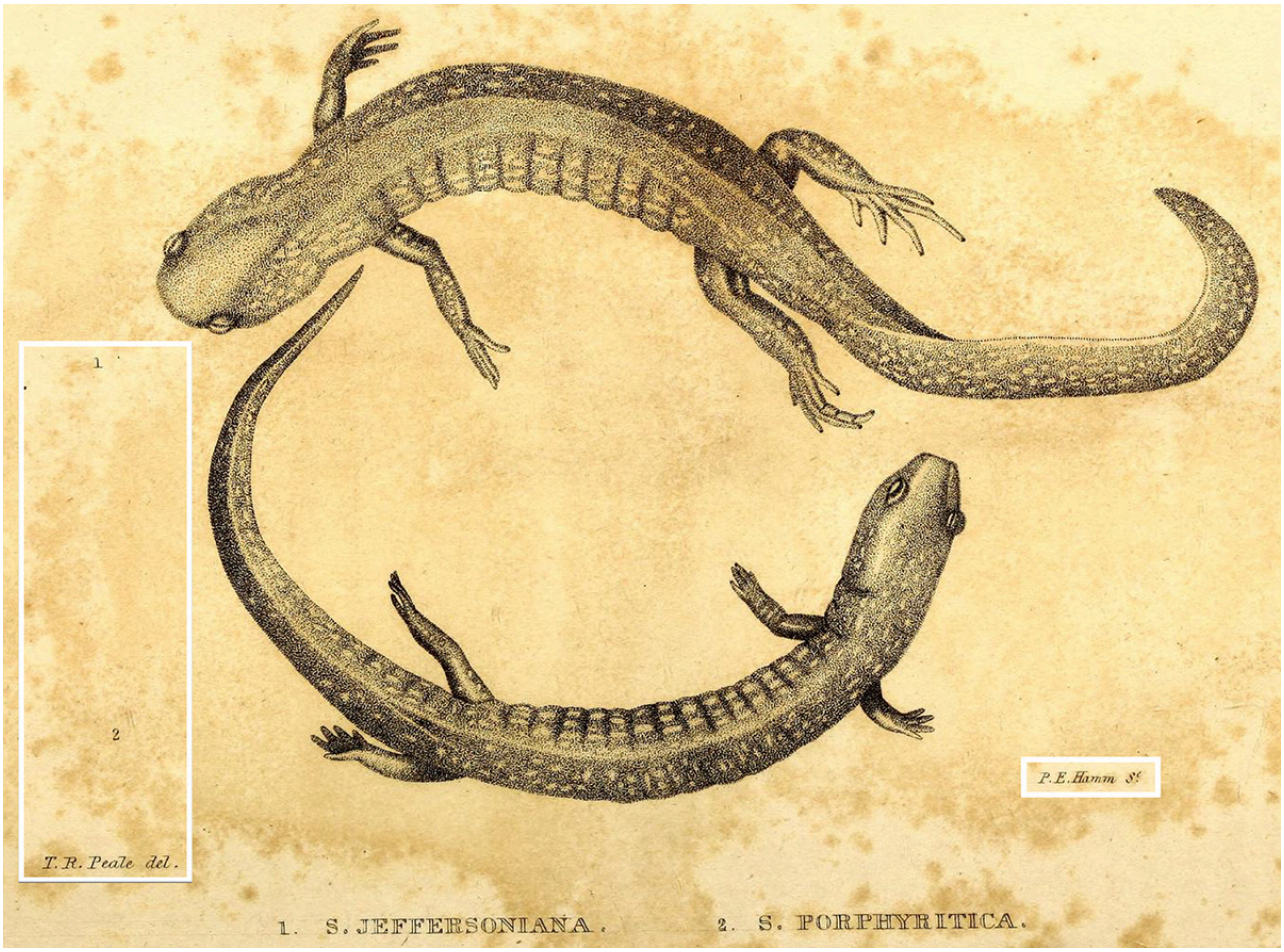

FIGURE 9. Green (1827a)'s figure (Pls. 1, 2) of the preserved holotypes of *Salamandra jeffersoniana* Green, 1827a (USNM 3968; see Fig. 10) and *S. porphyritica* Green, 1827a (unknown disposition; possibly USNM 3840), drawn by T.R Peale and engraved by P.E. Hamm. Notes and legend cropped from original.

Salamandra jeffersoniana Green, 1827a

The "Blue Spotted Salamander" (Jefferson Salamander; *Ambystoma jeffersonianum*); as with *Salamandra porphyritica* Green, 1827a, a type specimen referenced in the description in "Cabinet of the Maclurian Lyceum–my collection;" type locality given as "the marshy ground near Chartier's creek, in the vicinity of Jefferson College at Cannonsburg, Pa." Bizarrely, Harlan (1827b) states that *Salamandra jeffersoniana* Green, 1827b is a junior subjective synonym of *Salamandra variolata* Gilliams, 1818 (South Carolina Slimy Salamander; *Plethodon variolatus*), having first been described as a variety thereof described by Harlan (1827a). Green (1827b) was baffled by this

statement and disputed it vigorously. He first notes that Harlan (1827a) was published in February while Green (1827a) was published in January, negating an assertion of "priority." He then notes that he compared his species with Gilliams' at length and that both have been figured in print, with their differences evident to the observer. Finally, he notes that Harlan (1827a)'s account of *S. variolata* Gilliams, 1818 is not that species at all, but instead merely a variety of Green's own *S. glutinosa* Green, 1818, for which he gave an account in Green (1827a). He suggests Harlan's specimens were likely discolored in alcohol, causing this confusion.

Yarrow (1882) lists USNM 3968 from "Dr. J. Green," locality "Western Pennsylvania," as the "alc. type." This was reiterated by Cope (1889) and tentatively accepted by Uzzell (1967), but not mentioned by Cochran (1961). As with USNM 3738 for *S. bislineata* Green, 1818, examination reveals this to be a poorly preserved *Ambystoma jeffersonianum,* listed by the USNM catalogue as the "alleged holotype" (Fig. 10). Green (1827a, Pls. 1, 2) provides a figure drawn by Peale of the holotypes (presumably) of *S. jeffersoniana* Green, 1827a and *S. porphyritica* Green, 1827a in preservative (Fig. 9). From this, we can see that the specimen of *S. jeffersoniana* Green, 1827a is clearly USNM 3968; note in particular the semicircular leftward curve of the spine, right arm adpressed to the body, left arm extending directly away from the trunk, both legs adpressed to the tail, and an immediate rightward bend of the tail past the adpressed legs. Thus, we can reliably conclude that the specimens in Green's personal collection included some of his holotypes, that some of these passed into the care of Bache after his death, and that Bache distributed some of these to collections in the 1850's.

FIGURE 10. A poorly preserved specimen (USNM 3968; ventral view) listed as the "alleged holotype" of *Salamandra jeffersoniana* Green, 1827. Cope (1868) states that it was received from "Dr. F. Bache," while Yarrow (1882) records it as the "alc. type." from "Dr. J. Green," locality "Western Pennsylvania," which was reiterated by Cope (1889). Comparison with Peale's drawing of the holotype (Green 1827a, Pl. 2; Fig. 9) confirms its identity.

We can also conclude that there was originally a preserved holotype of *S. porphyritica* Green, 1827a, which may still be extant in the NMNH or other collections. Yarrow (1882) lists USNM 3840 from "Canonsburg, Pa." as originating from "Dr. J. Green." The difference from the type locality may simply be a later note from Green

or Bache based on the former's occasional residence in Canonsburg during his summer lectures at Jefferson College (Bennett 1949). Brandon (1966) did not mention examining USNM 3840, noting only that USNM 3852 (six specimens) were the earliest known material from the type locality but did not originate with Green. Examination of USNM 3840 in comparison with Peale's drawing (Green 1827a, Pl. 2; Fig. 9) will allow us to confirm or deny this possibility, which would preempt Brandon (1966)'s neotype designation of MCZ 35778. A global viral pandemic during the preparation of this paper forced the temporary closure of ANSP and NMNH, precluding us from examining this and other specimens, but an assessment will be provided at a later date.

Agama torquata Peale & Green, 1830

No common name given; (Wiegmann's Torquate Lizard; *Sceloporus torquatus*); holotype ANSP 8499; type locality "Temascaltepec, about eighty miles S. W. of the city of Mexico," collected by "Professor W. H. Keating." Amusingly, this name is both a junior secondary homonym and junior subjective synonym of *Sceloporus torquatus* Wiegmann, 1828, which is the type species of the genus *Sceloporus* Wiegmann, 1828 by subsequent designation of Wiegmann (1834). Peale and Green were apparently unaware of Wiegmann's publication; Baird (1857) seems to have been the first to designate their name a junior subjective synonym of Wiegmann's. Contra Bell *et al*. (2003), the two species-group names are not objective synonyms, as they do not share type specimens (Article 61.3.1). Smith & Taylor (1950) mistakenly restricted the type locality to "México, D.F." from the "Mexico" mentioned by Peale & Green (1830:231), but a detailed type locality was already given by Peale & Green (1830:232).

Scincus ventralis Peale & Green, 1830

No common name given; (Wiegmann's Alligator Lizard; *Gerrhonotus liocephalus*); type specimens designated as "three individuals … now in the cabinet of the Acad. Nat. Sciences," syntypes listed by Malnate (1971) as ANSP 9026–9027; type locality "from the mining districts of Mexico," brought by "Professor W. H. Keating." As with *Agama torquata* above, Peale and Green seem to have been unaware of *Gerrhonotus liocephalus* Wiegmann, 1828. Cope (1866) seems to have been the first to synonymize the two names. The syntypes ANSP 9026–9027, and presumably the holotype ANSP 8499 of *Agama torquata* Peale & Green, 1830 described in the same publication and also collected by Keating in Mexico, are among the few extant specimens that can be reliably associated with one of Green's original descriptions, having been present in an extant collection at the time of publication.

Peale and Green (1830:234) also state: "We have preferred to consider this animal for the present as a scink, but we are aware, that with a less violation of the arrangements of nature, than that which often occurs on this subject, that we might constitute with it a new genus, under the name of *Ptero-gastenes,* in allusion to the attachment of the ventral scales to the upper part of the body, by the lateral folds." While their formal intent to establish this as a new name is debatable based on the equivocal wording, many subsequent authors (e.g., Cope 1877 [as *Pterogasterus*]; Good 1988; Günther 1885; Tihen 1949) have treated this as establishing *Pterogastenes* Peale and Green, 1830 with the type species *P. ventralis* (Peale and Green, 1830). Thus, *Pterogastenes* Peale and Green, 1830 is a junior subjective synonym of *Gerrhonotus* Wiegmann, 1828.

As discussed by Smith & Taylor (1950), the third of Keating's ANSP specimens from Mexico seems to have been exchanged or mixed up at some point with a mutilated specimen apparently referable to the Old World skink genus *Dasia.* A number of specimen exchanges by the ANSP in the early 1850's (see Ruschenberger 1860) may explain both this discrepancy and the *Sceloporus graciosus* (ANSP 8348) in the putative type series of *Lacerta hyacinthina* Green, 1818. From this mysterious *Dasia* specimen (ANSP 9531), Hallowell (1856b) described *Euprepis microcephalus* Hallowell, 1856 from "Mexico," based on "one specimen presented by Mr. W. H. Keating," curiously listing the older name *Scincus ventralis* Peale & Green, 1830 as a synonym. This name is thus a *nomen dubium* (see Smith & Taylor 1950).

Salamandra cirrigera Green, 1831

The "Stewart's S[alamander]." (Southern Two-Lined Salamander; *Eurycea cirrigera*); four syntypes stated in the original description, current disposition unknown; type locality given as "near New Orleans." Green clearly describes a *Eurycea* with a yellowish back edged by black lines and prominent cirri, leaving little doubt as to the identity of this species. Cope (1870, 1889) stated that he had examined USNM 4734, which were "Green's type;" two specimens received from "Dr. F. Bache," locality "Southern States (La.?)." These specimens are not currently listed in the NMNH catalogue, and Dunn (1926) lists the type as "Not known to exist." When and how these speci-

mens were lost is unknown. While the broader applicability of this name to a "two-lined" *Eurycea* from eastern Louisiana is not in dispute, the *E. bislineata* species complex (including *E. cirrigera* from the New Orleans area) has a complex phylogeographic history (Kozak *et al.* 2006) that may result in additional cryptic species being described. Thus, a neotype designation may be warranted in future revisions.

Salamandra ingens Green, 1831

The "Great S[alamander]." (Tiger Salamander; *Ambystoma tigrinum*); a single type specimen, reported to be ANSP 1309 by Fowler & Dunn (1917), was sent to Green by Dr. Samuel M'Clellan from the type locality of "a fresh water stream near New Orleans." Green describes a very large animal ("nearly eleven inches) with a "dusky ferruginous or dirty red" color and "dark bluish blotches which are most distinct on the tail." Recall that Green frequently described white and yellow colors as "bluish." Green further notes that "outer toes of the hind feet fimbriated as in the Protonopsis horrida of Barton [*Salamandra horrida* Barton, 1807] or S. alleghaniensis of Daudin [*S. alleganiensis* Sonnini de Manoncourt & Latreille, 1801]—which animal [*Cryptobranchus alleganiensis*] it resembles so much, that at first sight I had no doubt of their identity." In contrast, the description clearly refers to a Tiger Salamander, and was applied to populations thereof by later authors (e.g., Holbrook 1842). Designated as a junior subjective synonym of *Salamandra tigrina* Green, 1825a by Cope (1868). We did not make a detailed examination of the putative holotype, but there is little apparent reason to dispute Cope's designation. This was the final taxon described or discussed by Jacob Green in print prior to his sudden period of rapidly declining health and early death in 1841.

Green's Types

As noted above, not all of Green's names can be associated with specimens, and few specimens currently associated with Green's names can be reliably authenticated as the original types. The history of systematics is replete with the kind of ambiguities seen here regarding the origin and disposition of type specimens. This stems from numerous factors, one of which is the lack of importance placed on individual name-bearing specimens prior to the Principle of Typification (Article 61) being codified and widely adopted (see Witteveen 2016). Another is the frequent lack of documentation and preservation of early natural history collections with the level of detail and record keeping we take for granted in the modern era (see Lane 1996).

It is entirely possible that additional specimens from Green (including types) are extant in collections, though locating them and validating their provenance and authenticity may prove difficult. The basis of USNM 3738, 3840, and 3968 purportedly originating with Green and the location of USNM 4734 is unknown (though all were likely donated by Bache), as is the fate of the Maclurian Lyceum collections, which Green may have simply reclaimed for his personal collection when that institution closed in 1829. At the ANSP, material may have been lost (and found) through various means over time; the re-discovery of ANSP 14001 attests to this. Workers in the late 19th and early 20th centuries apparently destroyed what they considered "duplicate" or otherwise "unnecessary" ANSP material (N. Gilmore, *pers. comm.*).

There may be international specimens as well. In a letter to Cuvier following his 1828 visit to Paris, Green (1830) notes that Cuvier mistakenly attributed some salamander species described by himself to Harlan instead. Green further notes that the MNHN collection has several of his specimens with his own labels attached, likely sent to Paris by Lesueur. The MNHN catalogue attributes several reptile and amphibian specimens, including some of the species listed here, to Harlan and Lesueur. It is thus possible that additional Green specimens are among them. Similarly, Gray (1850) notes nine larval specimens of *Proteus neocaesariensis* Green, 1818 in the BMNH collection, presented by Green. These were likely donated during Green's 1828 visit to London and may represent part or all of the original type series. Our understanding of Green's types may thus continue to evolve as new discoveries are made.

Conclusions

After 202 years, this review clarifies the status of all lizard and salamander taxa described or discussed by Jacob Green, and offers some additional insight regarding the taxonomy and nomenclature of some eastern USA sala-

manders and Mexican lizards. Reconciling the early history of systematic herpetology with modern-day concepts of typification and species delimitation is often difficult, due to epochal differences in techniques and standards for natural history collections, informal nomenclatural practices predating the Code, and pre-Darwinian concepts of speciation. Nevertheless, existing material and published accounts can occasionally yield satisfactory resolutions for the allocation of ambiguous nomina. We anticipate that the actions taken, and conclusions reached here will provide a firmer foundation for the rapidly shifting taxonomy of *Desmognathus* and other eastern USA salamander genera. Our investigations also yielded other significant material in the ANSP and other museums from authors such as Holbrook that bear heavily on the nomenclature of additional salamander species, but those are too complex to summarize here and will be dealt with in forthcoming publications.

Acknowledgements

We thank N. Gilmore and T. Daeschler (ANSP), S. G. Tilley (Smith), J. Hanken, J. Rosado, and J. Tonini (MCZ), and A. Wynn, S. Gotte, K. Tighe, R. C. Bell, and K. de Queiroz (NMNH) for information regarding and access to specimens, D. Frost (AMNH) and K. Adler (Cornell) for discussion, and M. Vences for comments. This work was funded in part by USA NSF grants DEB-1655737 to RAP and DEB-1656111 to DAB.

References

Adler, K.A. (1976) New genera and species described in Holbrook's "North American Herpetology." *In*: Adler, K.A. (Ed.), *Holbrook's North American Herpetology*. Society for the Study of Amphibians and Reptiles, Athens, Ohio, pp. 29–43.

Adler, K.A. (2007) *Contributions to the History of Herpetology. Vol. 2*. Society for the Study of Amphibians and Reptiles, Athens, Ohio, 396 pp.

Anonymous (1852) Donations to museum in January and February, 1851. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 5, 159–160.

Anonymous (1877) *Members and correspondents of the Academy of Natural Sciences of Philadelphia, 1877.* Printed for the Academy, Philadelphia, Pennsylvania, 48 pp.
https://doi.org/10.5962/bhl.title.22316

Anonymous (1956) Direction 57. Addition to the Official List of Specific Names in Zoology (a) of the specific names of forty-seven species belonging to the classes Cyclostomata, Pisces, Amphibia and Reptilia, each of which is the type species of a genus, the name of which was placed on the Official List of Generic Names in Zoology in the period up to the end of 1936 and (b) of the specific name of one species of the class Amphibia which is currently treated as a senior subjective synonym of the name of such a species. *Bulletin of Zoological Nomenclature*, 10, 365–388.

Anonymous (1963a) *Salamandra erythronota* Rafinesque, 1818 (Amphibia); suppression under the Plenary Powers. *Bulletin of Zoological Nomenclature*, 20, 199–200.
https://doi.org/10.5962/bhl.part.6612

Anonymous (1963b) *Ambystoma* Tschudi, 1838 (Amphibia); validation under the Plenary Powers. *Bulletin of Zoological Nomenclature*, 20, 102–104.
https://doi.org/10.5962/bhl.part.6587

Anonymous (1963c) *Salamandra tigrina* Green, 1825 (Amphibia); validation under the Plenary Powers. *Bulletin of Zoological Nomenclature*, 20, 193–194.
https://doi.org/10.5962/bhl.part.6609

Anonymous & Ride, W.D.L. (1999) *International Code of Zoological Nomenclature. 4th Edition*. International Trust for Zoological Nomenclature, c/o Natural History Museum, London, 306 pp.
https://doi.org/10.5962/bhl.title.50608

Baatz, S. (1988) Philadelphia patronage: the institutional structure of natural history in the new republic, 1800-1833. *Journal of the Early Republic*, 8 (2), 111–138.
https://doi.org/10.2307/3123808

Baird, S.F. (1850) Revision of the North American Tailed-Batrachia, with descriptions of new genera and species. *Journal of the Academy of Natural Sciences of Philadelphia*, 2, 281–294.

Baird, S.F. (1857) *Reptiles of the boundary*. C. Wendell, Washington, 86 pp.

Baird, S.F. & Girard, C. (1852) Characteristics of Some New Reptiles in the Museum of the Smithsonian Institution. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 6, 68–70.

Barton, B.S. (1804) Some Account of a New Species of North American Lizard. *Transactions of the American Philosophical Society*, 6, 108–112.
https://doi.org/10.2307/1004778

Barton, B.S. (1807) Miscellaneous facts and observations. *Philadelphia Medical and Physical Journal*, 2 (2), 193–198.
Beamer, D.A. & Lamb, T. (2020) Towards rectifying limitations on species delineation in dusky salamanders (*Desmognathus*: Plethodontidae): an ecoregion-drainage sampling grid reveals additional cryptic clades. *Zootaxa*, 4734 (1), 1–61. https://doi.org/10.11646/zootaxa.4734.1.1
Bell, E.L. (1996) Descriptions of neotypes for *Sceloporus undulatus undulatus*, the Southern Fence Lizard, and *Sceloporus undulatus hyacinthinus*, the Northern Fence Lizard, and a lectotype for *Sceloporus undulatus garmani*, the Northern Prairie Lizard. *Bulletin of the Maryland Herpetological Society*, 32, 81–103.
Bell, E.L., Smith, H.M. & Chiszar, D. (2003) An annotated list of the species-group names applied to the lizard genus Sceloporus. *Acta Zoológica Mexicana*, 90, 103–174.
Bennett, G.W. (1949) Pioneer Scientists of the Western Lea: III. "Old Jakey Green" at Canonsburg. *Proceedings of the Pennsylvania Academy of Science*, 23, 218–221.
Brandon, R.A. (1966) Systematics of the salamander genus *Gyrinophilus*. *Illinois Biological Monographs*, 35, 1–86. https://doi.org/10.5962/bhl.title.50088
Brandon, R.A. & Huheey, J.E. (1979) Distribution of the Dusky Salamander, *Desmognathus fuscus* (Green) in Illinois. *Chicago Academy of Sciences Natural History Miscellanea*, 205, 1–7.
Brimley, C.S. (1907) The salamanders of North Carolina. *Journal of the Elisha Mitchell Scientific Society*, 23, 150–156.
Brimley, C.S. & Sherman, F. (1908) Notes on the life-zones in North Carolina. *Journal of the Elisha Mitchell Scientific Society*, 24, 14–22.
Brygoo, E.R. (1989) Les types de Teiidés (Reptiles, Sauriens) du Muséum national d'Histoire naturelle Catalogue critique. *Bulletin du Muséum national d'histoire naturelle*, 11, 1–44. https://doi.org/10.2307/1445471
Buhlmann, K. (2001) A biological inventory of eight caves in northwestern Georgia with conservation implications. *Journal of Cave and Karst Studies*, 63, 91–98.
Byrne, M.W., Davie, E.P. & Gibbons, J.W. (2008) *Batrachochytrium dendrobatidis* Occurrence in *Eurycea cirrigera*. *Southeastern Naturalist*, 7, 551–555. https://doi.org/10.1656/1528-7092-7.3.551
Cassell, R.W. & Jones, M.P. (2005) Syntopic Occurrence of the Erythristic Morph of *Plethodon cinereus* and *Notophthalmus viridescens* in Pennsylvania. *Northeastern Naturalist*, 12, 169–172. https://doi.org/10.1656/1092-6194(2005)012[0169:SOOTEM]2.0.CO;2
Cochran, D.M. (1961) Type Specimens of Reptiles and Amphibians in the U.S. National Museum. *Bulletin of the United States National Museum*, 220, 1–291. https://doi.org/10.5479/si.03629236.220
Cope, E.D. (1866) Fifth Contribution to the Herpetology of Tropical America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 18, 317–323.
Cope, E.D. (1868) A review of the species of the Amblystomidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 19, 166–211.
Cope, E.D. (1869) A review of the species of Plethodontidae and Desmognathidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 21, 93–118.
Cope, E.D. (1870) Observations on the Fauna of the Southern Alleghanies. *The American Naturalist*, 4, 392–402. https://doi.org/10.1086/270612
Cope, E.D. (1877) Tenth Contribution to the Herpetology of Tropical America. *Proceedings of the American Philosophical Society*, 17, 85–98.
Cope, E.D. (1889) The Batrachia of North American. *Bulletin of the United States National Museum*, 34, 1–525. https://doi.org/10.5962/bhl.title.38254
Crother, B.I., Boundy, J., Campbell, J.A., de Queiroz, K., Frost, D.R., Green, D.M., Highton, R., Iverson, J.B., McDiarmid, R.W., Meylan, P.A., Reeder, T.W., Seidel, M.E., Sites, J.W.Jr., Tilley, S.G. & Wake, D.B. (2003) Scientific and standard English names of amphibians and reptiles of North America north of Mexico: Update. *Herpetological Review*, 34, 196–203.
Daudin, F.M. (1802a) *Histoire naturelle, générale et particulière, des reptiles. Tome Troisième*. F. Dufart, Paris, 452 pp.
Daudin, F.M. (1802b) *Histoire naturelle, générale et particulière, des reptiles. Tome Quatrième*. F. Dufart, Paris, 397 pp.
Daudin, F.M. (1803) *Histoire naturelle, générale et particulière, des reptiles. Tome Huitième*. F. Dufart, Paris, 439 pp.
Duméril, A.H.A. & Bibron, G. (1839) *Erpétologie Générale on Histoire Naturelle Complète des Reptiles. Tome Cinquième*. Roret, Paris, 871 pp.
Dunn, E.R. (1917) The salamanders of the genera *Desmognathus* and *Leurognathus*. *Proceedings of the United States National Museum*, 53, 393–433. https://doi.org/10.5479/si.00963801.53-2211.393
Dunn, E.R. (1926) *The salamanders of the family Plethodontidae*. Smith College, Northampton, 456 pp.
Dyer, W.G., Brandon, R.A. & Price, R.L. (1980) Gastrointestinal Helminths in Relation to Sex and Age of *Desmognathus fuscus* (Green, 1818) from Illinois. *Proceedings of the Helminthological Society of Washington*, 47, 95–99.
Fitzinger, L.J.F.J. (1843) *Systema reptilium.* Braumüller et Seidel, Vindobonae, 106 pp. https://doi.org/10.5962/bhl.title.4694
Fouquette, M.J. & Dubois, A. (2014) *A checklist of North American amphibians and reptiles: The United States and Canada.*

Vol. 1. Amphibians. 7th Edition. Xlibris, Bloomington, 613 pp.
Fowler, H.W. (1907) The amphibians and reptiles of New Jersey. *Annual Report of the New Jersey State Museum*, 1906, 29–250.
https://doi.org/10.5962/bhl.title.67220
Fowler, H.W. & Dunn, E.R. (1917) Notes on Salamanders. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 69, 7–28.
Frost, D.R. (2019) *Amphibian Species of the World: An Online Reference. Version 6.0*. American Museum of Natural History, New York, New York. Available from: http://research.amnh.org/herpetology/amphibia/index.html (October 29, 2019)
Garriock, C.S. & Reynolds, R. (2005) Results of a Herpetofaunal Survey of the Radford Army Ammunition Plant in Southwestern Virginia. *Banisteria*, 25, 3–22.
Gibson, C.A., Ratajczak Jr., R.E. & Grossman, G.D. (2004) Patch based predation in a southern Appalachian stream. *Oikos*, 106, 158–166.
https://doi.org/10.1111/j.0030-1299.2004.12911.x
Gilliams, J. (1818) Description of two new species of Linnaean *Lacerta*. *Journal of the Academy of Natural Sciences of Philadelphia*, 1 (1), 460–462.
Good, D.A. (1988) *Phylogenetic Relationships Among Gerrhonotine Lizards: An Analysis of External Morphology*. University of California Press, Berkeley, California, 139 pp.
Goodwin, G.H. (1960) Unrecorded Papers of Rafinesque and Jacob Green. *Systematic Zoology*, 9, 35–36.
https://doi.org/10.2307/2411540
Grant, E.H.C., Green, L.E. & Lowe, W.H. (2009) Salamander occupancy in headwater stream networks. *Freshwater Biology*, 54, 1370–1378.
https://doi.org/10.1111/j.1365-2427.2009.02166.x
Gravenhorst, J.L.C. (1807) *Vergleichende Uebersicht des Linneischen und einiger Neuern Zoologischen Systeme, nebst dem Eingeschaltenen Verzeichniss der Zoologischn Sammlung des Verfassers und den Beschreibungen neuer Theirarten die in Derselben Vorhanden Sind*. H. Dieterich, Göttingen, 504 pp.
Gray, J.E. (1831) A Synopsis of the Species of the Class Reptilia. *In:* Griffiths, E. (Ed.), *The Animal Kingdom Arranged in Conformity with its Organization, by the Baron Cuvier. Vol. 9. Part 2. Le Règne Animal.* Whittaker, Treacher, and Co., London, pp. 1–110.
Gray, J.E. (1838) Catalogue of the slender-tongued saurians, with descriptions of many new genera and species. Part 1. *Annals and Magazine of Natural History*, 1, 274–283.
https://doi.org/10.1080/00222933809512291
Gray, J.E. (1850) *Catalogue of the Specimens of Amphibia in the Collection of the British Museum. Part II. Batrachia Gradientia, etc.* Spottiswoodes and Shaw, London, 72 pp.
Green, A. (1858) Biographical Sketch of Jacob Green, M.D. *In:* Gayley, J.F. (Ed.), *A history of the Jefferson Medical College of Philadelphia: with biographical sketches of the early professors*. Joseph M. Wilson, Philadelphia, Pennsylvania, pp. 1–59.
Green, J. (1818) Descriptions of several species of North American Amphibia, accompanied with observations. *Journal of the Academy of Natural Sciences of Philadelphia*, 1, 348–359.
Green, J. (1821) Some curious facts respecting the Bones of the Rattle Snake. *American Journal of Science and Arts*, 3, 85–86.
Green, J. (1825a) Description of a new species of salamander. *Journal of the Academy of Natural Sciences of Philadelphia*, 5, 116–118.
Green, J. (1825b) Description of a new species of salamander. *The Port Folio, and New York Monthly Magazine*, 20, 159.
Green, J. (1827a) An account of some new species of salamanders. *Contributions of the Maclurian Lyceum to the Arts and Sciences*, 1 (1), 3–8.
Green, J. (1827b) Reply to a Note in Harlan's Synopsis of American Reptiles. *Contributions of the Maclurian Lyceum to the Arts and Sciences*, 1 (2), 39–41.
Green, J. (1830) Reclamation of Salamanders—in a Letter to the Baron F. Cuvier. *Transactions of the Albany Institute*, 1, 150–151.
Green, J. (1831) Description of two new species of salamander. *Journal of the Academy of Natural Sciences of Philadelphia*, 6, 253–255.
Günther, A.C.L.G. (1885) *Biologia Centrali-Americana: Reptilia and Batrachia.* R. H. Porter, London, 326 pp.
Hallowell, E. (1856a) Description of several species of Urodela, with remarks on the geographical distribution of the Caducibranchiate division of these animals and their classification. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 8, 6–11.
Hallowell, E. (1856b) On several new species of reptiles in the collection of the Academy of Natural Sciences. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 8, 153–156.
Hallowell, E. (1858) On the Caducibranchiate Urodele Batrachians. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 3, 337–366.
Harlan, R. (1825) Description of a new species of Salamandra. *Journal of the Academy of Natural Sciences of Philadelphia*, 5, 136.

Harlan, R. (1827a) Genera of North American Reptilia, and synopsis of the species. *Journal of the Academy of Natural Sciences of Philadelphia*, 5 (2), 317–372.
Harlan, R. (1827b) Genera of North American Reptilia, and synopsis of the species (continued,). *Journal of the Academy of Natural Sciences of Philadelphia*, 6 (1), 7–38.
Harlan, R. (1835) *Medical and physical researches*. L.R. Bailey, Philadelphia, Pennsylvania, 653 pp. https://doi.org/10.5962/bhl.title.107564
Herman, T.A. & Bouzat, J.L. (2016) Range-wide phylogeography of the four-toed salamander: out of Appalachia and into the glacial aftermath. *Journal of Biogeography*, 43 (4), 666–678. https://doi.org/10.1111/jbi.12679
Highton, R. (1960) The Scientific Name of the Red-Backed Salamander. *Herpetologica*, 16, 236–236.
Highton, R. (1961) Erythronota (Salamandra) Rafinesque, 1818; proposed suppression under the plenary powers (Amphibia, Caudata). *Bulletin of Zoological Nomenclature*, 18, 221–222.
Highton, R. (1962) Revision of North American salamanders of the Genus *Plethodon*. *Bulletin of the Florida State Museum*, 6, 235–367.
Highton, Richard., Maha, G.C. & Maxson, L.R. (1989) Biochemical evolution in the slimy salamanders of the Plethodon glutinosus Complex in the Eastern United States. *Illinois Biological Monographs*, 57, 1–153. https://doi.org/10.5962/bhl.title.49905
Holbrook, J.E. (1838) *North American Herpetology. Vol. 3. 1st Edition.* J. Dobson, Philadelphia, Pennsylvania, 122 pp.
Holbrook, J.E. (1840) *North American Herpetology. Vol. 4. 1st Edition*. J. Dobson, Philadelphia, Pennsylvania, 126 pp.
Holbrook, J.E. (1842) *North American Herpetology. Vol. 5. 2nd Edition.* J. Dobson, Philadelphia, Pennsylvania, 118 pp.
Holman, J.A. & Grady, F. (1989) The fossil herpetofauna (Pleistocene: Irvingtonian) of Hamilton Cave, Pendleton County, West Virginia. *National Speleological Society Bulletin*, 51, 34–41.
Hoogmoed, M.S. (1978) An annotated review of the Salamander types described in the Fauna Japonica. *Zoologische Mededelingen*, 53, 91–105.
Huntsman, B.M., Venarsky, M.P., Benstead, J.P. & Huryn, A.D. (2011) Effects of organic matter availability on the life history and production of a top vertebrate predator (Plethodontidae: *Gyrinophilus palleucus*) in two cave streams: cave salamander life history. *Freshwater Biology*, 56, 1746–1760. https://doi.org/10.1111/j.1365-2427.2011.02609.x
Jarocki, F.P. (1822) *Zoologiia Czyli Zwierzetopismo Ogolne Podlug Naynowszego Systematu, (Gady i plazy). Vol. 3*. Latkiewicz, Warsaw, 184 pp.
de Kay, J.E. (1842) *Zoology of New-York. Part III. Reptiles and Amphibia.* W. & A. White & J. Visscher, Albany, 98 pp.
Klein, J.A. (1989) A checklist of the reptiles and amphibians on the Department of Energy Oak Ridge Reservation, Anderson and Roane Counties, Tennessee. *Journal of the Tennessee Academy of Science*, 64, 228–230.
Kozak, K.H., Blaine, R.A. & Larson, A. (2006) Gene lineages and eastern North American palaeodrainage basins: phylogeography and speciation in salamanders of the *Eurycea bislineata* species complex. *Molecular Ecology*, 15 (1), 191–207. https://doi.org/10.1111/j.1365-294X.2005.02757.x
Kozak, K.H., Larson, A., Bonett, R.M. & Harmon, L.J. (2005) Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: *Desmognathus*). *Evolution*, 59 (9), 2000–2016. https://doi.org/10.1111/j.0014-3820.2005.tb01069.x
Lacépède, B.G.É. (1807) Sur une espèce de quadrupede ovipaire non encore décrite. *Annales du Muséum d'Histoire Naturelle, Paris*, 10, 230–233.
Lane, M.A. (1996) Roles of Natural History Collections. *Annals of the Missouri Botanical Garden*, 83, 536–545. https://doi.org/10.2307/2399994
Lanza, B., Catelani, T. & Lotti, S. (2004) Amphibia Gymnophiona and Caudata donated by Benedetto Lanza to the Museo di Storia Naturale, University of Florence. Catalogue with morphological, taxonomic, biogeographical and biological data. *Atti del Museo Civico di Storia Naturale di Trieste*, 51, 177–265.
Latreille, P.A. & Sonnini, C.S. (1801) *Histoire Naturelle des Reptiles, avec figures dessinées d'après nature. Tome II. Première partie. Quadrupèdes et bipèdes ovipares*. Imprimerie de Crapelet, Paris, 332 pp.
Laurenti, J.N. (1768) *Specimen Medicum, Exhibens Synopsin Reptilium Emendatum cum Experimentis Circa Venena et Antidota Reptilium Austriacorum*. Joan. Thom. nob. de Trattnern, Wien, 214 pp. https://doi.org/10.5962/bhl.title.5108
Le Conte, J. (1824) Description of a new species of Siren, with some observations on animals of a similar nature. *Annals of The Lyceum of Natural History of New York*, 1, 52–58. https://doi.org/10.1111/j.1749-6632.1824.tb00216.x
Leaché, A.D. & Reeder, T.W. (2002) Molecular Systematics of the Eastern Fence Lizard (*Sceloporus undulatus*): A Comparison of Parsimony, Likelihood, and Bayesian Approaches. *Systematic Biology*, 51 (1), 44–68. https://doi.org/10.1080/106351502753475871
Leidy, J. (1852) Report of the curators for 1851. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 5, 354–355.
Linnaeus, C. (1758) *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.* Salvius, Holmiae, 824 pp.

https://doi.org/10.5962/bhl.title.542
Linnaeus, C. (1766). *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio duodecima, reformata.* Salvius, Holmiae, 532 pp.
https://doi.org/10.5962/bhl.title.68927
Malnate, E.V. (1971) A Catalog of Primary Types in the Herpetological Collections of the Academy of Natural Sciences, Philadelphia (ANSP). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 123, 345–375.
Martof, B.S. (1975) *Pseudotriton ruber*. *Catalogue of American Amphibians and Reptiles*, 165, 1–3.
McAllister, C.T. & Bursey, C.R. (2004) Endoparasites of the Dark-Sided Salamander, *Eurycea longicauda melanopleura*, and the Cave Salamander, *Eurycea lucifuga* (Caudata: Plethodontidae), from Two Caves in Arkansas, U.S.A. *Comparative Parasitology*, 71, 61–66.
https://doi.org/10.1654/4076
McAllister, C.T., Bursey, C.R., Trauth, S.E. & Fenolio, D.B. (2006) Helminth Parasites of the Grotto Salamander, *Eurycea spelaea* (Caudata: Plethodontidae), from Northern Arkansas and Southern Missouri, U.S.A. *Comparative Parasitology*, 73, 291–297.
https://doi.org/10.1654/4196.1
Means, D.B. (2005) *Desmognathus fuscus* (Green, 1818) Northern Dusky Salamander. *In:* Lannoo, M. (Ed.), *Amphibian Declines: The Conservation Status of United States Species*. University of California Press, Berkeley, California, pp. 708–710.
Means, D.B., Lamb, J.Y. & Bernardo, J. (2017) A new species of dusky salamander (Amphibia: Plethodontidae: *Desmognathus*) from the Eastern Gulf Coastal Plain of the United States and a redescription of *D. auriculatus*. *Zootaxa*, 4263 (3), 467–506.
https://doi.org/10.11646/zootaxa.4263.3.3
Merrem, B. (1820) *Versuch eines Systems der Amphibien*. J.C. Kreiger, Marburg, 191 pp.
https://doi.org/10.5962/bhl.title.5037
Meshaka, W.E. & Layne, J.N. (2015) The herpetology of southern Florida. *Herpetological Conservation and Biology*, 10, 1–353.
Miller, B.T., Lamb, J.W. & Miller, J.L. (2005) The Herpetofauna of Arnold Air Force Base in the Barrens of South-Central Tennessee. *Southeastern Naturalist*, 4, 51–62.
https://doi.org/10.1656/1528-7092(2005)004[0051:THOAAF]2.0.CO;2
Moore, J.P. (1899) *Leurognathus marmorata*, a New Genus and Species of Salamander of the Family Desmognathidæ. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 51, 316–323.
Morris, M.A., Funk, R.S. & Smith, P.W. (1983) An Annotated Bibliography of the Illinois Herpetological Literature 1960-1980, and an Updated Checklist of Species of the State. *Illinois Natural History Survey Bulletin*, 33, 1–137.
https://doi.org/10.21900/j.inhs.v33.138
Mount, R.H. (1975) *The reptiles and amphibians of Alabama*. University of Alabama Press, Tuscaloosa, 347 pp.
Munshi-South, J., Zak, Y. & Pehek, E. (2013) Conservation genetics of extremely isolated urban populations of the northern dusky salamander (*Desmognathus fuscus*) in New York City. *PeerJ*, 1, e64.
https://doi.org/10.7717/peerj.64
Ohler, A. & Dubois, A. (2018) Article 23.9 of the *Code* cannot be used to reject the nomen *Hyla quoyi* Bory de Saint-Vincent, 1828 as a *nomen oblitum. Zoosystema,* 40 (2), 109–121.
https://doi.org/10.5252/zoosystema2018v40a6
Palisot de Beauvois, A.M.F.J. (1799) Translation of a memoir on a new species of Siren. *Transactions of the American Philosophical Society*, 4, 277–281.
https://doi.org/10.2307/1005106
Peale, T.R. & Green, J. (1830) Description of two new species of the Linnean genus *Lacerta*. *Journal of the Academy of Natural Sciences of Philadelphia*, 6, 231–234.
Petranka, J.W. (1998) *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, 587 pp.
Powell, R., Conant, R., & Collins, J.T. (2016) *Peterson field guide to reptiles and amphibians of eastern and central North America. 4th Edition.* Houghton Mifflin Harcourt, Boston, 494 pp.
Price, S.J., Eskew, E.A., Cecala, K.K., Browne, R.A. & Dorcas, M.E. (2012) Estimating survival of a streamside salamander: importance of temporary emigration, capture response, and location. *Hydrobiologia*, 679, 205–215.
https://doi.org/10.1007/s10750-011-0882-2
Pyron, R.A., O'Connell, K.A., Lemmon, E.M., Lemmon, A.R. & Beamer, D.A. (2020) Phylogenomic data reveal reticulation and incongruence among mitochondrial candidate species in Dusky Salamanders (*Desmognathus*). *Molecular Phylogenetics and Evolution*, 146, 106751.
https://doi.org/10.1016/j.ympev.2020.106751
Raffaëlli, J. (2007) *Les Urodèles du monde*. Penclen, Condé-sur-Noireau, 377 pp.
Rafinesque, C.S. (1818a) Description of a new American salamander—the red-backed salamander from the Highlands. *Scientific Journal of New York*, 1, 25–26.
Rafinesque, C.S. (1818b) Farther accounts of discoveries in natural history, in the western states. *American Monthly Magazine and Critical Review*, 4, 39–42.

Rafinesque, C.S. (1820) III Class. Erpetia.—The reptiles. *Annals of Nature*, 1, 4–6.
https://doi.org/10.5962/bhl.title.106763
Reed, C.F. (1960) *Plethodon erythronotus* (Raf.), the Red-Backed Salamander. *Herpetologica*, 16 (3), 207–213.
Rossman, D.A. (1958) A New Race of *Desmognathus fuscus* from the South-Central United States. *Herpetologica*, 14, 158–160.
Ruschenberger, W.S.W. (1860) *A notice of the origin, progress, and present condition of the Academy of natural sciences of Philadelphia*. Collins, Philadelphia, Pennsylvania, 102 pp.
Sager, A. (1839) On American Amphibia. *American Journal of Science and Arts*, 36, 320–324.
Say, T. (1818) Notes on Professor Green's paper on the Amphibia, published in the September number of this journal. *Journal of the Academy of Natural Sciences of Philadelphia*, 1, 405–407.
Schausberger, P. & Hoffmann, D. (2008) Maternal manipulation of hatching asynchrony limits sibling cannibalism in the predatory mite *Phytoseiulus persimilis*. *Journal of Animal Ecology*, 77, 1109–1114.
https://doi.org/10.1111/j.1365-2656.2008.01440.x
Schmidt, K.P. (1953) *A Check List of North American Amphibians and Reptiles. 6th Edition*. University of Chicago Press, Chicago, Illinois, 280 pp.
Schneider, J.G. (1799) *Historia Amphibiorum Naturalis et Literarariae. Fasciculus Primus. Continens Ranas, Calamitas*, *Bufones, Salamandras et Hydros in Genera et Species Descriptos Notisque suis Distinctos*. Frommanni, Jena, 264 pp.
https://doi.org/10.5962/bhl.title.4270
Schneider, J.G. (1801) *Historiae Amphibiorum naturalis et literariae. Fasciculus secundus continens Crocodilos, Scincos, Chamaesauras, Boas. Pseudoboas, Elapes, Angues. Amphisbaenas et Caecilias*. *2nd Edition*. Frommanni, Jena, 374 pp.
https://doi.org/10.5962/bhl.title.4270
Shaw, G. (1802) *General Zoology or Systematic Natural History. Vol. III. Part 1. Amphibia.* Thomas Davison, Whitefriars, London, 615 pp.
https://doi.org/10.5962/bhl.title.1593
Shaw, G. & Nodder, F.P. (1798) *The Naturalist's Miscellany; or Coloured Figures of Natural Objects Drawn and Described Immediately from Nature. Vol. 9*. Nodder & Co., London, no pagination.
https://doi.org/10.5962/bhl.title.79941
Simon, T.P., John, O., Whitaker, J., Castrale, J.S. & Minton, S.A. (2002) Revised Checklist of the Vertebrates of Indiana. *Proceedings of the Indiana Academy of Science*, 111, 182–214.
Sloane, H. (1725) *A Voyage to the Islands Madera, Barbados, Nieves, S. Christophers and Jamaica. Vol. II.* Printed for the author, London, 499 pp.
https://doi.org/10.5962/bhl.title.642
Smith, E.F. (1923) *Jacob Green, 1790–1841*, *Chemist*. University of Pennsylvania, Philadelphia, Pennsylvania, 34 pp.
Smith, H.M. (1938) Remarks on the status of the subspecies of *Sceloporus undulatus*, with descriptions of new species and subspecies of the *undulatus* group. *Occasional Papers of the Museum of Zoology, University of Michigan*, 387, 1–17.
Smith, H.M. (1948) The scientific name of the common northern fence lizard. *Natural History Miscellanea, Chicago Academy of Sciences*, 24, 1–2.
Smith, H.M. (2005) *Plestiodon*: a replacement name for most members of the genus *Eumeces* in North America. *Journal of Kansas Herpetology*, 14, 15–16.
Smith, H.M. & Kohler, A.J. (1977) A Survey of Herpetological Introductions in the United States and Canada. *Transactions of the Kansas Academy of Science*, 80, 1–24.
https://doi.org/10.2307/3627503
Smith, H.M. & Taylor, E.H. (1950) An Annotated Checklist and Key to the Reptiles of Mexico Exclusive of the Snakes. *Bulletin of the United States National Museum*, 1–253.
https://doi.org/10.5479/si.03629236.199
Smith, H.M. & Tihen, J.A. (1961) *tigrina* (Salamandra) Green, 1825: proposed validation under the Plenary Powers (Amphibia, Caudata). *Bulletin of Zoological Nomenclature*, 18, 214–216.
Sonnini de Manoncourt, C.S. & Latreille, P.A. (1801) *Histoire Naturelle des Reptiles. Tome IV. Seconde Partie, Serpens*. Deterville, Paris, 410 pp.
https://doi.org/10.5962/bhl.title.4688
Southerland, M.T., Jung, R., Mercurio, G., Chellman, I., Southerland, M., Baxter, D. & Vølstad, J. (2004) Stream salamanders as indicators of stream quality in Maryland, USA. *Applied Herpetology*, 2, 23–46.
https://doi.org/10.1163/1570754041231596
Stejneger, L. (1903) Rediscovery of one of Holbrook's salamanders. *Proceedings of the United States National Museum*, 26, 557–558.
https://doi.org/10.5479/si.00963801.1321.557
Stejneger, L. & Barbour, T. (1917) *A Check List of North American Amphibians and Reptiles*. Harvard University Press, Cambridge, Massachusetts, 125 pp.
https://doi.org/10.5962/bhl.title.4271
Stejneger, L. & Barbour, T. (1933) *A Check List of North American Amphibians and Reptiles. 3rd Edition*. Harvard University Press, Cambridge, Massachusetts, 185 pp.

https://doi.org/10.5962/bhl.title.6834
Stejneger, L.H. & Barbour, T.W. (1943) *A Check List of North American Amphibians and Reptiles. 5th Edition*. Harvard University Press, Cambridge, Massachusetts, 260 pp.
https://doi.org/10.2307/1438631
Stone, W. (1906) Notes on reptiles and batrachians of Pennsylvania, New Jersey and Delaware. *The American Naturalist*, 40, 159–170.
https://doi.org/10.1086/278611
Stranko, S.A., Gresens, S.E., Klauda, R.J., Kilian, J.V., Ciccotto, P.J., Ashton, M.J. & Becker, A.J. (2010) Differential Effects of Urbanization and Non-Natives on Imperiled Stream Species. *Northeastern Naturalist*, 17, 593–614.
https://doi.org/10.1656/045.017.0406
Taylor, E.H. (1932) *Eumeces inexpectatus*: a new American lizard of the family Scincidae. *The University of Kansas Science Bulletin*, 20, 251–261.
https://doi.org/10.5962/bhl.part.19197
Temminck, C.J. & Schlegel, H. (1838) *Fauna Japonica sive Descriptio animalium, quae in itinere per Japonianum, jussu et auspiciis superiorum, qui summum in India Batava Imperium tenent, suscepto, annis 1823–1830 colleget, notis observationibus et adumbrationibus illustratis. Vol. 3. Chelonia, Ophidia, Sauria, Batrachia.* J. G. Lalau, Leiden, 144 pp.
https://doi.org/10.5962/bhl.title.124951
Tihen, J.A. (1949) The Genera of Gerrhonotine Lizards. *The American Midland Naturalist*, 41, 580–601.
https://doi.org/10.2307/2421775
Uzzell, T. (1967) *Ambystoma jeffersonianum. Catalogue of American Amphibians and Reptiles*, 47, 1–2.
https://doi.org/10.15781/T2R785T43
Valentine, B.D. (1974) *Desmognathus quadramaculatus. Catalogue of American Amphibians and Reptiles*, 153, 1–4.
https://doi.org/10.15781/T2XD0R301
Waite, F.C. (1907) Specific name of *Necturus maculosus*. *The American Naturalist*, 41, 23–30.
https://doi.org/10.1086/278699
Wiegmann, A.F.A. (1828) Beyträge zur Amphibienkunde. *Isis von Oken*, 21, 364–383.
Wiegmann, A.F.A. (1834) *Herpetologia Mexicana, seu descriptio amphibiorum novae hispaniae*. Berolini, Luderitz, 54 pp.
Williams, C. (2015) The salamander species assemblage and environment of forested seeps of the Allegheny High Plateau, Northwestern Pennsylvania, USA. *Herpetology Notes*, 8, 99–106.
Witteveen, J. (2016) Suppressing synonymy with a homonym: the emergence of the nomenclatural type concept in nineteenth century natural history. *Journal of the History of Biology*, 49, 135–189.
https://doi.org/10.1007/s10739-015-9410-y
Wood, G.B. (1865) *Biographical memoir of Franklin Bache, M.D.: prepared at the request of the College of Physicians of Philadelphia and read before the college May 3d and June 7th, 1865*. J.B. Lippincott, Philadelphia, Pennsylvania, 66 pp.
Yarrow, H.C. (1882) Check list of North American Reptilia and Batrachia, with catalogue of specimens in U. S. National Museum. *Bulletin of the United States National Museum*, 1882, 1–249.
https://doi.org/10.5479/si.03629236.24.1