Allocation of *Salamandra auriculata* Holbrook, 1838, with a new species of swamp-dwelling dusky salamander (*Plethodontidae: Desmognathus*) from the Atlantic Coastal Plain

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Abstract

Most swamp-dwelling dusky salamanders of the genus *Desmognathus* from the Coastal Plain were long treated as a single species (*Desmognathus auriculatus*) ranging from east Texas to southeastern Virginia. This taxon concept was based on the name *Salamandra auriculata* Holbrook, 1838 with type locality Riceboro, Liberty County, Georgia and a type series that could not be located by later authors. Recent workers have been unable to locate or verify swamp-dwelling populations from east Texas and western Louisiana, which appear to be extirpated and may not have represented a distinct taxon from co-occurring lineages of *D. conanti*. Recent molecular phylogenies have supported at least four distinct species-level taxa within *D. auriculatus*. Populations from the Gulf Coastal Plain in eastern Louisiana, Mississippi, and southwestern Alabama were recently described as *D. valentinei* Means, Lamb, and Bernardo, 2017 and *D. pascagoula* Pyron, O’Connell, Lamb, and Beamer, 2022. This leaves two remaining species-level lineages with uncertain taxonomy and nomenclature: *D. auriculatus* A (Alabama, Florida, and Georgia), and *D. auriculatus* B/C (Georgia, South Carolina, and North Carolina), both of which occur near the type locality. We recently located a specimen at the Muséum national d’Histoire naturelle in Paris (MNHN 0.4675) that we concluded is one of Holbrook’s syntypes and designated it as the lectotype, but without allocation. Here, we use linear morphometrics to confidently allocate it to *D. auriculatus* A, bolstered by examination of three historical topotypic collections. This requires a new name for *D. auriculatus* B/C, which we describe as *D. valtos* sp. nov. (suggested common name: Carolina Swamp Dusky Salamander) from Otter Creek, Craven County, North Carolina. Other related and sympatric species of *Desmognathus* remain to be described from the Atlantic Coastal Plain and adjacent Piedmont of the southeastern United States.

Key words: Carolina Swamp Dusky Salamander, *Desmognathus valtos* sp. nov., taxonomy, nomenclature, cryptic species

Introduction

The Southern Dusky Salamander, *Desmognathus auriculatus* (Holbrook, 1838), has a long and contentious nomenclatural history, and knowledge of its distribution and taxonomy has changed substantially over time (Beamer & Lamb 2008; Grobman 1950; Pyron et al. 2022a; Valentine 1963). It was often treated as a single species ranging from Virginia to Texas (Bishop 1943; Means 1999). Historically reported swamp-dwelling populations from eastern Texas and western Louisiana (Burger *et al.* 1949; Livezey 1950; Sanders & Smith 1949) have not been recently verified (Beamer & Lamb 2008; Hibbits *et al.* 2015; Means *et al.* 2017) and may have been extirpated or may not have represented a distinct taxon from *D. conanti*. The known, extant populations previously referred to *D. auriculatus* are a polyphyletic assemblage of at least four species-level lineages (Beamer & Lamb 2020; Pyron *et al.* 2020). Of these, populations in Louisiana, Mississippi, and Alabama were recently described as *D. valentinei*...
Means, Lamb, and Bernardo, 2017, and populations of *D. valentinei* from southeastern Mississippi and southwestern Alabama were subsequently described as *D. pascagoula* Pyron, O’Connell, Lamb, and Beamer, 2022.

Remaining populations from southern Alabama to southeastern Virginia form two mito-nuclear candidate species (Pyron et al. 2020). The first occurs in south-central Alabama, northern and Peninsular Florida, and southern Georgia, representing the *D. auriculatus* A lineage (Beamer & Lamb 2008, 2020). It has recently been considered the nominotypical taxon, putatively encompassing the type locality of “Riceborough, [Riceboro, Liberty County,] in Georgia” (see Means et al. 2017). Dusky salamanders are now absent from this locality (Graham et al. 2010). This species-level taxon has undergone range-wide population declines starting in the late the 1960’s (Dodd 1998; Graham et al. 2010; Means 2015; Pyron et al. 2022a), more so than any of the other swamp-dwelling populations (C. Holzheuser and D. Means, pers. comm.). In contrast, the *D. auriculatus* B/C lineage from the Atlantic Coastal Plain in southeastern Georgia, South Carolina, and North Carolina (Pyron et al. 2022c) represents the fourth candidate species in this group and is widespread and abundant at numerous localities across its range (DAB and RAP, pers. obs.).

Despite recent assertions (Beamer & Lamb 2008, 2020; Means et al. 2017), allocation of *Salamandra auriculata* Holbrook, 1838 to *Desmognathus auriculatus* A is still unclear (see Pyron & Beamer 2022). Beamer & Lamb (2020) suggested that the Ogeechee River in southeastern Georgia was the boundary between *D. auriculatus* A (south) and *D. auriculatus* B/C (north), and Riceboro is south of the Ogeechee. However, Chandler et al. (2018) had reported a population of *D. auriculatus* B/C south of the Ogeechee in Candler County, which raises the possibility that both species occur near the type locality. We subsequently used the COI barcode locus (unpubl. data) to genetically confirm a population of *D. auriculatus* B/C at the coincidentally named “Holbrook Pond” on Ft. Stewart in Liberty County, Georgia,~23 airline km NW of Riceboro and ~23 airline km SW of the Ogeechee. Allocation of the name *D. auriculatus* therefore comes down to the specific identity of the type specimens, of which Holbrook reported a series.

**Systematics**

We previously reported discovering one of Holbrook’s syntypes in the Muséum national d’Histoire naturelle (MNHN 0.4675), which we designated as the lectotype (Pyron & Beamer 2022). We did not allocate it at the time but do so here based on linear morphometrics. Following a modification of Bingham et al. (2018) from our recent study (Pyron et al. 2022b), we used Adobe Photoshop to measure the high-resolution photographs of MNHN 0.4675 (Pyron & Beamer 2022: fig. 3) to 0.01mm precision, setting a 20mm scale bar from the 1cm reference grid. The measurements are: SVL (snout-vent length = 55.27), TL (tail length = 49.02), AG (axilla-groin length = 30.75), CW (chest width = 5.53), FL (femur length = 2.35), HL (humerus length = 3.78), SG (snout-gular length = 9.23), TW (tail width at rear of vent = 5.04), TO (length of third toe = 2.29), FI (length of third finger = 1.53), HW (head width = 7.28), ED (eye diameter = 2.52), IN (internarial distance = 2.15), ES (eye-snout distance = 2.30), ON (orbito-narial distance = 1.51), IO (inter-orbital distance = 2.39), and IC (inter-canthal distance = 2.94).

We combined these with the same measurements from 33 *D. auriculatus* B/C and 41 *D. auriculatus* A from the RAP collection, pooled across sex and age (Appendix S1). These specimens represent populations sampled from across the range of both lineages and should therefore incorporate the range of species-level variation in both taxa. We used SVL plus the residuals of the other 16 measurements regressed against SVL for a MANCOVA and linear discriminant analysis of the two lineages. The MANCOVA revealed significant differences in overall size and shape across the two lineages ($F_{16,57} = 7.5$, Pillai = 0.68, $P = 4.7 \times 10^{-3}$), while the classifier was 92% accurate overall, correctly identifying 28/33 *D. auriculatus* B/C (85%) and 40/41 *D. auriculatus* A (98%). It estimated that MNHN 0.4675 is *D. auriculatus* A with ~100% probability (Fig. 1). We repeated the measurements of MNHN 0.4675 five times, revealing modest variability in classification probability due to landmark uncertainty, but never less than 80% and always greater than any *D. auriculatus* B/C. While the differences and potential interaction of size-corrected shape variables are difficult to interpret, AG–SVL is the heaviest-loading measurement in the LDA with a significant median difference, and we therefore offer it as an example of a diagnostic morphological trait.

This allocation is bolstered in our estimation by examination of three historical topotypic collections from Riceboro. The first is USNM 3901 & 271136–45, collected prior to 1858 by Dr. William L. Jones, an associate, contemporary, and neighbor of Dr. Joseph M. B. Harden, the original collector of Holbrook’s syntypes (see Pyron
The second is ANSP 26539 & 35016 from “1 m W Riceboro,” collected 8 April 1933 by Ernest Bacon. The third is six of 15 individuals from the lot DBM-1545 (now possibly in the FLMNH), collected 13 April 1971 by D. Bruce Means in a tributary of Riceboro Creek on the Riceboro city limits (Means 1974: fig. 25). All give a strong impression of belonging to *D. auriculatus* A based on their more heavily keeled tails, black or dark-grey dorsal coloration, darker and less distinctly patterned venters, and more prominent and well-defined white “porthole” markings in up to three rows along the lateral surfaces (see Means 1999: fig. 1; Means *et al.* 2017: fig. 14, 15, 18). In contrast, *D. auriculatus* B/C tends to have less heavily keeled tails, greenish or lighter-grey dorsal ground color, more granular and colorfully patterned venters, and less-distinct portholes.

As additional evidence for Holbrook’s specimens having been *Desmognathus auriculatus* A, one might also include the disappearance of populations from the vicinity of Riceboro (like elsewhere throughout its range), while *D. auriculatus* B/C is still present and even abundant at most surveyed historical localities, including several in southeastern Georgia near Riceboro. As a result, we corroborate the previous allocation (Beamer & Lamb 2008, 2020) and re-description (Means *et al.* 2017) of *Salamandra auriculata* Holbrook, 1838 to the *Desmognathus auriculatus* A lineage. We tentatively accept the proposed historic range of *D. auriculatus* described by Means *et al.* (2017) and Pyron *et al.* (2022a, b) in southern Alabama, northern Florida, and southern Georgia, noting that many apparently extirpated historical populations in Alabama and Florida have yet to be verified genetically.

Our previous work (Pyron *et al.* 2020, 2022c) demonstrated that *D. auriculatus* B/C is a phylogenetically distinct mito-nuclear candidate species exhibiting no apparent gene flow with *D. auriculatus*. Its sister species is the *D. fuscus* D lineage, with which it exhibits small amounts of detectable admixture in both directions that we did not previously consider significant (Pyron *et al.* 2022c). Similarly, some individuals of the closely related *D. fuscus* C lineage exhibit significant ancestry from *D. auriculatus* B/C, but the reverse is not true, suggesting asymmetry in hybridization or gene flow. Consequently, we conclude that *D. auriculatus* B/C represents a genetically, geographically, and morphologically distinct species and recognize it here as:
Desmognathus valtos sp. nov.

*Desmognathus auriculatus* Holbrook, 1838 (part: see Means 1999; most historical concepts of *D. auriculatus* included populations from GA, SC, and NC)

**Holotype:** MNHN 2021.0131 (RAP0955; Fig. 2), collected 30 August 2019 by DAB at Otter Creek (NC: Craven; 34.968, -76.958; 4m ASL).

**Paratypes:** NCSM 108360–1 (RAP 2289 & 2293), collected 22 April 2022 by RAP at the type locality (Fig. 3). BMNH 2021.7566, GSU 26900, & GMNH 52996 (RAP1646 & 1648–9), collected 9 January 2021 by RAP, DAB, and Dirk J. Stevenson at Holbrook Pond (GA: Liberty; 31.914, -81.554; 7m ASL). AMNH A-193889 (RAP2294; Fig. 4), collected 22 April 2022 by RAP at Jasons Branch (NC: Carteret; 34.768, -76.943; 6m ASL).

**Etymology:** The specific epithet is a non-Latin noun used in apposition, from the Greek váltos (βάλτος) for “swamp,” in reference to the primary habitat of the species. We suggest the common name “Carolina Swamp Dusky Salamander.”

**Diagnosis:** In comparison with the re-description of *Desmognathus auriculatus* (Holbrook, 1838) by Means et al. (2017), *D. valtos* is a moderately-sized Dusky Salamander (17.2–62.4mm SVL for transformed specimens), typically with a dark greenish-grey ground color and orangish wash on the dorsal surfaces (Fig. 2). Smaller individuals often have visible remnants of orangish or reddish paired larval spots on the dorsum; differentiation between dorsal and lateral color pattern is typically absent in *D. auriculatus*, and larval patterning is usually obscured by darkening in even the smallest specimens. Differs significantly in overall size and shape from *D. auriculatus*, the greatest difference being proportionally longer torsos (longer AG). Tail is thick, girthy, and long, up to 106% SVL, typically less keeled than *D. auriculatus*, but still flattened at the terminus. Dorsal surface of tail typically exhibits a yellowish or orangish stripe with indistinct margins even in larger individuals (Fig. 2–5); such stripes are usually less colorful and prominent in *D. auriculatus*, particularly older specimens. Ventrolateral porthole markings with whitish, yellowish, orangish, or reddish pigment may occur in up to three rows (see Pyron et al. 2022b and references therein), but these are generally less prominent than in *D. auriculatus*. Ventral color pattern is typically relatively bright and granular, consisting of interspersed flecking of darkened melanophores, lighter xanthophores, and whitish speckling, while in *D. auriculatus* “the belly is unmistakably black but may be densely peppered with small whitish or silvery speckling (Fig. 14c)” (Means et al. 2017).

**FIGURE 2.** Holotype (MNHN 2021.0131/RAP0955) of *Desmognathus valtos*. Specimen is an adult (53.1mm SVL), possibly a female based on apparent lack of mental gland and lack of peramorphic or hypertrophied jaw musculature. The holotype exhibits the diagnostic greenish-grey ground color with a reddish-orange dorsal wash, orangish stripe with indistinct margins on the dorsal surface of the tail, yellowish or orangish portholes on the lateral surfaces in three rows, and granular ventral color-pattern with clusters of xanthophores and melanophores interspersed with white flecks and speckles.
FIGURE 3. Paratype (NCSM 108360/RAP2289) of Desmognathus valtos. Specimen is a juvenile or small adult (32.1 mm SVL) showing the same diagnostic features as the holotype, with more prominent dorsal color-pattern and lateral white flecking that is characteristic of younger individuals.

FIGURE 4. Paratype (AMNH A-193889/RAP2294) of Desmognathus valtos. Specimen is a small adult (41.2 mm SVL) showing the same diagnostic features as the holotype, with more prominent dorsal color-pattern and lateral white flecking or speckling that is characteristic of younger individuals, with the latter extending noticeably onto the dorsal surfaces.
FIGURE 5. Comparative specimen (AMNH A-193891/RAP2303) of Desmognathus valtos. Specimen is a large adult (62.4 mm SVL) showing the same diagnostic features as the holotype, with very prominent reddish or orangish wash or stripe on the dorsal surface and very indistinct margins on the tail.

FIGURE 6. Comparative specimen (AMNH A-193890/RAP2297) of Desmognathus valtos. Specimen is transformed juvenile (17.2 mm SVL) with remnants of gill nubs, showing general approximation of the adult color pattern. This specimen exhibited substantial metachrosis after capture and rapid fading in preservative; in life, it exhibited more prominent differentiation of lateral, dorsal, and ventral surfaces and a bolder stripe on the dorsal surface of the tail.
Notes: Little is known about reproduction, larval morphology, or ecological interactions; a few notes were given by Robertson & Tyson (1950) in comparison to D. “fuscus” (potentially representing multiple distinct species) and D. brimleyorum. Sexual dimorphism has not been characterized, but adult males appear to exhibit peramorphic hypertrophied jaw musculature as in most other Desmognathus. Ontogenetic change in color pattern is minimal; a 17mm juvenile (Fig. 6) was mostly transformed with barely any gill nubs visible, and a less colorful but essentially adult pattern. That specimen exhibited substantial metachrosis (primarily dorsal lightening) ~24 hours after capture, but this was not observed in adults.

Discussion

Here, we offer a taxonomic and nomenclatural resolution to the complex and long-standing uncertainty regarding many populations of swamp-dwelling Coastal Plain dusky salamanders (see Beamer & Lamb 2008, 2020; Means et al. 2017; Pyron & Beamer 2022; Pyron et al. 2022a–c). Historically reported swamp-dwelling populations from west of the Mississippi River in Texas and Louisiana remain a mystery (Hibbitts et al. 2015). Similar questions remain about the identity of apparently extirpated populations from southern Alabama and the northwestern Panhandle of Florida (Pyron et al. 2022a). A combination of formalin sequencing (O’Connell et al. 2022; Pyron et al. 2022c) and morphometric approaches such as the one implemented here may help to allocate historical specimens. An obvious limitation of the latter is difficulty in identifying genetic hybrids or new cryptic groups without a priori classification.

Swamp-dwelling populations from east of the Mississippi River in Louisiana and south-central Mississippi represent Desmognathus valentinei, while those in southeastern Mississippi and southwestern Alabama represent D. pascagoula. We restrict the name D. auriculatus (Holbrook, 1838) to populations from southern Alabama, northern Florida, and southern Georgia, terminating near the Ogeechee River in Georgia and representing the former D. auriculatus “A” lineage. This species has undergone notable declines, far more so than any other known Desmognathus species (Means 2015). Finally, we describe the Atlantic Coastal Plain populations from the Ogeechee River in Georgia to northern North Carolina as D. valtos, representing the former D. auriculatus “B/C” lineage.

Genetically verified populations of Desmognathus valtos are known from Liberty County, Georgia to Beaufort County, North Carolina (Pyron et al. 2022: fig. 1). We doubt that it occurs in Virginia (see Robertson & Tyson 1950); examination of hundreds of specimens at the NMNH did not yield any unambiguous individuals. Recently encountered specimens from a swampy tributary of the Northwest River in Chesapeake County, Virginia appeared to represent D. fuscus C (D. Weisenbeck, pers. comm.). Some geographically and phylogenetically distant populations of D. fuscus E from the Blue Ridge mountains of Virginia apparently captured mitochondrial haplotypes of D. valtos during a past hybridization event, likely facilitated by range shifts during glacial cycles (Beamer & Lamb 2020). Additional work is needed to clarify the history of genetic interactions between Desmognathus in the Coastal Plain and Piedmont.

Little is known about the biology of this species; despite its widespread abundance, few studies have been conducted (e.g., Robertson & Tyson 1950). It is found in low-relief, low-elevation swampy areas with muddy or mucky substrates and is particularly abundant in stick piles and debris dams formed by water currents on the margins of swampy areas. We consider the mating and nesting behaviors reported by Neill & Rose (1949) and Verrell (1997) from near Augusta, Georgia to be of dubious allocation to this species. Instead, they likely represent Desmognathus conanti A or D. fuscus C (see Pyron et al. 2022c). Observations by the authors (2002–2022) revealed widespread and abundant populations of D. valtos across their range, corroborated by numerous recent citizen-science records on iNaturalist, including extensive state and federal protected areas. Consequently, we suggest that this species be classified as “LC” under the IUCN Red List criteria (see Maes et al. 2015). However, swamp-dwelling Coastal Plain Desmognathus (particularly D. auriculatus) have exhibited substantial apparent declines elsewhere (Pyron et al. 2022a), and this species may be vulnerable to future land-use alterations, emerging infectious diseases, or global climate change.

A key question of ecological and evolutionary interest is how swamp-specific microhabitats and other niche preferences vary between Desmognathus valtos, D. auriculatus, D. pascagoula, and D. valentinei. Whether or not their similar phenotypes are convergent or parallel and share a primitive or derived genetic basis may help to illuminate the history of ecomorphological diversification in the genus. To our knowledge, D. valtos is never found
syntopically with other *Desmognathus*, though *D. fuscus C* are found in close proximity (<1km) at some sites, with which it exhibits some degree of gene flow (Pyron et al. 2022c). Other salamanders found in these communities include common swamp-dwelling species such as *Amphiuma means*, *Eurycea chamberlaini*, *E. cirrigera*, *E. guttolineata*, *E. quadridigitata*, *Pseudotriton montanus*, *Siren intermedia*, and *Stereochilus marginatus*. Finally, its sister taxon, *D. fuscus D*, is found in the adjacent Coastal Plain and Piedmont of North and South Carolina, though there is little genetic evidence for any substantial admixture (Pyron et al. 2022c).

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