

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/352465131>

Glow and Behold: Biofluorescence and New Insights on the Tails of Pitvipers (Viperidae: Crotalinae) and Other Snakes

Article in *Herpetological Review* · June 2021

CITATIONS

0

READ

1

2 authors, including:



[Robert W Mendyk](#)

Audubon Zoo

46 PUBLICATIONS 249 CITATIONS

[SEE PROFILE](#)

ARTICLES

Herpetological Review, 2021, 52(2), 221–237.

© 2021 by Society for the Study of Amphibians and Reptiles

Glow and Behold: Biofluorescence and New Insights on the Tails of Pitvipers (Viperidae: Crotalinae) and Other Snakes

Biofluorescence, the absorption of photons by biological tissues that are then reemitted at longer lower-energy wavelengths, occurs naturally in a broad range of organisms. In recent years, biofluorescence in tetrapods has emerged as an increasingly common phenomenon, with many examples documented in mammals (Jeng 2019; Kohler et al. 2019; Anich et al. 2020), birds (Pearn et al. 2003; McGraw et al. 2007; Barreira et al. 2012; Camacho et al. 2019; Wilkinson et al. 2019), amphibians (Nowogrodzki 2017; Taboada et al. 2017a,b; Deschepper et al. 2018; Goutte et al. 2019; Gray 2019; Thompson et al. 2019; Lamb and Davis 2020; Whitcher 2020) and reptiles (Hulse 1971; Gruber and Sparks 2015; Prötzel et al. 2018, 2021; Sloggett 2018; Seiko and Terai 2019; Eipper et al. 2020; Eto 2020; Top et al. 2020; Mendyk 2021). The extent of this phenomenon in reptiles and its ecological and evolutionary underpinnings, however, remain poorly studied, though various fluorescent emission patterns have been identified in reptiles including the carapaces of sea turtles (Gruber and Sparks 2015), bony cranial protuberances of lizards, (Prötzel et al. 2018), skeletal elements of geckos (Sloggett 2018; Top et al. 2020), and the body scalation of various snakes and lizards (Hulse 1971; Seiko and Terai 2019; Eipper et al. 2020; Eto 2020; Prötzel et al. 2021). Taken together, these few examples suggest that biofluorescence may be more widespread in, and important to reptiles than previously envisaged.

Snakes offer new opportunities for exploring biofluorescence in reptiles. To date, biofluorescence has been recorded in several snake species across various families, including fossorial taxa such as the leptotyphlopids *Rena humilis* (Hulse 1971) and various members of the typhlopids genus *Anilius* (Eipper et al. 2020), the marine elapid *Laticauda laticaudata* (Seiko and Terai 2019), the terrestrial lamprophiids *Limaformosa crossi* and *Mehelya poensis* (Eto 2020), and rattlesnakes (Klauber 1956). Fluorescent pteridine-derived substances have also been extracted from the skin of three colubrids (*Elaphe climacophora*, *E. quadrivirgata*,

Euprepophis conspicillata) and the pitviper *Gloydus blomhoffii* (Odate et al. 1959). Given the dramatic differences in body size, morphology, coloration, ecology, behavior and phylogenetic relatedness between these taxa and considering that there are more than 3,800 extant snake species (Uetz et al. 2020) that vary widely in these characters, it is almost certain that additional examples of biofluorescence await discovery in snakes.

Recently, a cursory search for ultraviolet (UV) induced visible fluorescence in a private collection of captive reptiles by one of us (LP) revealed remarkable tail fluorescence in a captive-bred sibling group of juvenile Hagen's Pitvipers, *Trimeresurus hageni*. Here, we dramatically increase the number of snake taxa known to exhibit biofluorescence by describing tail fluorescence in several genera of pitvipers (Viperidae: Crotalinae) for the first time.

MATERIALS AND METHODS

From our initial observations of fluorescence in *T. hageni*, we expanded our sampling to include a total of 28 pitviper species representing ten genera to determine whether tail fluorescence occurs in additional taxa within the group. To establish whether the character is inherent to members of Crotalinae rather than a potential artifact of captivity, a combination of living captive and field specimens were examined, and several frozen and fluid-preserved specimens of both wild and captive origins were analyzed. Fifteen snake species representing the outgroups Boidae, Colubridae, Elapidae, Lamprophiidae, and Viperinae also were examined for tail fluorescence (Table 1).

For visualizing fluorescent tissues, we scanned the entirety of each snake's body in darkness with a 3-watt, 365 nm LED UV torch (model UV301D; Shenzhen LIGHTFE Lighting Co., Ltd., Shenzhen, China) and recorded qualitative data on any tail fluorescence observed. Because 365 nm LED torches also cast a faint blue light that could interfere with or obscure detection of more subtle biofluorescent tissues, torches were fitted with UV pass filters to reduce the overall residual visible light emitted. Although not included as part of our original analysis, we also later examined several specimens using 395 nm LED UV torches (model KJ-C6404; YMMYP Technology Co., Shenzhen, China; and model UV301A; Shenzhen LIGHTFE Lighting Co., Ltd., Shenzhen, China) and a 100 µW 405 nm blue-violet laser (model D8-LASER100; Walfront LLC, Lewes Delaware, USA) for evidence of fluorescent excitation under greater wavelengths.

LAURENCE PAUL

e-mail: laurencepaul@outlook.com

ROBERT W. MENDYK

Department of Herpetology, Audubon Zoo, 6500 Magazine Street
New Orleans, Louisiana 70118, USA

Department of Herpetology, Smithsonian National Zoological Park,
3001 Connecticut Ave NW, Washington, DC 20008, USA

e-mail: rmendyk@auduboninstitute.org

TABLE 1. Snake taxa examined for evidence of UV-induced tail fluorescence.

Family	Subfamily	Taxa (N)
Boidae	Boinae	<i>Corallus annulatus</i> (9), <i>C. caninus</i> (2), <i>C. hortulanus</i> (3)
Colubridae	Colubrinae	<i>Heterodon kennerlyi</i> (1), <i>Masticophis flagellum</i> (2), <i>Pituophis catenifer</i> (1), <i>P. ruthveni</i> (15)
	Dipsadinae	<i>Conopsis lineatus</i> (3)
	Natricinae	<i>Nerodia erythrogaster transversa</i> (1), <i>N. fasciata confluens</i> (1)
Elapidae	Elapinae	<i>Acanthophis laevis</i> (2), <i>Dendroaspis angusticeps</i> (1)
Lamprophiidae	Pseudoxyrhophiinae	<i>Langaha madagascariensis</i> (4)
Viperidae	Crotalinae	<i>Agkistrodon contortrix</i> (2), <i>A. laticinctus</i> (2), <i>A. piscivorus</i> (6), <i>Bothriechis marchi</i> (2), <i>B. lateralis</i> (2), <i>B. schlegelii</i> (10), <i>Crotalus adamanteus</i> (1), <i>C. aquilus</i> (8), <i>C. atrox</i> (2), <i>C. horridus</i> (3), <i>C. lepidus klauberi</i> (10), <i>C. l. lepidus</i> (6), <i>C. morulus</i> (13), <i>C. polystictus</i> (2), <i>C. ravus</i> (2), <i>Ophryacus smaragdinus</i> (2), <i>Lachesis muta</i> (2), <i>Mixcoatlus melanurus</i> (3), <i>Protobothrops cornutus</i> (5), <i>P. mangshanensis</i> (2), <i>P. mucrosquamatus</i> (8), <i>P. tokarensis</i> (3), <i>P. xiangchengensis</i> (2), <i>Sistrurus tergeminus edwardsii</i> (2), <i>Trimeresurus hageni</i> (18), <i>T. mcgregori</i> (6), <i>T. sumatranus</i> (3), <i>T. trigonocephalus</i> (1), <i>Tropidolaemus wagleri</i> (1)
	Viperinae	<i>Bitis nasicornis</i> (3), <i>Vipera ammodytes ammodytes</i> (5)

Captive specimens were examined from Audubon Zoo's herpetology department and a private reptile collection while the animals were inside their terrariums, or during the course of routine husbandry practices such as feeding, enclosure cleaning, weight measurements or veterinary procedures. To minimize the risk of venomous snakebite, handling live captive specimens including restraint and physical manipulation was minimized or avoided. Field specimens were encountered opportunistically. Road-killed individuals were examined in situ at night, and nuisance snakes were retrieved and examined in darkness before relocation.

Fluorescent photography.—For photographing fluorescence, we used a Nikon P950 and Canon Rebel T5i (fitted with an 18–55 mm, 3.5–5.6 IS lens) with apertures of F/8, ISOs of 100–200, and shutter speeds of 2–4 sec. Specimens were illuminated with two of the aforementioned 365 nm LED torches.

Statistical analysis.—A two-tailed Fisher's Exact Test was used to compare the presence or absence of tail fluorescence in taxa with potentially relevant physical or behavioral characters. Statistical significance was assessed at $p < 0.05$.

RESULTS

We recorded tail fluorescence in 22 species of pitvipers representing eight genera and 78.6% of the total number of crotaline taxa examined in this study (Table 2). Tail fluorescence occurred in two principal tissue types: tail scalation including the distal tail tip and the rattle. The color of observed fluorescence varied between species and their age groups from white to blue to bluish-green, and to greenish-yellow. Fluorescence was observed in both wild and captive individuals, confirming a natural presence in pitvipers. The character was also detected in frozen, formalin-, and alcohol-preserved specimens, although the latter two experienced fading. Although this study focused primarily on fluorescent excitation under 365 nm UV light, fluorescence was also observed under longer lower energy wavelengths (395 and 405 nm) in all of the species that were examined under these additional wavelengths (Table 2).

Tail scalation.—The proportion of the tail that fluoresced (and intensity) varied across taxa and between age groups, ranging from roughly the distal $\frac{1}{3}$ – $\frac{1}{2}$ of the tail in several species including *Agkistrodon piscivorus*, *A. laticinctus*, *Bothriechis marchi*, *Crotalus aquilus*, *C. lepidus*, *C. morulus*, *Protobothrops cornutus*, *Trimeresurus hageni* and *T. sumatranus* (Fig. 1), to just a few terminal scales on the distal tail tip in *P. mangshanensis*, *P. mucrosquamatus*, *P. tokarensis* and *Tropidolaemus wagleri* (Fig. 2).

Examination of three successive years of captive-bred *T. hageni* siblings and their wild-caught parents revealed a gradual reduction in tail fluorescence over time. Fluorescence became considerably reduced dorsally by the age of three. While some yearling individuals still exhibited their conspicuous white juvenile tail coloration, others had already transitioned to mostly reddish tails more characteristic of adults; both groups still fluoresced under UV light. A similar difference in tail fluorescence was also observed between juvenile and adult *A. piscivorus*. We also observed a noticeable difference in the degree of tail fluorescence between the adult male and female *T. hageni* examined, with fluorescence much more prominent in the lighter-colored ventral scalation of the male than the reddish-pink scalation of the female. Similar differences were also observed in adult *T. sumatranus*.

In our study, 81.3% of the species that exhibited fluorescent tail scalation are also known to have conspicuous tail coloration (usually as neonates and juveniles) ($N = 13$; $p = 0.0497$), excluding species such as *P. mangshanensis*, *P. mucrosquamatus*, *P. tokarensis*, *P. xiangchengensis*, and *T. wagleri* that did not have conspicuously colored tails but rather slightly lighter colored distal tail tips (Fig. 2). Fifty percent of the species with fluorescent tail scalation are also known to, or are suspected to perform caudal luring behavior ($N = 8$; $p = 0.2530$; Table 2). Because it is likely that the behavior simply has not yet been recorded in some poorly-studied species, we expanded this cohort to include taxa that belong to genera in which caudal luring has been documented or is suspected to occur (Table 2). This number increased to 100% of species with fluorescent tail scalation ($N = 16$; $p = 0.4286$). Of the thirteen species with fluorescent tail scalation that are also known to have conspicuous tail coloration, all belong to genera that contain

TABLE 2. Breakdown of pitvipers examined in this study with descriptions of the tail fluorescence observed. Abbreviations used: N = neonate; J = juvenile; S = subadult; A = adult; C = captive specimen; F = field specimen; PC = preserved captive specimen; PF = preserved field specimen; KTS = known to species; ATF = accompanied tail fluorescence; KTG = known to genus; S = suspected.

Genus	Species	N	Specimens examined			Presence of tail fluorescence				Extent of tail fluorescence		Conspicuous tail coloration		Caudal luring		Comments
			Age class (N,I,S,A)	Type/Origin (C,F,PC,PF)		N	J	S	A	Tail scalation	Rattle	KTS	ATF	KITS	KTG	
<i>Agkistrodon</i>	<i>contortrix</i>	2	0.2.0.0	0.1.0.1		-	Y	-	-	Y	n/a	Y	Y	Y	Y	Distal 1/3–1/2 of tail scalation fluoresced strongly in juveniles.
	<i>laticinctus</i>	2	0.1.0.1	1.1.0.0		-	Y	-	Y	Y	n/a	Y	Y	S	Y	Distal 1/3–1/2 of tail scalation fluoresced strongly in juveniles, but less intensely in adult.
	<i>piscivorus</i>	6	1.2.1.2	2.3.0.1		Y	Y	Y	N	Y	n/a	Y	Y	Y	Y	Faded in juveniles and sub-adults, absent in adults
	<i>marchi</i>	2	0.0.0.2	2.0.0.0		-	-	-	Y	Y	n/a	Y	Y	Y	S	Y
<i>Crotalus</i>	<i>lateralis</i>	2	0.0.0.2	2.0.0.0		-	-	-	N	N	n/a	Y	n/a	S	Y	No fluorescence observed
	<i>schlegelii</i>	10	0.0.0.10	10.0.0.0		-	-	-	N	N	n/a	Y	n/a	Y	Y	No fluorescence observed in adults of multiple color phases (yellow, green, mixed)
	<i>adamanteus</i>	1	1.0.0.0	0.0.0.1		N	-	-	-	N	-	N	n/a	N	Y	No fluorescence observed
	<i>aquilus</i>	8	5.0.0.3	8.0.0.0		Y	-	-	Y	Y	Y	Y	Y	Y	N	Y
	<i>atrox</i>	2	0.0.0.2	0.1.0.1		-	-	-	Y	N	Y	N	n/a	N	Y	Rattle fluoresced
	<i>horridus</i>	3	1.0.2.0	2.1.0.0		N	-	Y	-	N	Y	N	n/a	N	Y	Rattle fluoresced
	<i>lepidus klauberi</i>	10	4.0.0.6	10.0.0.0		Y	-	-	Y	Y	Y	Y	Y	Y	Y	Rattle fluoresced; distal 1/3–1/2 of tail scalation fluoresced moderately in neonates, but dully in adults. Fluorescence also observed under 395 and 405 nm light.
	<i>lepidus lepidus</i>	6	0.3.1.2	6.0.0.0		-	Y	Y	Y	Y	Y	Y	Y	Y	Y	Rattle fluoresced; distal 1/3–1/2 of tail scalation fluoresced moderately in juveniles, but dully in adults. Fluorescence also observed under 395 and 405 nm light.
	<i>morulus</i>	13	7.2.0.4	11.0.2.0		Y	Y	-	Y	N	Y	Y	Y	N	Y	Rattle fluoresced; distal 1/3–1/2 of tail scalation fluoresced moderately in neonates, but dully in adults. Fluorescence also observed under 395 and 405 nm light.
	<i>polystictus</i>	2	0.0.0.2	2.0.0.0		-	-	-	Y	N	Y	N	n/a	N	Y	Rattle fluoresced; fluorescence also observed under 395 nm light
	<i>ravus</i>	2	0.0.0.2	2.0.0.0		-	-	-	Y	N	Y	Y	N	N	Y	Rattle fluoresced
	<i>smaragdinus</i>	2	2.0.0.0	0.0.2.0		Y	-	-	-	Y	n/a	Y	Y	N	S	Distal 1/3–1/2 of tail scalation fluoresced strongly. Fluorescence also observed in supraocular horns.
<i>Lachesis</i>	<i>muta</i>	2	0.0.0.2	2.0.0.0		-	-	-	N	N	n/a	Y	n/a	S	S	No fluorescence observed.

TABLE 2. Continued.

Genus	Species	N	Specimens examined			Presence of tail fluorescence			Extent of tail fluorescence		Conspicuous tail coloration		Caudal luring		Comments
			Age class (N.J.S.A)	Type/Origin (C.EPC.PF)	N	J	S	A	Tail scalation	Rattle	KTS	ATF	KITS	KTG	
<i>Mixocoatlus</i>	<i>melanurus</i>	3	0.0.0.3	3.0.0.0	-	-	-	N	N	n/a	N	n/a	N	N	Possible fluorescence of supraocular horns.
	<i>cornutus</i>	5	1.0.0.4	4.0.1.0	Y	-	-	Y	Y	n/a	Y	Y	N	Y	Distal 1/3–1/2 of tail scalation fluoresced strongly in neonate. In adults tail fluorescence was less intense and restricted dorsally to the distal tip, and ventrally to the last several distal scales. Fluorescence also observed under 395 nm light.
<i>Protobothrops</i>	<i>mangshanensis</i>	2	0.0.0.2	2.0.0.0	-	-	-	Y	Y	n/a	Y	N	Y	Y	Fluorescence observed in last few scales on distal tail tip in adult male and female.
	<i>muerosquamatus</i>	8	8.0.0.0	5.0.3.0	Y	-	-	-	Y	n/a	N	N	N	Y	Intense fluorescence observed in last 1–3 scales on distal tail tip in both sexes. Entire body fluoresced dullly. Fluorescence also observed under 395nm light.
<i>Sistrurus</i>	<i>tokarensis</i>	3	3.0.0.0	3.0.0.0	Y	-	-	-	Y	n/a	N	N	N	Y	Fluorescence observed in last 1–3 scales on distal tail tip in both sexes. Fluorescence also observed under 395 nm light.
	<i>xiangchengensis</i>	2	0.0.0.2	0.0.2.0	-	-	-	Y	Y	n/a	N	N	N	Y	Fluorescence observed in last 1–3 scales on distal tail tip in both sexes.
<i>Trimeresurus</i>	<i>tergeminus edwardsii</i>	2	0.1.1.0	2.0.0.0	-	Y	Y	-	Y	Y	Y	N	Y	Y	Entire body and rattle fluoresced. Tail scalation fluoresced more intensely than the rest of the body and with a slightly different hue. Fluorescence also observed under 395 and 405 nm light.
	<i>hageni</i>	18	7.7.1.3	16.0.2.0	Y	Y	Y	Y	Y	n/a	Y	Y	N	Y	Distal 1/3–1/2 of tail scalation fluoresced strongly in neonates. In adults tail fluorescence was less intense and restricted dorsally to the distal tip, and ventrally to the last several distal scales. Fluorescence in adults more intense in the male than the female. Fluorescence also observed under 395 and 405 nm light.
<i>mgregori</i>	<i>mgregori</i>	6	0.0.0.6	6.0.0.0	-	-	-	N	N	n/a	N	n/a	N	Y	No fluorescence observed in adults of multiple color phases (yellow, white, brown, black).
	<i>sumatranus</i>	3	0.0.0.3	2.0.1.0	-	-	-	Y	Y	n/a	Y	N	N	Y	Fluorescence was restricted dorsally to the distal tip, and ventrally to the last several distal scales. Fluorescence was more intense in the male than the female. Fluorescence also observed under 395 and 405 nm light.
<i>Tropidolaemus</i>	<i>trigonocephalus</i>	1	0.0.0.1	1.0.0.0	-	-	-	N	N	n/a	N	n/a	N	Y	No fluorescence observed.
	<i>wagleri</i>	1	0.0.0.1	0.0.1.0	-	-	-	Y	Y	n/a	Y	N	S	Y	Fluorescence restricted to extreme distal tail tip.

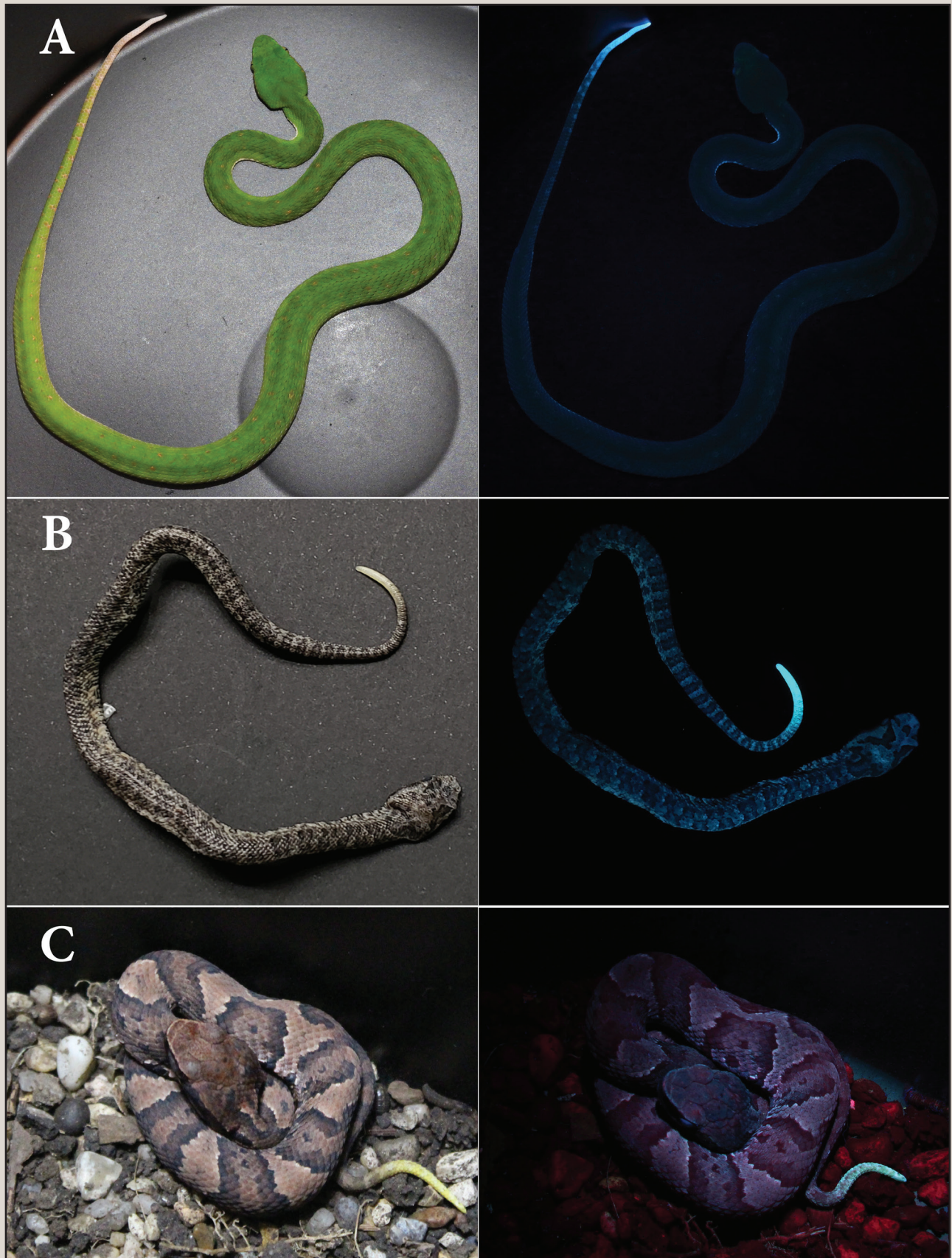


FIG. 1. Tail fluorescence in: A) a live juvenile *Trimeresurus hageni*; B) a preserved neonatal *Protobothrops cornutus*; and C) a live neonatal *Agkistrodon piscivorus*.

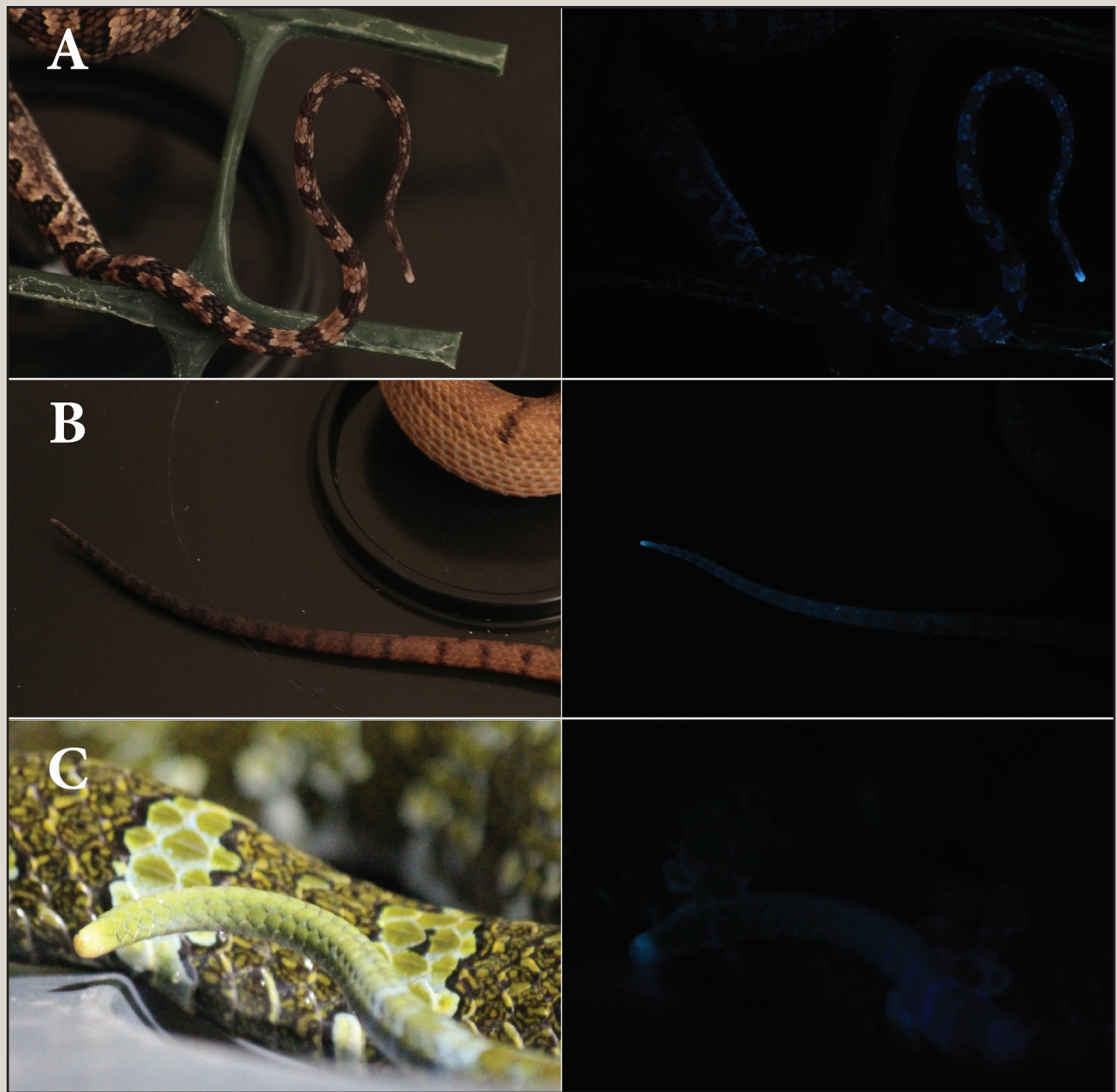


FIG. 2. Fluorescence of the distal tail tips of A) live neonate *Protobothrops mucrosquamatus*, B) live neonate *P. tokarensis*, C) live adult *P. mangshanensis*.

confirmed or suspected caudal luring species ($p = 1.0000$; Table 2).

In addition to tail fluorescence, *P. mucrosquamatus* and *S. tergeminus edwardsii* appeared to exhibit blue fluorescence of the body scalation which was not seen in congeners. Additionally, although closer examination is needed, the horn-like projections over the eyes of *O. smaragdinus* and possibly *Mixcoatlus melanurus* also appeared to fluoresce. Although we did not observe fluorescence in the tails of polymorphic adult *B. schlegelii*, for which several naturally-occurring color phases were examined, a small piece of retained shed skin on the distal tail tip of a yellow adult *B. schlegelii* following ecdysis did fluoresce a bluish color under 365 nm light.

Rattlesnake rattles.—Fluorescence was observed in the entirety of all rattle segments for all rattlesnake species examined (*Crotalus* and *Sistrurus*; Fig. 3) except *C. adamanteus*, for which

only a preserved pre-button neonatal specimen was available. Also, fluorescence was observed in the buttons of captive-born *C. aquilus*, *C. lepidus klauberi*, *C. l. lepidus*, and *C. morulus* which were added following their first shed ca. 7–15 days after birth. Although not examined in this study or included in our analyses, the rattle segments of wild *S. miliarius barbouri* have also been reported to fluoresce (S. Sweet, pers. comm.).

With 62.5% of the rattlesnake species examined in this study known to feature both rattle fluorescence and conspicuously colored tail scalation, there was no apparent association between these characters ($p = 1.000$; Table 2). Additionally, with only two of the rattlesnake species examined in this study known to perform vermiform caudal luring (*C. lepidus* and *S. tergeminus*), there was no apparent relationship between rattle fluorescence and vermiform caudal luring ($p = 1.000$; Table 2).

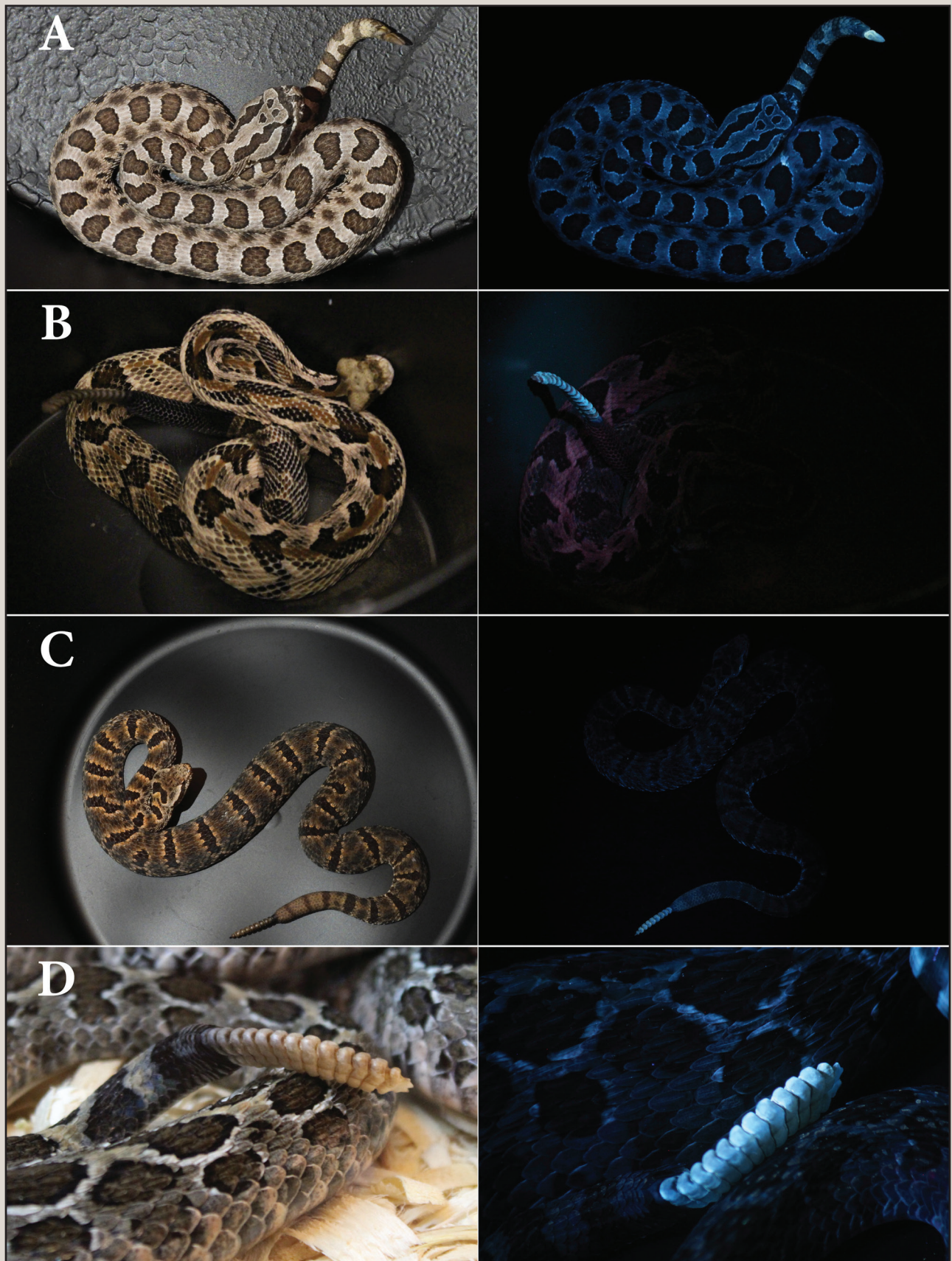


FIG. 3. Ultraviolet-induced fluorescence in the rattles of: A) *Sistrurus tergeminus edwardsii*; B) *Crotalus horridus*; C) *C. morulus*; and D) *C. polystictus*.



FIG. 4. Fluorescence of the extreme distal tail tips in: A) preserved adult *Langaha madagascariensis*; and B) live adult *Acanthophis laevis*.

Additional snake taxa.— In non-crotaline species, we observed UV-induced visible fluorescence in the extreme distal tail tips of *Langaha madagascariensis* (N = 3) and *Acanthophis laevis* (N = 2) (Fig. 4), which was similar in appearance to the tail fluorescence observed in several species of *Protophthops* (Fig. 2) and *T. wagleri*.

DISCUSSION

Our discovery of tail fluorescence across eight genera of pitvipers represents an important further case of widespread biofluorescence in non-avian reptiles (Prötzel et al. 2018; Eipper et al. 2020), and the only known examples in tetrapods where biofluorescence is localized to a specific appendage. Unlike other reptile taxa which display fluorescence as part of their general body coloration (Gruber and Sparks 2015; Seiko and Terai 2019; Eto 2020; Prötzel et al. 2021), skeletal elements (Sloggett 2018; Top et al. 2020) or bony cranial protuberances (Prötzel et al. 2018), the restriction of fluorescence to the tails of various pitvipers suggests a close association with a specialized behavior or function of the appendage. We offer several hypotheses for the ecological relevance and function of this remarkable phenomenon.

Tail fluorescence in pitvipers.—Aggressive (luring) mimicry has evolved in many different organisms as a way to manipulate the behavior of other species, particularly prey (Jackson and Cross 2013). Caudal luring, the use of the tail as a deceptive lure to attract prey, is a specialized hunting technique employed by many snake species across at least seven families (Neill 1960; Heatwole and Davison 1976; Murphy et al. 1978; Radcliffe et al.

1980; Leal and Thomas 1994; Sazima and Puerto 1993; Antunes and Haddad 2009; Sheehy 2016). In caudal luring pitvipers, including rattlesnakes (Schuett et al. 1984; Reiserer and Schuett 2016), the tail is usually conspicuously colored relative to the rest of the body, especially in neonates and juveniles, and undulated in a manner that mimics the writhing movements of a worm or vermiform insect larva (Neill 1960; Greene and Campbell 1972; Martins et al. 2002; Reiserer and Schuett 2008). Since most of the species observed with fluorescent tail scalation in the present study are known to perform caudal luring or belong to genera in which the behavior has been documented or is suspected to occur, we suspect that tail fluorescence facilitates or enhances caudal luring in these species by increasing the conspicuousness and visual attractiveness of the lure to certain prey species under certain light conditions. In many cases tail fluorescence co-occurred with conspicuous tail coloration, a key adaptation associated with caudal luring in pitvipers and other snake taxa (Neill 1960; Green and Campbell 1972; Heatwole and Davison 1976; Martins et al. 2002), further supporting our hypothesis.

Since biofluorescence is dependent upon excitation by external light sources, fluorescent tissues may only be detectable in certain light environments. At present, there is little understanding of how species visualize fluorescence especially in terrestrial environments, but perceptibility is likely to vary based on species-specific visual sensitivities as well as the ambient wavelengths present. Ultraviolet radiation reaches its peak intensity during midday in open environments (e.g., Buntoun et al. 2012), but fluorescence may not be perceptible or as conspicuous under such conditions due to interference from other wavelengths present, particularly visible light.



FIG. 5. UV-fluorescent lepidopteran larvae may serve as a model for the fluorescent vermiform caudal lure in some pitvipers. Examples of biofluorescent North American taxa: A) *Hemaris thysbe*; B) *H. diffinis*; and C) *Manduca sexta*.

Instead, fluorescence may be better visualized in low visible light conditions such as heavily shaded forest environments or between dusk and dawn when the overall proportion of shorter-wavelength light present including UV radiation is much greater (Johnsen et al. 2006). For species with exceptional visual sensitivities in low light environments, detectability of fluorescent tissues under such conditions may require very minimal excitation from UV or other low wavelengths (e.g., Kohler et al. 2019), and likely far less intensity than what was generated by the LED torches used in this study.

In snakes, vermiform caudal luring primarily targets anuran and lizard prey (Neill 1960; Heatwole and Davison 1976), which both factor prominently into the natural diets of many pitviper species (Orlov et al. 2002a,b; Campbell and Lamar 2004; Martins et al. 2012). Studies on the foraging abilities of anurans (Larsen and Pedersen 1982; Aho et al. 1993; Buchanan 1998) and visual acuities of lizards (Roth and Kelber 2004; Fleishman et al. 2011) under different light conditions have shown that at least some species from these groups have exceptional visual sensitivities in low light environments that are many times greater than that of the human eye. Moreover, the discovery of biofluorescence in various anuran and lizard taxa which is suspected to aid intraspecific signaling or identification (Taboada et al. 2017a,b; Prötzel et al. 2018, 2021; Sloggett 2018; Goutte et al. 2019; Top et al. 2020; Whitcher 2020) suggests that at least some species within these groups are capable of visualizing fluorescent tissues and that biofluorescence already plays an active role in their visual and behavioral ecologies. Many terrestrial invertebrate groups preyed upon by lizards and anurans also include biofluorescent species including, but not limited to larval lepidopterans (Messenger et al. 2019; Moskowitz 2018; Sourakov 2017, 2019), which could serve as a mimicry model for vermiform caudal luring in some tail-fluorescent pitvipers (Fig. 5).

It appears that at least some of the fluorescent pitvipers documented in this study experience reductions in tail scalation fluorescence over time. We have observed this transition in *T. hageni* and several species of rattlesnake (*C. aquilus*, *C. lepidus*, *C. morulus*) in captivity and suspect that other fluorescent pitvipers follow a similar trend. Here, the reduction in fluorescence appears to parallel the loss of conspicuous tail color in various pitviper species which has been linked to ontogenetic shifts in diet (Neill 1960; Heatwole and Davison 1976). Although our limited sample sizes preclude statistical analysis, we also observed differences in fluorescent emission patterns between adult male and female *T. hageni* and *T. sumatranus*, with males displaying a greater degree of tail fluorescence than females. If tail fluorescence in these species is linked to caudal luring, such differences in emission patterns could be reflective of intraspecific differences in dietary preferences or foraging habits. While dietary studies for *T. hageni* and *T. sumatranus* appear to be lacking, several other pitviper taxa have been shown to exhibit intraspecific sexual variation in

diet (Daltry et al. 1998; Vincent et al. 2004; Lin and Tu 2008). A greater sampling of adult males and females in these species will be needed to confirm whether these differences are inherently dimorphic.

Several species of rattlesnake (*Crotalus*, *Sistrurus*) are also known to use vermiform caudal luring to attract ectothermic prey such as lizards and frogs (Kauffeld 1943; Jackson and Martin 1980; Schuett et al. 1984; Starrett and Holycross 2000; Reiserer and Schuett 2008, 2016). However, with the possible exceptions of *S. miliarius* (Jackson and Martin 1980) and *C. cerastes* (Reiserer and Schuett 2008; Clark et al. 2016), this behavior appears to be mostly limited to neonates and juveniles with very limited or no rattle segmentation, and is rarely observed in larger specimens with fully-developed rattles. Unlike the prehensile tail in other caudal-luring pitvipers, rattle segments are autonomous from the tail musculature and therefore may have reduced capacity for undulation in the same vermiform manner. Moreover, since the natural diets of many rattlesnake species tend to shift away from ectothermic to endothermic prey with ontogeny (Campbell and Lamar 2004; Ernst and Ernst 2012; Schuett et al. 2016a), there may be less of a need for a vermiform lure in larger individuals and species. Thus, even though the structure itself does bear physical resemblance to segmented invertebrates (see Reiserer and Schuett 2016), some of which may even biofluoresce, vermiform caudal luring might not account for fluorescence of the rattle. Instead, fluorescence of the structure, as first noted by Klauber (1956), might serve a slightly different deceptive function.

Rattlesnakes are often associated with ecosystems that support grass communities (Campbell and Lamar 2004; Ernst and Ernst 2012; Schuett et al. 2016a), and grasslands may have played a key role in the origin and diversification of rattlesnakes (see Reiserer and Schuett 2016). In addition to providing refuge and other resources that may be utilized by rattlesnakes, grasses are also important for sustaining small mammal communities, particularly granivorous rodents that are heavily dependent on harvesting and caching their seeds throughout the year (e.g., Monson 1943; Chapman 1972; Brown and Heske 1990; Hesk et al. 1993, 1994; Longland 1994). Through our observations of tail fluorescence in captive rattlesnakes, we noticed that the stems and spikelets of grasses planted in their terrariums (*Chasmanthium latifolium*, *Bromus catharticus* [Poaceae; Pooideae]) also fluoresced at a similar color and intensity as the snakes' rattles under the same 365 and 395 nm UV torches (Fig. 6), which corroborates Baby et al.'s (2013) discovery of widespread UV-induced fluorescence in the reproductive structures of several subfamilies of grasses with a peak excitation wavelength of 366 nm. We also could not help but notice the resemblance of the rattle in terms of its general morphology and appearance to the paired spikelets of various pooid grass genera (e.g., *Chasmanthium*, *Eragrostis*, *Glyceria*, *Uniola*, *Hordeum*,

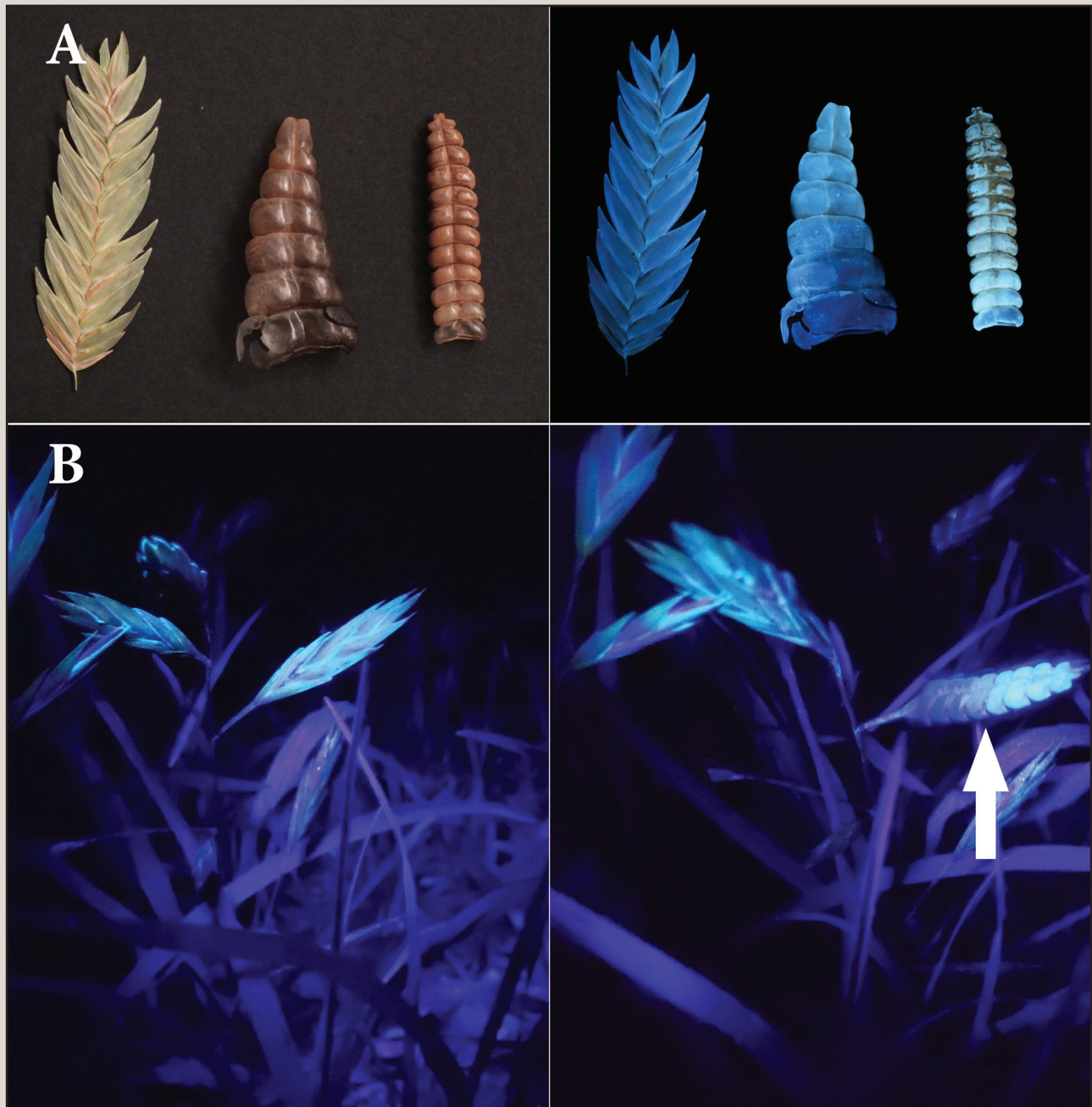


FIG. 6. A) Comparison of fluorescent *Chasmanthium latifolium* spikelet (left) to the rattles of *C. atrox* (center) and *C. lepidus klauberi* (right) under room lighting and UV light; B) fluorescent *Bromus catharticus* spikelets under UV light, with a *C. lepidus klauberi* rattle (arrow) mounted on a stem to demonstrate similarities in fluorescence and general appearance under UV light. Although neither grass species depicted here is indigenous to the New World, they illustrate a general spikelet morphology that is conserved across many pooid genera naturally distributed throughout the world including the Americas; biofluorescence is also widely distributed in grasses (Baby et al. 2013).

Bromus, *Distichlis*), especially under UV light (Fig. 6); such morphological similarities have apparently long been recognized by botanists and reflected in the vernacular names assigned to several pooid species distributed throughout the world (e.g., Rattlesnake Grass [*Briza maxima*], Rattlesnake Mannagrass [*Glyceria canadensis*], Rattlesnake Brome [*Bromus briziformis*]). Given these considerations and since granivorous rodents comprise an important dietary component of many rattlesnakes (Campbell and Lamar 2004; Reiserer et al. 2018; Ernst and Ernst 2012; Schuett et al. 2016a), we consider the possibility that the

fluorescent rattle may function as a deceptive lure that mimics the biofluorescent spikelets of grasses and possibly the seeds of other biofluorescent plants to attract seed-harvesting rodents.

Biofluorescence is well known in plants (Buschmann et al. 2000), but its apparent usage by grasses as a visual signal for insect pollinators and possibly seed predators represents a newly recognized phenomenon (Baby et al. 2013). Although it has not yet been tested experimentally, with retinal receptors that are highly sensitive in low-light environments (Jacobs et al. 1991, 2001), rodents are suspected of visualizing and exploiting

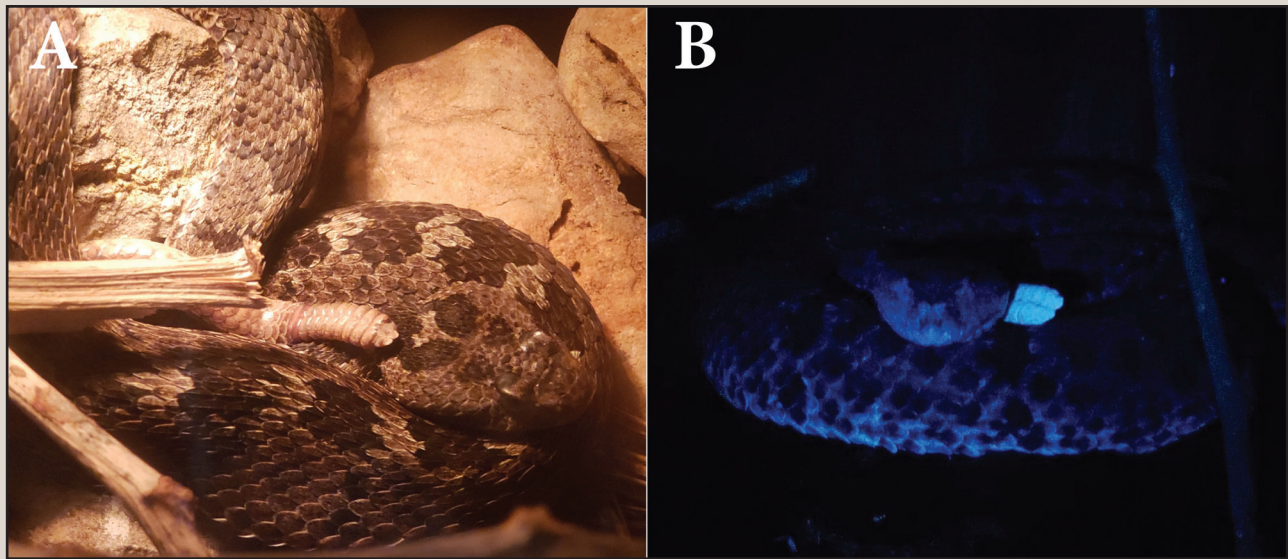


FIG. 7. Rattlesnakes resting with their rattles positioned close to the head; A) *Crotalus aquilus* under ambient room lighting; B) *C. lepidus klauberi* under UV light.

biofluorescent grasses to locate their seeds and flowers (Baby et al. 2013). If this is true, rattlesnakes, in turn, could be exploiting a foraging tactic of rodents by mimicking a biofluorescent dietary staple. Such deceptive luring could complement the predatory repertoires of at least some rattlesnake species that are known to take up ambush positions along small mammal runways or near rodent dens (e.g., Tevis 1943; Fitch and Twining 1946; Hennessy and Owings 1988; Duvall et al. 1990; Reinert et al. 1984, 2011; Dugan and Hayes 2012), and might also explain why rattlesnakes are sometimes observed at rest or in ambush with their rattles exposed and positioned close to the head (Fig. 7; Rabatsky and Farrell 1996; Theodoratus and Chiszar 2000).

We consider deceptive prey luring to be the most likely explanations for tail fluorescence in pitvipers, but we recognize that fluorescence could serve other functions in these species that may not necessarily be mutually exclusive. For instance, since various antipredator displays are known to snakes including those that involve specialized tail movements and posturing (e.g., Greene 1973; Kochva and Golani 1993; Rabatsky and Waterman 2005; Melvinsevan and Nibedita 2016), fluorescence could increase the conspicuousness of the tail as a visual display to distract or deter attackers. Rattlesnakes are best known for their use of the rattle in producing an audible warning signal, but it is unclear whether the shaking rattle itself, which is typically raised above the body and made visible to the attacker, might also serve as a visual aposematic display. Here, in a similar light to Vogel's (1964) presumption that the contrasting black and white tail banding of *C. atrox* enhances the visibility of the species' rattling threat display, fluorescence could enhance the conspicuousness of the vibrating rattle as a visual aposematic display in low-light environments (Fig. 8), possibly to crepuscular or nocturnal mammalian predators such as canids, felids, mustelids, or procyonids.

Many other pitvipers including members of *Agkistrodon*, *Bothrops*, *Lachesis*, *Protobothrops*, and *Trimeresurus* also exhibit defensive tail shaking or vibrating behavior when threatened or distressed (Greene and Campbell 1972; Greene 1973; Campbell and Lamar 2004; Mendyk and Paul, unpubl.). However, unlike rattlesnakes, the tail in most of these species is not elevated above the body to increase its conspicuousness or visibility to

the attacker. Instead, the tail is usually kept low and pressed against the substrate (Sisk and Jackson 1997) and used to rustle leaf litter or vegetation, where it probably would not benefit from increased visibility via fluorescence. Additionally, since some species do not appear to retain tail fluorescence into adulthood yet still perform defensive tail shaking or vibrating as adults, a defensive role may not account for this character in some taxa.

For some reptiles including chameleons (Prötzel et al. 2018), geckos (Sloggett 2018; Top et al. 2020; Prötzel et al. 2021) and anoles (Mendyk, in review), biofluorescence may play a role in intraspecific communication by highlighting or accentuating certain body markings, skeletal elements or bony protuberances. While snakes rely heavily on chemical cues for intraspecific communication (Madison 1977; Ford 1986; Mason 1992; Mason and Parker 2010), there is increasing evidence that visual displays play an important role in their sociality as well (Carpenter 1977; Putman and Clark 2015; Schuett et al. 2016b). Such communicative displays can include tail signaling, which has been recorded in adults of at least two New World pitvipers shown to exhibit tail fluorescence in the present study—*A. contortrix* (Schuett 1997) and *C. atrox* (Schuett et al. 2016b)—as well as in *C. oreganus* (Putman and Clark 2015). In species with communicative tail signaling, fluorescence could enhance the visibility of the signal to conspecifics. Yet again, while this could potentially account for tail fluorescence in rattlesnakes and other pitviper species that display the character as adults, we are less inclined to consider this as a possible explanation for species that do not appear to fluoresce as adults or experience marked reductions in fluorescence over time.

Phylogenetic and evolutionary implications.—Is tail fluorescence plesiomorphic to Crotalinae, or did it arise independently in multiple genera like other shared characters of the group (e.g., Sanders et al. 2004)? Although our preliminary sampling of pitviper taxa is incomplete, our data clearly show tail fluorescence to be phylogenetically widespread within Crotalinae (Fig. 9). If tail fluorescence tends to co-occur with conspicuous tail coloration and caudal luring in pitvipers as has largely been the case in this study, all pitviper genera could potentially harbor species with this trait (Fig. 9). Clearly, a more

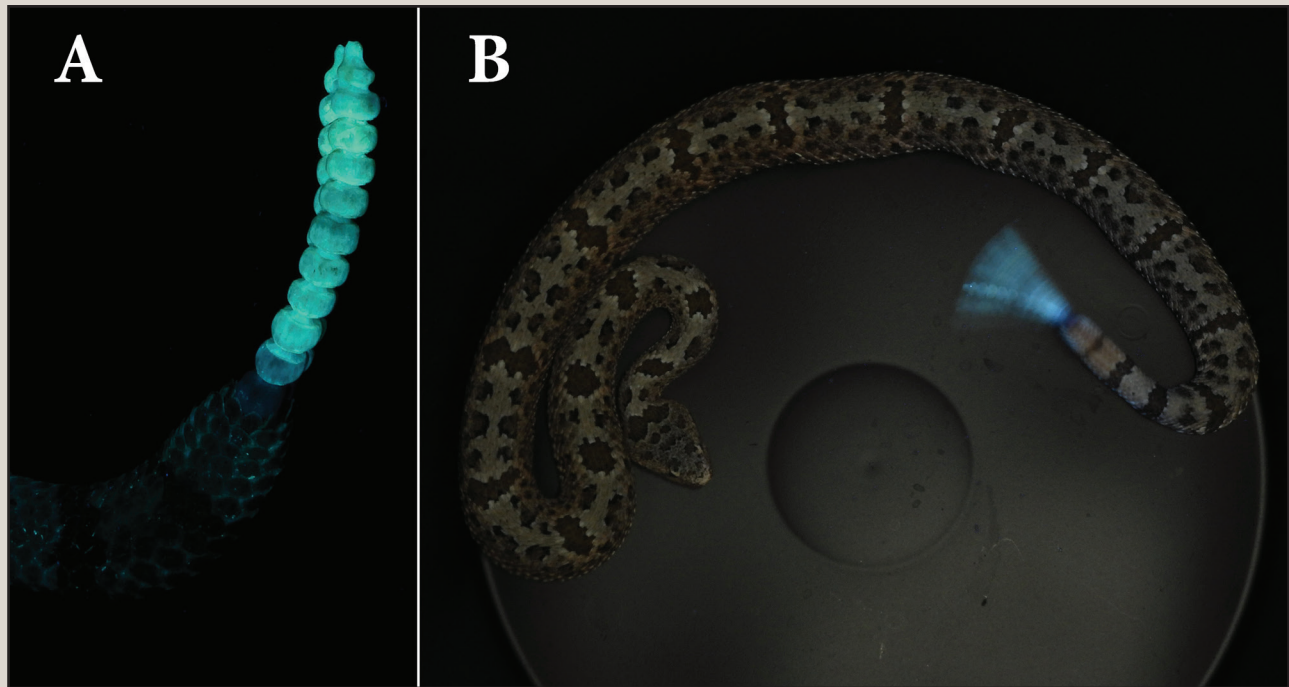


FIG. 8. Fluorescence of the rattle (A) and defensive rattling display of *Crotalus lepidus klauberi* (B).

robust sampling of taxa, sexes and age classes is needed to determine the full extent of tail fluorescence within individual species as well as across Crotalinae.

Our observations of fluorescence in the extreme distal tail tips of *Langaha madagascariensis* (Lamprophiidae) and *Acanthophis laevis* (Elapidae) confirm that this character has also arisen outside Crotalinae. Since there appears to be an association between tail fluorescence and both caudal luring and conspicuous tail coloration in pitvipers, it will be useful to determine if tail fluorescence occurs in additional taxonomic groups that also possess these characters, such as true vipers (Henderson 1970; Heatwole and Davison 1976; Parellada and Santos 2002; Reiserer 2002), boids (Radcliffe et al. 1980), colubrids (Leal and Thomas 1994; Tiebout 1997; but see Reiserer and Schuett [2016] for a refutation of the latter), dipsadids (Sazima and Puerto 1993; Stender-Oliveira et al. 2016), elapids (Neill 1960; Carpenter et al. 1978; Khan and Tasnim 1986a; Chiszar et al. 1990; Hagman et al. 2008), pseudoxyrhopiids (Sheehy 2016), pythonids (Murphy et al. 1978; Whittaker and Shine 1999; McFadden 2005) and tropidophiids (Antunes and Haddad 2009).

The origin of the crotaline rattle and the circumstances of its evolutionary development have been long-debated topics in herpetology with many hypotheses proposed over the last century (reviewed by Reiserer and Schuett 2016). Tail fluorescence adds vital new information to this discussion, lending further support to Schuett et al.'s (1984) hypothesis of a caudal luring origin for the rattle. Since rattlesnakes represent a more recently derived lineage within Crotalinae (Wüster et al. 2008; Alencar et al. 2016), tail fluorescence, which appears to be plesiomorphic to the monophyletic clade encompassing *Crotalus*, *Sistrurus*, and *Agkistrodon*, would have originated prior to the rattle (Fig. 9). If tail fluorescence is closely associated with caudal luring, this would suggest that the long-perceived primary role of the rattle as an audible aposematic alarm may have evolved secondarily to its role as a biofluorescent lure (see Reiserer and Schuett 2016). Such a scenario would account for

incipient stages in the evolutionary development of the rattle from a “normal” biofluorescent tail tip used for vermiform caudal luring, such as that seen in the sister group *Agkistrodon*, to a possible fluorescent proto-rattle also aimed at vermiform caudal luring, to the fluorescent present day rattle, which does not appear to be used in such a capacity but may serve a slightly different deceptive role.

Implications for future studies.—Tail fluorescence in pitvipers raises many new questions about the biology of this group and opens up various avenues for future research. Since it is apparent that tail fluorescence occurs over a range of wavelengths and because we were unable to collect spectral data, studies that determine the optimal excitation and emission wavelengths of tail fluorescence across these taxa (e.g., Prötzel et al. 2018, 2021) will be crucial for pairing this phenomenon with specific light environments where fluorescence would be best visualized as well as the species that may be best suited for visualizing it. Information gained through spectral analyses will also be important for developing behavioral studies aimed at testing the hypotheses presented in this study.

Much remains to be learned about the visual systems of reptiles and amphibians, and little is presently known about how visual sensitivities to certain wavelengths may influence aspects of their behavioral ecology or how different light environments may have helped shape the evolution of key physical features such as conspicuous tail coloration and biofluorescence, or behavioral innovations such as caudal luring. While some studies have looked into the effects of light intensity on foraging behavior in snakes including caudal luring specifically (Neill 1960; Rabatsky and Farrell 1996; Chiszar et al. 1990), none appear to have focused on specific wavelengths, nor has biofluorescence been considered a potential influencing factor. Neill (1960) may have unknowingly hinted a potential connection between UV-induced biofluorescence and caudal luring in juvenile *A. contortrix*, reporting that luring behavior under artificial room lighting did not occur until the animals were exposed to low

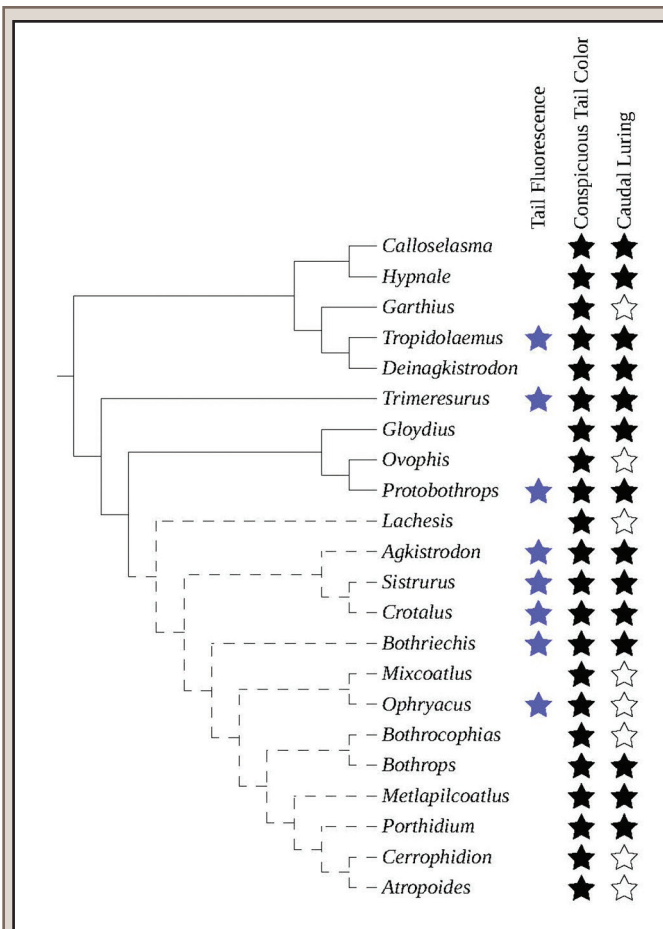


FIG. 9. Preliminary generic-level distribution of tail fluorescence in Crotalinae from the current study based on phylogenetic relationships inferred from molecular data (Alencar et al. 2016) and recent taxonomic revisions by Campbell et al. (2019). Tail coloration and caudal luring data were derived from multiple published sources (Ditmars 1907; Steiner 1907; Henry 1925; Smith 1943; Neill 1948; Allen 1949; Burger and Smith 1950; Wharton 1960; Antonio 1980; Murphy and Mitchell 1984; Schuett 1984; Tryon 1985; Khan and Tasnim 1986b; Sazima 1991; Strimple 1995; Andrade et al. 1996, 2010; Daltry et al. 1998; Whitaker and Captain 2004; Farrell et al. 2011; Freitas and Silva 2011; Martins et al. 2012 [and references therein]; McCleary et al. 2015; Owens 2016; Barnes and Knierim 2019; da Fonseca et al. 2019; de Plecker and Dwyer 2020; Zhang et al. 2020) and unpublished data of the authors. Solid line and dashed branches distinguish Old and New World taxa, respectively. Blue stars denote confirmed tail fluorescence from this study; solid black stars represent a confirmed character in the genus; outlined stars denote the suspected presence of a character in the genus.

levels of natural light filtered through a window. This raises additional questions relating to whether the snakes themselves are cognizant of, or capable of visualizing their own fluorescence under certain light conditions and whether this may influence performance of caudal luring behavior.

Histologically, there appear to be many interesting aspects of tail fluorescence in pitvipers that warrant further study. For instance, despite having a uniform appearance under visible light, there are clearly structural differences between scales on the tail that fluoresce and more proximal neighboring scales that do not. Additionally, it is unclear how these fluorescent tissues might change structurally over time, what mechanisms may be responsible for reductions in fluorescence, and whether this

coincides with the ontogenetic loss of conspicuous tail coloration observed in various pitviper species (e.g., Neill 1960; Heatwole and Davison 1976). It will also be important to compare the structural and biochemical basis for fluorescence in the crotaline rattle to that of fluorescent tail scalation in pitvipers to shed light on the relationship between these tissues and the evolution of tail fluorescence in the group.

Most studies on fluorescence in reptiles to date have relied on 365 or 395 nm UV torches for exciting, visualizing and photographing biofluorescent tissues (Prötzel et al. 2018, 2021; Sloggett 2018; Seiko and Terai 2019; Eipper et al. 2020; Eto 2020; Top et al. 2020). One drawback to these torches is that they inevitably emit some residual visible light that could interfere with or obscure detection of more subtle biofluorescent tissues, especially when examined on semi-reflective or lighter-colored backgrounds, in faded fluid-preserved specimens (e.g., Eipper et al. 2020), or when attempting to examine active, uncooperative specimens. Therefore, our results should be considered preliminary, and the confirmation of, but not necessarily the absence of, tail fluorescence from the species examined. Additionally, due to the potential effects of this residual light, the color of fluorescence observed with these torches may not necessarily reflect the true colors visualized by species in nature. Studies are clearly needed to determine if and how fluorescence may be visualized by reptiles and amphibians under natural conditions; here, the important work by Gruber et al. (2016) on biofluorescence in marine elasmobranchs could serve as a useful model for developing similar approaches for herpetofauna.

Finally, our findings, together with other recent discoveries of biofluorescence in reptiles (Gruber and Sparks 2015; Prötzel et al. 2018, 2021; Sloggett 2018; Seiko and Terai 2019; Eipper et al. 2020; Eto 2020) and other tetrapods (e.g., Nowogrodzki 2017; Taboada et al. 2017a,b; Camacho et al. 2019; Jeng 2019; Kohler et al. 2019; Wilkinson et al. 2019; Anich et al. 2020) call attention to the limitations of our own sensory modalities when studying and interpreting the ecology, behavior and functional morphology of other species (e.g., Martin 2012). The fact that tail fluorescence has gone largely undetected for so long in pitvipers including rattlesnakes, a group that has been intensively kept and studied in captivity over two centuries (Bennett 1829; Harlan 1830; Mitchell 1860; Murphy 2017), raises an important question: what other key biological attributes of species may we be missing due to our visual biases? For instance, UV-reflectance, which like biofluorescence also falls outside of the human-visible spectrum and utilizes wavelengths in the UV range, was only recently shown to play an important role in the behavioral ecology of reptiles, namely lizards (e.g., Font et al. 2009; Bajer et al. 2011; Abramjan et al. 2020). Furthermore, given that both high UV-reflectance and biofluorescence have been described in various vertebrates and invertebrates and closely interact with one another (e.g., Lim et al. 2007; Barreira et al. 2012; Finkbeiner et al. 2017), and considering the widespread fluorescence described in this study, it is likely that some snake species possess both of these traditionally-overlooked colorations. In the case of pitvipers, it appears that interpreting caudal luring behavior and the function of the crotaline rattle solely through the lens of our human vision may have contributed to an incomplete understanding of these specialized adaptations. Placing greater emphasis on the roles that different wavelengths play in the ecology and behavior of species will be especially important as further examples of biofluorescence inevitably continue to be discovered and described.

Acknowledgments.—We thank Samuel Sweet for collecting and sharing useful field data and observations with us, and Clinton Szymanski for valuable insight on the subject of caudal luring. Bob Thomas loaned specimens, Craig Gagne provided access to additional specimens, and Michelle Hatwood, Richard Dunn, Adrienne Atkins, Christopher St. Romain, and Karen Ross assisted with securing field specimens. Melanie Litton, Will Fullerton, and Adam Weisse provided husbandry support. Wolfgang Wüster, Bree Putman, and the Smithsonian Institution Libraries provided useful literature and David Moskowitz generously contributed photographs. Lastly, we thank the Audubon Nature Institute and Smithsonian National Zoological Park for institutional support (RWM), and Gordon Schuett, Joe Mendelson, and Jady Sethna for helpful comments on this manuscript.

LITERATURE CITED

- ABRAMJAN, A., V. BARANOVÁ, P. FRÝDLOVÁ, E. LANDOVÁ, AND D. FRYNTA. 2020. Ultraviolet reflectance and pattern properties in leopard geckos (*Eublepharis macularius*). *Behav. Processes* 173:104060.
- AHO, A.-C., K. DONNER, S. HELENUS, L.O. LARSEN, AND T. REUTER. 1993. Visual performance of the toad (*Bufo bufo*) at low light levels: retinal ganglion cell responses and prey-catching accuracy. *J. Comp. Physiol. A* 172:671–682.
- ALENCAR, L. R. V., T. B. QUENTAL, F. G. GRAZZIOTIN, M. L. ALFARO, M. MARTINS, M. VENZON, AND H. ZAHER. 2016. Diversification in vipers: Phylogenetic relationships, time of divergence and shifts in speciation rates. *Mol. Phylog. Evol.* 105:50–62.
- ALLEN, E. R. 1949. Observations of the feeding habits of the juvenile cantil. *Copeia* 1949:225–226.
- ANDRADE, D. V., S. A. S. ABE, AND M. C. DOS SANTOS. 1996. Is the venom related to diet and tail color during *Bothrops moojeni* ontogeny? *J. Herpetol.* 30:285–288.
- ANDRADE, D. V., O. A. V. MARQUES, R. S. B. GAVIRA, F. E. BARBO, R. L. ZACARIOTTI, AND I. SAZIMA. 2010. Tail luring by the golden lancehead (*Bothrops insularis*), an island endemic snake from south-eastern Brazil. *S. Amer. J. Herpetol.* 5:175–180.
- ANICH, P. S., S. ANTHONY, M. CARLSON, A. GUNNELSON, A. M. KOHLER, J. G. MARTIN, AND E. R. OLSON. 2020. Biofluorescence in the platypus (*Ornithorhynchus anatinus*). *Mammalia* 85:179–181.
- ANTONIO, F. B. 1980. Mating behavior and reproduction of the eyelash viper (*Bothrops schlegelii*) in captivity. *Herpetologica* 36:231–233.
- ANTUNES, A. P., AND C. F. B. HADDAD. 2009. *Tropidophis paucisquamis* (Brazilian dwarf boa): diet and caudal luring. *Herpetol. Rev.* 40:104.
- BABY, S. A., J. JOHNSON, B. GOVINDAN, S. LUKOSE, B. GOPAKUMAR, AND K. C. KOSHY. 2013. UV induced visual cues in grasses. *Sci. Rep.* 3:2738.
- BAJER, K., O. MOLNÁR, J. TÖRÖK, AND G. HERCZEG. 2011. Ultraviolet nuptial colour determines fight success in male European green lizards (*Lacerta viridis*). *Biol. Lett.* 7:866–868.
- BARNES, C. H., AND T. K. KNIERIM. 2019. Brief insight into the behavior, activity, and interspecific interactions of urban *Trimeresurus (Cryptelytrops) albolabris* (Reptilia: Squamata: Viperidae) vipers in Bangkok, Thailand. *J. Threat. Taxa* 11:14503–14510.
- BARREIRA, A. S., M. G. LAGORIO, D. A. LIJTMAR, S. C. LOUGHEED, AND P. L. TUBARO. 2012. Fluorescent and ultraviolet sexual dichromatism in the bluewinged parrotlet. *J. Zool.* 288:135–142.
- BENNETT, E. T. 1829. The Tower Menagerie: Comprising the Natural History of the Animals Contained in that Establishment, with Anecdotes of their Characters and History. R. Jennings, London.
- BROWN, J. H., AND E. J. HESKE. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250:1705–1707.
- BUCHANAN, B. W. 1998. Low-illumination prey detection by squirrel treefrogs. *J. Herpetol.* 32:270–274.
- BUNTOUNG, S., P. CHOOSRI, A. DECHLEY, I. MASIRI, R. WATTAN, AND S. JANJAI. 2012. An investigation of total solar ultraviolet radiation at Nakhon Patho, Thailand. *Procedia Engin.* 32:427–432.
- BURGER, W. L., AND P. W. SMITH. 1950. The coloration of the tail tip of young fer-de-lance: Sexual dimorphism rather than adaptive coloration. *Science* 112:431–433.
- BUSCHMANN, C., G. LANGSDORF, AND H. K. LICHTENTHALER. 2000. Imaging of the blue, green, and red fluorescent emission of plants: An overview. *Photosynthetica* 38:483–491.
- CAMACHO, C., J. J. NEGRO, I. REDONDO, S. PALACIOS, AND P. SÁEZ-GÓMEZ. 2019. Correlates of individual variation in the porphyrin-based fluorescence of red-necked nightjars (*Caprimulgus ruficollis*). *Sci. Rep.* 9:19115.
- CAMPBELL, J. A., D. R. FROST, AND T. A. CASTOE. 2019. New generic name for jumping pitvipers (Serpentes: Viperidae). *Rev. Latinoamer. Herpetol.* 2:52–53.
- , AND W. W. LAMAR. 2004. The Venomous Reptiles of the Western Hemisphere. Comstock Publishing Associates, Ithaca, New York. 870 + 28 pp.
- CARPENTER, C. C. 1977. Communication and displays of snakes. *Amer. Zool.* 17:217–223.
- , J. B. MURPHY, AND G. C. CARPENTER. 1978. Tail luring in the death adder, *Acanthophis antarcticus* (Reptilia, Serpentes, Elapidae). *J. Herpetol.* 12:574–577.
- CHAPMAN, B. R. 1972. Food habits of Loring's kangaroo rat, *Dipodomys elator*. *J. Mammal.* 53:877–880.
- CHISZAR, D., D. BOYER, R. LEE, J. B. MURPHY, AND C. W. RADCLIFFE. 1990. Caudal luring in the southern death adder, *Acanthophis antarcticus*. *J. Herpetol.* 24:253–260.
- CLARK, R. W., S. W. DORR, M. D. WHITFORD, G. A. FREYMLER, AND B. J. PUTMAN. 2016. Activity cycles and foraging behaviors of free-ranging sidewinder rattlesnakes (*Crotalus cerastes*): The ontogeny of hunting in a precocial vertebrate. *Zoology* 119:19–206.
- DA FONSECA, W. L., A. DE SOUZA OLIVEIRA, R. R. CORREA, AND P. S. BERNARDE. 2019. Caudal luring in the neotropical two-striped forest pitviper *Bothrops bilineatus smaragdinus* Hoge, 1966 in the western Amazon. *Herpetol. Notes* 12:365–374.
- DALTRY, J. C., W. WÜSTER, AND R. S. THORPE. 1998. Intraspecific variation in the feeding ecology of the crotaline snake *Calloselasma rhodostoma* in Southeast Asia. *J. Herpetol.* 32:198–205.
- DE PLECKER, R., AND Q. DWYER. 2020. First breeding of the black-headed bushmaster (*Lachesis melanocephala*) in Costa Rica. *Herpetol. Rev.* 51:57–64.
- DESCHÉPPER, P., B. JONCKHEERE, AND J. MATTHYS. 2018. A light in the dark: The discovery of another fluorescent frog in the Costa Rican rainforests. *Wild. Environ. Med.* 29:421–422.
- DITMARS, R. L. 1907. The Reptile Book. Doubleday, Page and Co., Garden City, New York. 465 pp.
- DUGAN, E. A., AND W. K. HAYES. 2012. Diet and feeding ecology of the red diamond rattlesnake, *Crotalus ruber* (Serpentes: Viperidae). *Herpetologica* 68:203–217.
- DUVALL, D., M. J. GOODE, W. K. HAYES, J. K. LEONHARDT, AND D. G. BROWN. 1990. Prairie rattlesnake vernal migration: Field experimental analyses and survival value. *Nat. Geogr. Res.* 6:457–469.
- EIPPER, S. C., A. ELLIOTT, AND T. EIPPER. 2020. Notes on the discovery of fluorescence in Australian scolecophidians in the genus *Anilius* Gray 1845 (Serpentes: Typhlopidae). *The Captive Field Herpetol. J.* 4:27–30.
- ERNST, C. H., AND E. M. ERNST. 2012. Venomous Reptiles of the United States, Canada, and Northern Mexico. Volume 2. *Crotalus*. John Hopkins University Press, Baltimore, Maryland. 391 pp.
- ETO, K. 2020. *Limaformosa crossi* (Crosse's file snake) and *Mehelya poensis* (western forest file snake): coloration/biofluorescence. *Herpetol. Rev.* 51:622–623.
- FARRELL, T. M., P. G. MAY, AND P. T. ANDREADIS. 2011. Experimental manipulation of tail color does not affect foraging success in a caudal luring rattlesnake. *J. Herpetol.* 45:291–293.
- FATHINIA, B., N. RASTEGAR-POUYANI, E. RASTEGAR-POUYANI, F. TODEHDEGHAN, AND F. AMIRI. 2015. Avian deception using an elaborate caudal lure in *Pseudocerastes urarachnoides* (Serpentes: Viperidae). *Amphibia-Reptilia* 36:223–231.
- FITCH, H. S., AND H. TWINING. 1946. Feeding habits of the Pacific rattlesnake. *Copeia* 1946:64–71.

- FINKBEINER, S. D., D. A. FISHMAN, D. OSORIO, AND A. D. BRISCOE. 2017. Ultraviolet and yellow reflectance but not fluorescence is important for visual discrimination of conspecifics by *Heliconius erato*. J. Exp. Biol. 220:1267–1276.
- FLEISHMAN, L. J., E. R. LOEW, AND M. J. WHITING. 2011. High sensitivity to short wavelengths in a lizard and implications for understanding the evolution of visual systems in lizards. Proc. R. Soc. B. 278:2891–2899.
- FONT, E., G. P. I. DE LANUZA, AND C. SAMPEDRO. 2009. Ultraviolet reflectance and cryptic sexual dichromatism in the ocellated lizard, *Lacerta (Timon) lepida* (Squamata: Lacertidae). Biol. J. Linn. Soc. 97:766–780.
- FORD, N. B. 1986. The role of pheromone trails in the sociobiology of snakes. In D. Duvall, D. Müller-Schwarze, and R. M. Silverstein (eds.), Chemical Signals in Vertebrates 4, pp. 261–278. Springer, Boston, Massachusetts.
- FREITAS, M. A., AND T. F. S. SILVA. 2011. *Bothrops leucurus* (Bahia lance-head). Caudal luring. Herpetol. Rev. 42:436.
- GOUTTE, S., M. J. MASON, M. A. ANTONIAZZI, C. JARED, D. MERLE, L. CAZES, L. F. TOLEDO, H. EL-HAFICI, S. PALLU, H. PORTIER, S. SCHRAMM, P. GUERIAU, AND M. THOURY. 2019. Intense bone fluorescence reveals hidden patterns in pumpkin toadlets. Sci. Rep. 9:5388.
- GRAY, R. J. 2019. Biofluorescent lateral patterning on the mossy bush-frog (*Philautus macrocelis*): The first report of biofluorescence in a rhacophorid frog. Herpetol. Notes 12:363–364.
- GREENE, H. W. 1973. Defensive tail display by snakes and amphisbaenians. J. Herpetol. 7:143–161.
- , AND J. A. CAMPBELL. 1972. Notes on the use of caudal lures by arboreal green pit vipers. Herpetologica 28:32–34.
- GRUBER, D. E., E. R. LOEW, D. D. DEHEYN, D. AKKAYANAK, J. P. GAFFNEY, W. L. SMITH, M. P. DAVIS, J. H. STERN, V. A. PIERBONE, AND J. S. SPARKS. 2016. Biofluorescence in catsharks (Scyliorhinidae): Fundamental description and relevance for elasmobranch visual ecology. Sci. Rep. 6:24751.
- , AND J. S. SPARKS. 2015. First observation of fluorescence in marine turtles. Amer. Mus. Nov. 3845:1–7.
- HAGMAN, M., B. L. PHILLIPS, AND R. SHINE. 2008. Tails of enticement: Caudal luring by an ambush-foraging snake (*Acanthophis praelongus*, Elapidae). Funct. Ecol. 22:1134–1139.
- HARLAN, R. 1830. Experiments made on the poison of the rattlesnake: In which the powers of the *Hieraceum venosum*, as a specific, were tested; together with some anatomical observations on this animal. Trans. Amer. Phil. Soc. 3:300–314.
- HEATWOLE, H., AND E. DAVISON. 1976. A review of caudal luring in snakes with notes on its occurrence in the Saharan sand viper *Cerastes vipera*. Herpetologica 32:332–336.
- HENDERSON, R. W. 1970. Caudal luring in a juvenile Russel's viper. Herpetologica 26:276–277.
- HENNESSY, D. E., AND D. H. OWINGS. 1988. Rattlesnakes create a context for localizing their search for potential prey. Ethology 77:317–329.
- HENRY, G. M. 1925. Notes on *Ancistrodon hypnale*, the hump-nosed viper. Ceylon J. Sci. B 13:257–258.
- HESKE, J. E., J. H. BROWN, AND Q. GUO. 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. Oecologia 95:520–524.
- , ———, AND S. MISTRY. 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. Ecology 75:438–445.
- HULSE, A. C. 1971. Fluorescence in *Leptotyphlops humilis* (Serpentes: Leptotyphlopidae). Southwest. Nat. 16:123–124.
- JACKSON, R. R., AND F. R. CROSS. 2013. A cognitive perspective on aggressive mimicry. Zoology 290:161–171.
- JACKSON, J. F., AND D. L. MARTIN. 1980. Caudal luring in the dusky pigmy rattlesnake, *Sistrurus miliarius barbouri*. Copeia 1980:926–927.
- JACOBS, G. H., J. NETZ, AND J. F. DEEGAN II. 1991. Retinal receptors in rodents maximally sensitive to ultraviolet light. Nature 353:655–656.
- , J. A. FENWICK, AND G. A. WILLIAMS. 2001. Cone-based vision of rats for ultraviolet and visible lights. J. Exp. Biol. 204:2439–2446.
- JENG, M. -L. 2019. Biofluorescence in terrestrial animals, with emphasis on fireflies: A review and field observation. In H. Suzuki (ed.), Analytical Applications and Basic Biology, pp. 1–25. Intech Open, DOI: 10.5772/intechopen.86029.
- KAUFFELD, C. F. 1943. Growth and feeding of new-born Price's and green rock rattlesnakes. Amer. Midl. Nat. 29:607–614.
- KHAN, M. S., AND R. TASNIM. 1986a. Balling and caudal luring in young *Bungarus caeruleus*. The Snake 18:42–46.
- , AND ———. 1986b. Notes on the Himalayan pit viper, *Agkistrodon himalayanus* (Günther). Litteratura Serpentina 6:46–55.
- KLAUBER, L. M. 1956. Rattlesnakes: Their Habits, Life Histories and Influence on Mankind. University of California Press, Berkeley, California. 1476 pp.
- KOCHVA, E., AND I. GOLANI. 1993. Tail display in *Atractaspis engaddensis* (Atractaspididae, Serpentes). Copeia 1993:226–228.
- KOHLER, A. M., E. R. OLSON, J. G. MARTIN, AND P. S. ANICH. 2019. Ultraviolet fluorescence discovered in New World flying squirrels (*Glaucomys*). J. Mammal. 100:21–30.
- SÖNKE, J., A. KELBER, E. WARRANT, A. M. SWEENEY, E. A. WIDDER R. L. LEE JR, AND J. HERNANDEZ-ANDRES. 2006. Crepuscular and nocturnal illumination and its effects on color perception by the nocturnal hawkmoth *Deilephila elpenor*. J. Exp. Biol. 209:789–800.
- LAMB, J. Y., AND M. P. DAVIS. 2020. Salamanders and other amphibians are aglow with biofluorescence. Sci. Rep. 10:2821.
- LARSEN, L. O., AND J. N. PEDERSEN. 1982. The snapping response of the toad, *Bufo bufo*, towards prey dummies at very low light intensities. Amphibia-Reptilia 2:321–327.
- LEAL, M., AND R. THOMAS. 1994. Notes on the feeding behavior and caudal luring by juvenile *Alsophis portoricensis* (Serpentes: Colubridae). J. Herpetol. 28:126–128.
- LIM, M. L., M. F. LAND, AND D. LI. 2007. Sex-specific UV and fluorescence signals in jumping spiders. Science 315:481.
- LIN, C. F., AND M. C. TU. 2008. Food habits of the Taiwanese mountain pitviper, *Trimeresurus gracilis*. Zool. Stud. 47:697–703.
- LONGLAND, W. S. 1994. Seed use by desert granivores. In S. B. Monsen and S. G. Kitchen (eds.), Ecology and Management of Annual Rangelands Proceedings, pp. 233–237. United States Department of Agriculture, Ogden, Utah.
- MADISON, D. M. 1977. Chemical communication in amphibians and reptiles. In D. Müller-Schwarze and M. M. Mozell (eds.), Chemical Signals in Vertebrates, pp. 135–168. Springer, Boston.
- MASON, R. T. 1992. Reptilian pheromones. In C. Gans and D. Crews (eds.), Biology of the Reptilia: Hormones, Brain, and Behavior, pp. 114–128. University of Chicago Press, Chicago, Illinois.
- , AND M. R. PARKER. 2010. Social behavior and pheromonal communication in reptiles. J. Comp. Physiol. A 196:729–749.
- MARTIN, G. R. 2012. Through birds' eyes: Insights into avian sensory ecology. J. Ornithol. 153:S23–S48.
- MARTINS, M. A., O. A. MARQUES, AND I. SAZIMA. 2002. Ecological and phylogenetic correlates of feeding habits in neotropical pitvipers of the genus *Bothrops*. In G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (eds.), Biology of the Vipers, pp. 307–328. Eagle Mountain Publishing, Eagle Mountain, Utah.
- MCCLEARY, R. J. R., M. -R. LOW, AND D. P. BICKFORD. 2015. Intracatch characteristics of the Wagler's viper, *Tropidolaemus wagleri* (Serpentes: Viperidae), in Singapore. Herpetol. Notes 8:629–631.
- MCFADDEN, M. 2005. Evidence for caudal luring in a captive water python (*Liasis fuscus*). Herpetofauna (Sydney) 35:42.
- MCGRAW, K. J., M. B. TOOMEY, P. M. NOLAN, N. I. MOREHOUSE, M. MASSARO, AND P. JOUVENTIN. 2007. A description of unique fluorescent yellow pigments in penguin feathers. Pigm. Cell Res. 20:301–304.
- MEIK, J. M., AND G. W. SCHUETT. 2016. Structure, ontogeny, and evolutionary development of the rattlesnake rattle. In G. W. Schuett, M. J. Feldner, R. S. Reiserer and C. F. Smith (eds.), Rattlesnakes of Arizona. Vol. 2, pp. 277–300. ECO Publishing, Rodeo, New Mexico.
- MELVINSELVAN, G., AND D. NIBEDITA. 2016. Defensive caudal display in *Uropeltis pulneyensis* Beddome 1863 (Serpentes: Uropeltidae) from Palani Hills, Western Ghats, India. Russian J. Herpetol. 23:77–80.

- MENDYK, R. W. 2021. Biofluorescence in the Sri Lankan house gecko (*Hemidactylus parvimaculatus*). *Taprobanica* 10:61–63.
- MESENGER, K. R., Y. YI, AND A. BORZEE. 2019. UV biofluorescence in swallowtail butterfly larvae. *Front. Ecol. Envir.* 17:444.
- MITCHELL, S. W. 1860. Researches upon the Venom of the Rattlesnake with an Investigation of the Anatomy and Physiology of the Organs Concerned. Smithsonian Contributions to Knowledge. Smithsonian Institute, Washington.
- MONSON, G. 1943. Food habits of the banner-tailed kangaroo rat in Arizona. *J. Wildl. Manag.* 7:98–102.
- MOSKOWITZ, D. 2018. Hunting caterpillars with a UV flashlight - part 2. *News of the Lepidopterists' Soc.* 60:169–171.
- MURPHY, J. B. 2017. Rattlesnakes and zoos. *Herpetol. Rev.* 48:887–898.
- , C. C. CARPENTER, AND J. C. GILLINGHAM. 1978. Caudal luring in the green tree python, *Chondropython viridis* (Reptilia, Serpentes, Boidae). *J. Herpetol.* 12:117–119.
- , AND L. A. MITCHELL. 1984. Miscellaneous notes on the reproductive biology of reptiles. 6. Thirteen varieties of the genus *Bothrops* (Serpentes, Crotalidae). *Acta Zool. Pathol. Antverp.* 78:199–214.
- MURPHY, R. W., J. FU, A. LATHROP, J. V. FELTHAM, AND V. KOVAC. 2002. Phylogeny of the rattlesnakes (*Crotalus* and *Sistrurus*) inferred from the sequences of five mitochondrial DNA genes. In G. W. Schuett, M. Höggren, and M. E. Douglas (eds.), *Biology of the Vipers*, pp. 69–92. Eagle Mountain Publishing, Eagle Mountain, Utah.
- NEILL, W. T. 1948. The yellow tail of juvenile copperheads. *Herpetologica* 4:161.
- . 1960. The caudal lure of various juvenile snakes. *Quart. J. Florida Acad. Sci.* 23:173–200.
- NOWOGRODZKI, A. 2017. First fluorescent frog found. *Nature* 543:297.
- ODATE, S. Y., TATEBE, M., OBIKA, AND T. HAMA. 1959. Pteridine derivatives in reptilian skin. *Proc. Jap. Acad.* 35:567–570.
- ORLOV, N., N. ANANJEVA, A. BARABANOV, S. RYABOV, AND R. KHALIKOV. 2002a. Diversity of vipers (Azemiopinae, Crotalinae) in East, Southeast, and South Asia: Annotated checklist and natural history data (Reptilia: Squamata: Serpentes: Viperidae). *Faunistische Abhandlungen Staatliches Museum für Tierkunde Dresden* 23:177–218.
- , AND R. KHALIKOV. 2002b. Natural history of pitvipers in eastern and southeastern Asia. In G. W. Schuett, M. Höggren, and M. E. Douglas (eds.), *Biology of the Vipers*, *Biology of the Vipers*, pp. 345–359. Eagle Mountain Publishing, Eagle Mountain, Utah.
- OWENS, T. 2016. Mangshan pit viper *Protobothrops mangshanensis*. In Peeling, C. and I. Recchio (eds.), *Regional Collection Plan. AZA Snake Advisory Group*. 4th Edition, pp. 68–70. Association of Zoos and Aquariums, Silver Spring, Maryland.
- PARRELLADA, X., AND X. SANTOS. 2002. Caudal luring in free-ranging adult *Vipera latasti*. *Amphibia-Reptilia* 23:343–347.
- PEARNS, S. M., A. T. BENNETT, AND I. C. CUTHILL. 2003. The role of ultraviolet-A reflectance and ultraviolet-A induced fluorescence in the appearance of budgerigar plumage: Insights from spectrofluorometry and reflectance spectrophotometry. *Proc. R. Soc. Lond. B* 270:859–865.
- PRÖTZEL, D., M. HESS, M. D. SCHERZ, M. SCHWAGER, A. V. PADJE, AND F. GLAW. 2018. Widespread bone-based fluorescence in chameleons. *Sci. Rep.* 8:698.
- , M. SCHWAGER, F. GLAW, AND M. D. SCHERZ. 2021. Neon-green fluorescence in the desert gecko *Pachydactylus rangei* caused by iridophores. *Sci. Rep.* 11:297.
- RABATSKY, A. M., AND T. M. FARRELL. 1996. The effects of age and light level on foraging posture and frequency of caudal luring in the rattlesnake, *Sistrurus miliarius barbouri*. *J. Herpetol.* 30:558–561.
- , AND J. N. WATERMAN. 2005. Non-rattling defensive tail display in the dusky pygmy rattlesnake, *Sistrurus miliarius barbouri*: A previously undescribed behavior. *Herpetol. Rev.* 36:236–238.
- RADCLIFFE, C. W., D. CHISZAR, AND H. B. SMITH. 1980. Prey-induced caudal movements in *Boa constrictor* with comments on the evolution of caudal luring. *Bull. Maryland Herpetol. Soc.* 16:19–22.
- REINERT, H. K., D. CUNDALL, AND L. M. BUSHAR. 1984. Foraging behavior of the timber rattlesnake, *Crotalus horridus*. *Copeia* 1984:976–981.
- , G. A. MACGREGOR, M. ESCH, L. M. BUSHAR, AND R. T. ZAPPALORTI. 2011. Foraging ecology of timber rattlesnakes, *Crotalus horridus*. *Copeia* 2011:430–442.
- REISERER, R. S. 2002. Stimulus control of caudal luring and other feeding responses: Visual perception in vipers. In G. W. Schuett, M. Höggren, M. E. Douglas and H. W. Greene (eds.), *Biology of the Vipers*, pp. 361–383. Eagle Mountain Publishing, Eagle Mountain, Utah.
- , AND G. W. SCHUETT. 2008. Aggressive mimicry in neonates of the sidewinder rattlesnake, *Crotalus cerastes* (Serpentes: Viperidae): Stimulus control and visual perception of prey luring. *Biol. J. Linn. Soc.* 95:81–91.
- , AND ———. 2016. The origin and evolution of the rattlesnake rattle: Misdirection, clarification, theory, and progress. In G. W. Schuett, M. J. Feldner, C. F. Smith, and R. S. Reiserer (eds.), *Rattlesnakes of Arizona*. Vol. 2, pp. 245–276. ECO Publishing, Rodeo, New Mexico.
- , AND H. W. GREENE. 2018. Seed ingestion and germination in rattlesnakes: Overlooked agents of rescue and secondary dispersal. *Proc. R. Soc. B* 285:20172755.
- ROTH, L. S. V., AND A. KELBER. 2004. Nocturnal colour vision in geckos. *Proc. R. Soc. Lond. B* 271:S485–S487.
- SANDERS, K. L., A. MALHOTRA, AND R. S. THORPE. 2004. Ecological diversification in a group of Indomalayan pitvipers (*Trimeresurus*): Convergence in taxonomically important traits has implications for species identification. *J. Evol. Biol.* 17:721–731.
- SAZIMA, I. 1991. Caudal luring in two neotropical pitvipers, *Bothrops jararaca* and *B. jararacussu*. *Copeia* 1991:245–248.
- , AND G. PUERTO. 1993. Feeding technique of juvenile *Tropidodryas striaticeps*: Probable caudal luring in a colubrid snake. *Copeia* 1993:222–226.
- SCHUETT, G. W. 1984. *Calloselasma rhodostoma* (Malayan pit viper): feeding mimicry. *Herpetol. Rev.* 15:112.
- . 1997. Body size and agonistic experience affect dominance and mating success in male copperheads, *Agkistrodon contortrix*. *Anim. Behav.* 54:213–224.
- , D. L. CLARK, AND F. KRAUS. 1984. Feeding mimicry in the rattlesnake *Sistrurus catenatus*, with comments on the evolution of the rattle. *Anim. Behav.* 32:625–626.
- , M. J. FELDNER, R. S. REISERER, AND C. F. SMITH (eds.). 2016a. *Rattlesnakes of Arizona*. Vol. 1. ECO Publishing, Rodeo, New Mexico.
- , R. W. CLARK, R. A. REPP, M. AMARELLO, C. F. SMITH, AND H. W. GREENE. 2016b. Social behavior of rattlesnakes: A shifting paradigm. In G. W. Schuett, M. J. Feldner, R. S. Reiserer, and C. F. Smith (eds.), *Rattlesnakes of Arizona*. Volume 2, pp. 161–244. ECO Publishing, Rodeo, New Mexico.
- SEIKO, T., AND Y. TERAI. 2019. Fluorescence emission in a marine snake. *Galaxea* 21:7–8.
- SHEEHY, C. M. 2016. On the structure and function of tails in snakes: Relative length and arboreality. Unpublished Dissertation. University of Florida, Gainesville.
- SISK, N. R., AND J. E. JACKSON. 1997. Test of two hypotheses for the origin of the crotaline rattle. *Copeia* 1997:485–295.
- SLOGGETT, J. J. 2018. Field observations of putative bone-based fluorescence in a gecko. *Curr. Zool.* 64:319–320.
- SMITH, H. M. 1943. Summary of the collections of snakes and crocodilians made in Mexico under the Walter Rathbone Bacon Traveling Scholarship. *Proc. U.S. Nat. Mus.* 93:393–504.
- SOURAKOV, A. 2017. Studying Lepidoptera in different lights. *News of the Lepidopterists' Soc.* 59:96–101.
- . 2019. Scientific note: Evaluating potential aposematic signals in caterpillars using fluorescent microscope and spectrometer. *Trop. Lepidopt. Res.* 29:52–55.
- STARRETT, B. L., AND A. T. HOLYCROSS. 2000. *Crotalus lepidus klauberi* (banded rock rattlesnake): caudal luring. *Herpetol. Rev.* 31:245.

- STEJNEGER, L. 1907. Herpetology of Japan and adjacent territory. U.S. Nat. Mus. Bull. 58:1–577.
- STENDER-OLIVEIRA, F. M., MARTINS, AND O. A. V. MARQUES. 2016. Food habits and reproductive biology of tail-luring snakes of the genus *Tropidodryas* (Dipsadidae, Xenodontinae) from Brazil. *Herpetologica* 72:73–79.
- STRIMPLE, P. 1995. Comments on caudal luring in snakes with observations on this behaviour in two subspecies of cantils, *Agkistrodon bilineatus* ssp. *Litteratura Serpentina* 15:74–77.
- TABOADA, C., A. E. BRUNETTI, C. ALEXANDRE, M. G. LAGORIO, AND J. FAIVOVICH. 2017a. Fluorescent frogs: A herpetological perspective. *S. Amer. J. Herpetol.* 12:1–13.
- , ———, F. N. PEDRON, F. C. NETO, D. A. ESTRIN, S. E. BARI, L. B. CHMES, N. P. LOPES, M. G. LAGORIO, AND J. FAVOVICH. 2017b. Naturally occurring fluorescence in frogs. *PNAS* 114:3672–3677.
- TEVIS, L. 1943. Field notes on a red rattlesnake in lower California. *Copeia* 1943:242–245.
- THEODORATUS, D. H., AND D. CHISZAR. 2000. Habitat selection and prey odor in the foraging behavior of western rattlesnakes (*Crotalus viridis*). *Behaviour* 137:119–135.
- THOMPSON, M. E., R. A. SAVORITO, D. H. RUIZ-VALDERRAMA, G. F. MEDINA-RANGEL, AND M. A. DONNELLY. 2019. A field-based survey of fluorescence in tropical tree frogs using an LED UV-B flashlight. *Herpetol. Notes* 12:987–990.
- TIEBOUT, H. H. 1997. Caudal luring by a temperate colubrid snake, *Elaphe obsoleta*, and its implications for the evolution of the rattle among rattlesnakes. *J. Herpetol.* 31:290–292.
- TOP, M. M., C. L. PUAN, M. -F. CHUANG, S. N. OTHMAN, AND A. BORZEE. 2020. First record of ultraviolet fluorescence in the bent-toed gecko *Cyrtodactylus quadrivirgatus* Taylor, 1962 (Gekkonidae: Sauria). *Herpetol. Notes* 13:211–212.
- TRYON, B. W. 1985. *Bothrops asper* (terciopelo): caudal luring. *Herpetol. Rev.* 16:28.
- UETZ, P., P. FREED, AND J. HOSEK (eds.). 2020. The Reptile Database. <http://www.reptile-database.org/>. Last accessed 2 October 2020.
- VINCENT, S. E., A. HERREL, AND D. J. IRSCHICK. 2004. Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). *J. Zool.* 264:53–59.
- VOGEL, Z. 1964. *Reptiles and Amphibians: Their Care and Behaviour*. Viking Press, New York. 228 pp.
- WHARTON, C. H. 1960. Birth and behavior of a brood of cottonmouths, *Agkistrodon piscivorus* with notes on tail-luring. *Herpetologica* 16:125–129.
- WHITCHER, C. 2020. New accounts of biofluorescence in several anuran genera (Hylidae, Microhylidae, Ranidae, Leptodactylidae) with comments on intraspecific variation. *Herpetol. Notes* 13:443–447.
- WHITTAKER, S. P., AND R. SHINE. 1999. *Morelia spilota* (Australian carpet python): caudal luring. *Herpetol. Rev.* 30:102–103.
- WILKINSON, B. P., M. E. JOHNS, AND P. WARZYBOK. 2019. Fluorescent ornamentation in the rhinoceros auklet *Cerorhinca monocerata*. *Ibis* 161:694–698.
- WÜSTER, W., L. PEPPIN, C. E. POOK, AND D. E. WALKER. 2008. A nesting of vipers: Phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes). *Mol. Phylog. Evol.* 49:445–459.
- ZHANG, B. B. WU, D. YANG, X. TAO M. ZHANG, S. HU, J. CHEN, AND M. ZHENG. 2020. Habitat association in the critically endangered Mangshan pit viper (*Protobothrops mangshanensis*), a species endemic to China. *PeerJ* 8:e9439.

Herpetological Review, 2021, 52(2), 237–245.

© 2021 by Society for the Study of Amphibians and Reptiles

Terrestrial Microhabitats of Plethodontid Salamanders in the Southern Blue Ridge Mountains

The streams and forests of the southern Blue Ridge Mountains (USA) support a diverse fauna of stream-dwelling, streamside, and woodland species of lungless salamanders (Plethodontidae) (Beane et al. 2010). In the warmer months terrestrial forest-floor ecosystems are enriched by an influx of streamside species which co-occur with resident woodland species (Hairston 1981; Petranks and Smith 2005). During daylight hours these salamanders remain concealed beneath cover objects on the forest floor, to emerge after dark to forage (e.g., Ash 2020; Hocking et al. 2021). Cover objects represent an important resource for salamanders (and other small animals), providing moisture and a source of invertebrate prey, as well as a refuge from predators (Caruso 2016). A principal category of cover object is referred to as down woody debris (DWD), which includes round wood (trunks and limbs of trees and shrubs), as well as bark and other

woody material, all in contact with the ground and in varying states of decay. DWD is an important component of biomass in temperate North American forests (Woodall et al. 2013), and supports a diverse animal community (Stokland et al. 2012). Other cover objects include rocks, leaf litter, and moss.

In a study in the Great Smoky and Balsam Mountains, Caruso (2016) surveyed cover object use by plethodontid salamanders on two 3 × 50 m forest plots at each of 40 sites. The categories of cover objects were logs, bark piles, and rocks. Caruso (2016) observed 624 individual salamanders in 4 genera and 11 species. Salamanders showed a preference for larger woody retreats, mainly logs, which Caruso (2016) ascribed to the higher moisture content and greater prey abundance of such cover objects. Among four species of *Desmognathus* the tiny *D. wrighti* used smaller retreats than the larger *D. santeetlah*, *D. ocoee*, and *D. imitator*.

Rossell et al. (2018) examined cover object use by Northern and Southern Pygmy Salamanders (*D. organi*, *D. wrighti*) at 73 sites in the southern Blue Ridge of North Carolina. They recorded size and type of cover object used by these salamanders, as well as a number of environmental variables. Both species preferred woody cover objects rather than rocks, and apparently selected

RICHARD C. BRUCE

Department of Biology, Western Carolina University,
Cullowhee, North Carolina 28723, USA

Current address: 50 Wagon Trail, Black Mountain, North Carolina 28711, USA
e-mail: ebruce1563@aol.com