REPTILES & AMPHIBIANS

Preliminary Observations of Skeletal UV Fluorescence in Fresh and Preserved Snakes

Justin M. Bernstein[1], Eric N. Rittmeyer[2], and Sara Ruane[3]

[1]Department of Biological Sciences, Rutgers University-Newark, Newark, New Jersey 07102, USA (Current Address: Department of Biology, University of Texas at Arlington, Arlington, Texas 07102, USA) (justin.bernstein@uta.edu [corresponding author]; ORCID ID: 0000-0002-5249-3340)
[2]Department of Biological Sciences, Rutgers University-Newark, Newark, New Jersey 07102, USA
[3]Life Sciences Section, Negaunee Integrative Research Center, Field Museum, Chicago, Illinois 60605, USA (sruane@fieldmuseum.org; ORCID ID: 0000-0002-9543-1297)

Abstract.—Biofluorescent tissues in vertebrates are commonly observed phenomena that have been found in a wide variety of taxonomic groups. The fluorescence of bone has recently been found visible through the skin in some squamates, although its function is poorly known. While this phenomenon has been observed in lizards, no published records of ultraviolet (UV)-based fluorescence exist for snakes. We present the first published record of bone-based fluorescence of snakes using museum skeletal specimens and fresh dead-on-the-road (DOR) specimens (24–48 h postmortem) gathered during field observations. Nine of 11 families tested fluoresced in the presence of a UV alternative light source. We found that snake bones emitted brighter blue/green light in DOR specimens than the dull green color in older museum specimens. Fluorescence, though brighter in fresh specimens, was still observed in museum specimens as old as 95 years. We herein present observations to provide baseline data for fluorescence-related studies in snakes. We remain uncertain if the light emitted from bones is visible through the skin and scales of living snakes and identify this as an important area for future investigations.

Invertebrates and vertebrates use a variety of signals to communicate with predators, prey, and conspecifics, and these signals include coloration, behavioral displays, chemical cues, and vocalizations (Narins 1990; Fonseca 2014; Surov and Maltsev 2016; Bruinjé et al. 2019). Although not as well documented outside of anthozoan cnidarians, biofluorescence, the absorption of lower wavelength and reemission of higher wavelength light, is taxonomically more widespread than previously thought. Biofluorescent tissues and compounds have been found in cnidarians, lepidopterans, psittaciform birds, arthropods, and even some plants (Lawrence 1954; Arnold et al. 2002; Gandía-Herrero et al. 2005; Nowogrodzki 2017). This phenomenon is especially prevalent in ray-finned fishes, which exhibit a diversity of emission spectra (Sparks et al. 2014), and amphibians that show different patterns and levels of fluorescence intensity across frogs, salamanders, and caecilians (Goutte et al. 2019; Lamb and David 2020). Along with the diversity of organisms that possess biofluorescent proteins, or fluorophores, variation also exists in the mechanisms of their expression. These proteins have been shown to be distributed nonrandomly in some taxa (Gruber et al. 2008), are phenotypically variable in others (Sparks et al. 2014), and can exist through multiple mechanisms across substrates such as guanine crystals in reef fish (Michiels et al. 2008), feathers in birds (Arnold et al. 2002), storage of fluorophores in the hemolymph of spiders (Andrews et al. 2007), or fluorescent hyloins in the lymph and skin of hylid frogs (Taboada et al. 2017). In harder tissues, such as bone, fluorescence is likely a byproduct of the tyrosine in the bony matrix, which is composed heavily of collagen type I (Shen et al. 2018). Bone fluorescence has been known for decades and is likely present in most, if not all, vertebrates (Bachman and Ellis 1965). However, bone-based fluorescence in squamate reptiles has just recently been documented in light of function (e.g., Prötzel et al. 2018), and fluorescence in any tissue in snakes (e.g., scales; Fuentes et al. 2021) is beginning to open up new avenues of research and hypotheses regarding the evolution of structures and respective functions (Paul et al. 2021).

Field observations and laboratory experiments have shown that the bones or keratinized structures of some reptilian species fluoresce in the presence of blue or ultraviolet (UV) light. The carapace (and while not bone, the fins) of Loggerhead (*Caretta caretta*) and Hawksbill (*Eretmochelys imbricata*) Sea Turtles exhibit red and green fluorescence in the presence of high-intensity blue lights (Gruber and Sparks 2015). External fluorescence, albeit blue-green in color, also has been observed in amphisbaenids (Maitland and Hart 2008). Additionally, the skull, vertebral column, pelvis, and some limb bones of *Chondrodactylus bibronii* and

Reptiles & Amphibians ISSN 2332-4961
https://doi.org/10.17161/randa.v31i1.21588

Cyrtodactylus quadrivirgatus, two gekkonid geckos, fluoresce blue under different levels of UV light (Sloggett 2018; Tah et al. 2020). The degree of light emitted from the bones and the ability for this light to be seen may be correlated with the dermal structure of the organism itself, as is seen in some species of chameleons. For example, species in the chamaeleonid genus *Calumma* have tubercles scattered on the head, which are positioned beneath a thinner layer of skin covering the bone in comparison to regions lacking tubercles, minimizing the attenuation of bone fluorescence (Prötzel et al. 2018). These studies identify cases in which hard dermal or subdermal elements fluoresce in representatives of several major groups of reptiles (amphisbaenids, chelioniids, chamaeleonids, and gekkonids), but skeletal biofluorescence of any kind has not yet been documented in snakes.

To the best of our knowledge, we herein provide the first observations of skeletal fluorescence in snakes using museum specimens and field observations of roadkills. Indeed, the bones of all vertebrates are expected to fluoresce due to their conserved composition, and while an ecological function of this phenomenon is largely dependent on the visibility of fluorescence from outside a live animal, documenting fluorescence in multiple lineages and at different points in time (historically preserved vs. fresh tissue) serves as a baseline to determine if bone fluorescence in snakes has an ecological role and changes over time. The aims of this study were to: (1) confirm and report the first observations of skeletal UV fluorescence in both fresh and old (museum) snake specimens, (2) provide a preliminary assessment of the taxonomic breadth in which skeletal fluorescence occurs in snakes, and (3) lay a foundation of hypotheses and observations for future studies of fluorescence in snake systems.

Methods

Collection and Sampling.—While collecting salvage specimens in the Pine Barrens of New Jersey (USA) in August 2018 (New Jersey Department of Environmental Protection [NJDEP] salvage permit SW 2018011) for a separate project, we opportunistically checked for and observed fluorescence of the skeletons of roadkilled snakes. Twelve dead-on-road (DOR) snakes were found throughout forested habitats in the Pine Barrens and were designated field numbers (see Table 1). We did not manipulate (i.e., dissect or reposition) any bones within the DOR specimens. Roads with DOR specimens were driven multiple times on consecutive nights, so we assumed that DOR specimens in this study were killed within 24–48 h of observations of skeletal fluorescence. We also checked an additional specimen salvaged in August 2017 (NJDEP salvage permit SW 2017040) for skeletal fluorescence in a laboratory at Rutgers University-Newark (New Jersey, USA). To look for differences in fluorescence intensity of fresh vs. old specimens, as well as assess the taxonomic breadth of skeletal fluorescence in snakes, we examined whole and partial skeletons of 43 specimens (31 species in 11 families) from the American Museum of Natural History (AMNH, New York, USA; Table 1).

Detection of Skeletal Fluorescence.—We used a TaoTronics® 12 LEDs UV flashlight (wavelength = 395 nm) to check for fluorescing bones in snakes that were recently killed (roadkill). We shined the flashlight on entire specimens, focusing on bones that were sticking out of bodies and any tissue seen through lacerations in the skin. The UV flashlight was held about 10 cm from the specimen in a room with no light. To check the distribution of colors in the images, we used the 'Color Inspected 3D' plugin in ImageJ (Schindelin et al. 2012). Photographs of fluorescence were taken using a Samsung Galaxy S9 smartphone and a Canon EOS 70D Digital SLR camera with a Tamron AF 90mm lens.

We checked for fluorescence on skeletal specimens at the AMNH using the same TaoTronics® UV flashlight and the same lighting conditions as the DOR specimens (Table 1). Although fluorescence can be confirmed using the flashlight in this study, we do not consider absence of fluorescence as 'not fluorescent,' as temporal and environmental factors can potentially alter the fluorescence of tissues. Additionally, the use of different flashlights emitting differing wavelengths and imaging equipment such as cameras with UV and non-UV filters might or might not allow fluorescence to be apparent. Familial status of taxa is based on Burbrink et al. (2020).

Results

Fresh Specimens.—We observed fluorescence in 12 DOR specimens of nine species from four families found in the Pine Barrens in 2017 and 2018: *Coluber constrictor*, *Crotalus horridus*, *Heterodon platirhinos, Lampropeltis getula*, *Nerodia sipedon*, *Opheodrys aestivus*, *Pantherophis alleghaniensis, Storeria occipitomaculata*, and *Thamnophis sirtalis* (Table 1). All twelve specimens exhibited skeletal fluorescence of the teeth and, most notably, the ribs and vertebrae (Fig. 1). Bones did not have to be exposed to show fluorescence, as in some fresh specimens, we observed blue/green light emitted from bones that were embedded in muscle tissue (Fig. 2). Bones from these snakes fluoresced bright blue when exposed to UV light in daytime conditions, but were more noticeable in darker conditions (e.g., at night while in the field or in a dark room with no visible light). Any DOR specimens that were frozen for several weeks maintained their fluorescent properties with no visible changes. Although not the focus of this paper, we also observed fluorescence in DOR specimens of the bufonid toad *Anaxyrus fowleri* (limb bones) and emydid turtles *Chrysemys picta* and *Terrapene carolina* (carapace and plastron). Although we held the flashlight 10 cm from the DOR specimens, bright fluorescence was still observed when the flashlight was held up to 30.5 cm away from the bone. No scales or skin fluoresced in any of the specimens observed.

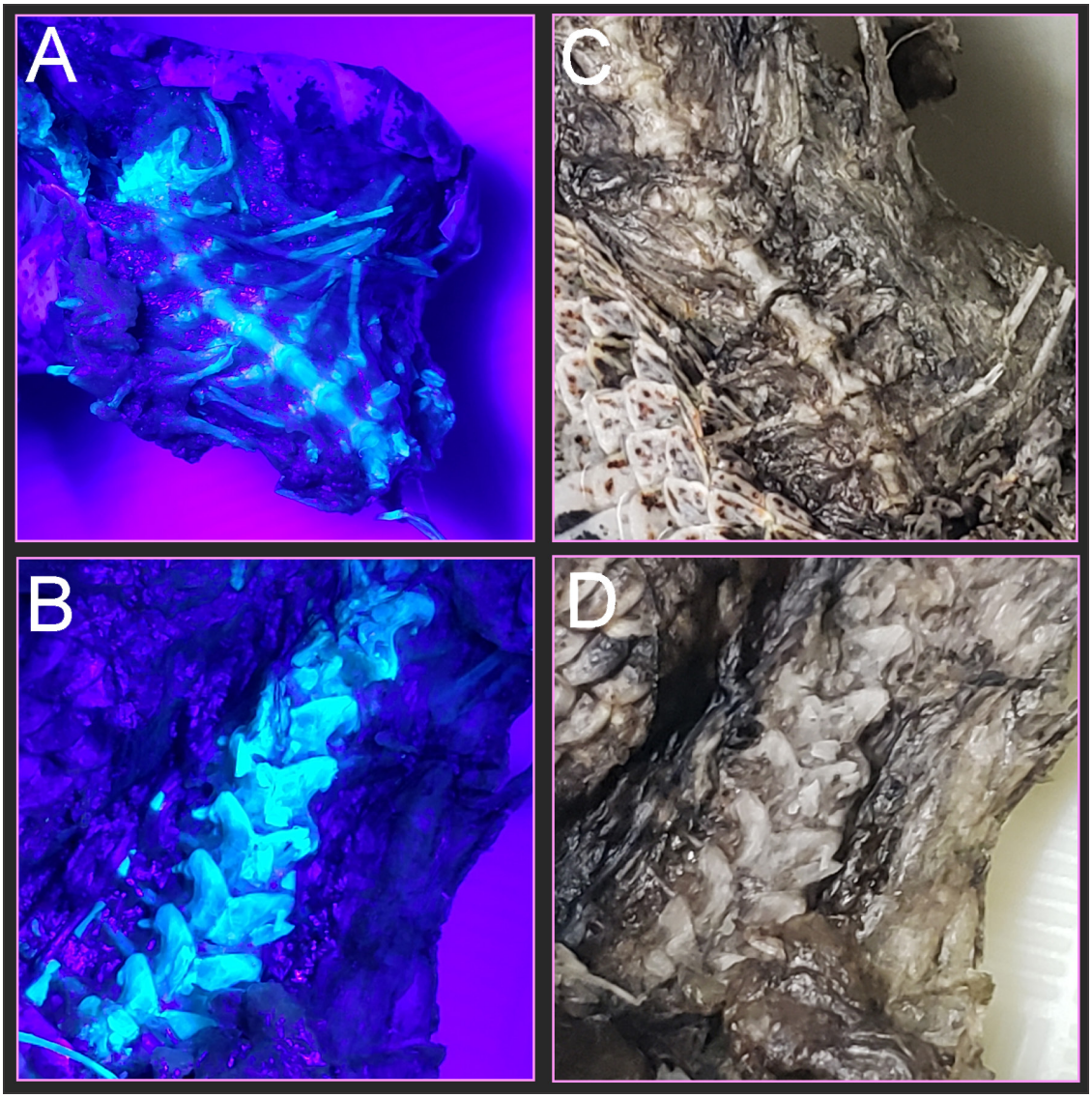

Figure 1. Fresh scale, muscle, and bone of a DOR *Crotalus horridus* (SR 490) under ultraviolet (A, B) and white (C, D) light. Fresh ribs (only visible in A and C) and vertebra emit a bright blue light when subjected to UV light of 395 nm. Photographs taken with a Samsung Galaxy S9 smartphone by JMB.

The color distributions of all images under UV light showed higher levels of color in the blue-green range (shown for *C. horridus*; Fig. 2).

Museum Specimens.—The museum snake skeletons showed varying degrees of fluorescence, including none, fluorescence observable only in complete darkness (faintly fluorescent), or fluorescence observable under normal daylight conditions (Table 1). In contrast to the DOR specimens, light emitted from museum skeletons was dull green; 25 of 31 species (9 of 11 families) tested exhibited skeletal fluorescence. Specimens that had fluorescent bones were from species in Acrochordidae, Boidae, Colubridae, Cylindrophiidae, Dipsadidae, Elapidae, Grayiidae, Natricidae, and Viperidae, representing ~22.5% of snake families (Fig. 3; Table 1). In contrast, we noted no observable emission when the UV light was shined on bones of the one homalopsid, one aniliid, and some of the colubrids and natricids examined (Table 1). The oldest specimens found to fluoresce were from 1925 (Table 1). We also observed an instance in which only some vertebrae of a single specimen of *Opheodrys vernalis* from the museum collection fluoresced, suggesting that age, preservation method, and/or storage conditions could affect our ability to detect fluorescence. Due to unavailable data for some tested specimens, we made no correlations between the amount of fluorescence and collection year of museum skeletons. Overall, however, fresher (DOR) samples appeared to fluoresce more brightly than any of the museum specimens.

Discussion

Given the conserved morphological composition of bones in animals and the selective constraints of the collagen type I-coding gene (*COL1a1*; Stover and Verrelli 2011), most (if not all) bones are expected to fluoresce when subjected to UV light. However, our results provide support for skeletal

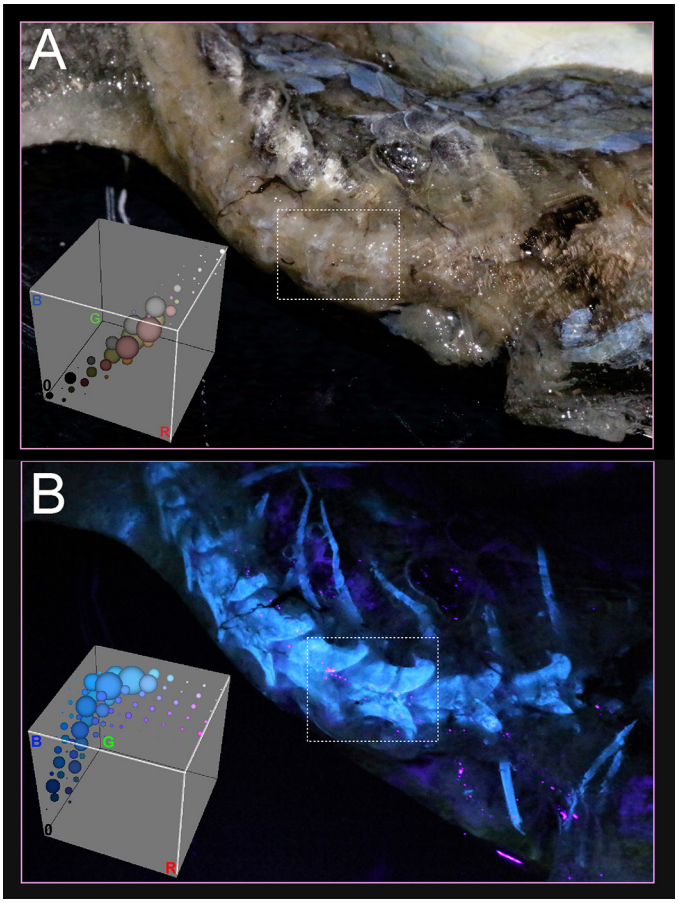

Figure 2. Images of fresh tissue from a DOR *Opheodrys aestivus* (SR 615) in white light (A) and UV light of 395 nm (B). Note that details of the vertebrae and ribs are not apparent through the soft tissues and are visible only under UV light. Distribution of red (R), green (G), blue (B), and black (0) for two vertebrae (outlined in dashed rectangle) inset; larger spheres indicate higher levels of a color within the coordinate plane. Photographs taken with a Canon EOS 70D Digital SLR camera with a Tamron AF 90mm lens by JMB.

fluorescence in the presence of UV light across multiple snake lineages, we show evidence for change in fluorescence intensity over time, and we discuss areas for further investigation.

We documented the presence of fluorescence in nine families of snakes: Acrochordidae, Boidae, Colubridae, Cylindrophiidae, Dipsadidae, Elapidae, Grayiidae, Natricidae, and Viperidae (Crotalinae). As stated, if fluorescence was not observed, we did not assume that taxon does not have fluorescent bones. Fluorescent properties could decrease and degrade over time, indicated by the observation of most recently collected bone tissue fluorescing the brightest and a different color than the museum specimens. This degradation in fluorescence also has been shown in whole voucher specimens (Prötzel et al. 2018) and in bones of humans ranging from hundreds to >1000 years (Swaraldahab and Christensen 2016). What environmental or biological determinants lead to changes in fluorescence magnitude (e.g., level of sunlight on DORs, preparatory methods for skeletal specimens in museum collections) is difficult to discern. Although some compounds have been discovered to be the source of biofluorescence in soft tissues (e.g., green fluorescent protein (GFP) and GFP-like proteins in a variety of taxa, coumarins in scorpions [Frost et al. 2001], hyloins in hylid frogs [Taboada et al. 2017]; fatty-acid-binding-protein in eels [Kumagi et al. 2013]), the fluorescence of bones in snakes is likely attributable to collagen, hydroxyapatite, and calcium phosphate (Bachman and Ellis 1965).

As habitat preferences and diets of the tested snake taxa differ, the presence and function of fluorescence probably does not pertain wholly to either of these life history traits. Furthermore, as of yet, no evidence indicates that the fluorescence of bones is visible through the scales and skin of live snakes. Fluorescence of various tissues in other organisms presumably plays a primary role in signaling and communication, but these are all instances in which other organisms can perceive fluorescent properties from outside the fluorescing animal. These scenarios might involve interspecific and intraspecific interactions, as well as attraction (mate selection) and repulsion (e.g., aposematism, competition) mechanisms. Such visual signals are not limited to any particular taxonomic group, for example, squirrels (Kohler et al. 2019), some fishes (Garcia et al. 2002), and birds (Hunt et al. 1998; Arnold et al. 2002) appear to use fluorescent signaling in species recognition and mating, and greater fluorescence apparently increases the likelihood of attracting a mate. Numerous mechanisms for species recognizing conspecifics or congenerics have evolved via visual communication. Even in lineages that typically use auditory signals, visual cues can develop. For example, members of the Brazilian-endemic frog genus *Brachycephalus* (pumpkin toadlets) are deaf to their own calls, and the biofluorescence of these species might be linked to the loss of hearing, aiding in the perception of individuals that cannot be heard (Goutte et al. 2017; Taboada et al. 2017). Many marine fishes that are found at great depths in dark environments will fluoresce or have adaptations to enhance the perception of fluorescence (Heinermann 1984; Sparks et al. 2014; Anthes et al. 2016). Finally, evidence suggests that fluorescence is used as an anti-predator defense, like camouflage and aposematism, as seen in pumpkin toadlets (Pires et al. 2002; Taboada et al. 2017), butterflies (Olofsson et al. 2010), and fishes (Sparks et al. 2014). Although not as widespread, other less common functions, some of which do not depend on visual perception from outside the animal, include photoprotection (Salih et al. 2000), antioxidation (Bou-Abdallah et al. 2006), regulation of symbiotic relationships (Field et al. 2006), photoacclimation (Roth et al. 2010), general health (Roth et al. 2013), and visual contrast (Gruber et al. 2008), all of which occur in corals.

Given the wide taxonomic scope of skeletal fluorescence we observed in snakes and the possibility that it is not visible

Table 1. Specimens examined in this study, with corresponding collection and voucher data (if available). AMNH = American Museum of Natural History (Herpetology Collection); SR = Sara Ruane field series. Dashes indicate no data or data unavailable. Asterisks (*) indicate that the status of fluorescence was uncertain due to specimen quality. Two asterisks (**) indicate that only some vertebrae fluoresced.

Catalogue number	Species	Locality	Fluorescence	Year collected
Squamata: Acrochordidae				
AMNH-R 89839, 140813	*Acrochordus javanicus*	—	Present	—
Squamata: Aniliidae				
AMNH —	*Anilius scytale*	—	Absent*	—
Squamata: Boidae				
AMNH-R 76200	*Aspidites melanocephalus*	—	Present	—
AMNH-R 102222	*Eryx johnii*	—	Present	—
AMNH-R 84494	*E. miliaris*	Uzbekistan	Present	1956
Squamata: Colubridae				
SR 699	*Coluber constrictor*	USA: New Jersey	Present	2018
AMNH-R 71084	*Gonyosoma oxycephalum*	—	Present	—
AMNH-R 88243	*Gyalopion canum*	USA: Arizona	Present	1961
AMNH-R 99346	*G. canum*	USA: Arizona	Present	1966
AMNH-R 102526	*G. canum*	USA: Arizona	Present	1968
AMNH-R 115590	*G. canum*	USA: Arizona	Present	1971
SR 611	*Lampropeltis getula*	USA: New Jersey	Present	2018
AMNH-R 58326, 58327	*L. triangulum*	USA: Texas	Present	—
AMNH-R 140807	*L. t. hondurensis*	—	Present	—
AMNH-R 29933	*L. t. microlophis*	—	Present	1928
AMNH-R 155326	*L. t. nelsoni*	Mexico: Puebla	Present	1950
AMNH-R 155325	*L. t. nelsoni*	Mexico: Sinaloa	Present	1962
AMNH-R 76198	*L. t. polyzona*	No data	Present	—
AMNH-R 155324	*L. t. triangulum*	USA: Michigan	Present	1957
SR 615	*Opheodrys aestivus*	USA: New Jersey	Present	2018
AMNH-R 155358	*O. vernalis*	USA: Michigan	Present**	—
SR 621	*Pantherophis alleghaniensis*	USA: New Jersey	Present	2018
Squamata: Cylindrophiidae				
AMNH-R 12872	*Cylindrophis lineatus*	Singapore	Present	1937
AMNH-R 58647	*C. rufus*	Thailand	Present	1960
Squamata: Dipsadidae				
AMNH-R 74842	*Heterodon nasicus*	—	Present	—
SR 701	*H. platirhinos*	USA: New Jersey	Present	2018
AMNH —	*Hypsiglena* sp.	—	Absent*	—
AMNH-R 75825	*Ninia atrata*	Trinidad	Present	1956

(continued)

(continued)

Catalogue number	Species	Locality	Fluorescence	Year collected
Squamata: Elapidae				
AMNH-R 73804	*Dendroaspis angusticeps*	—	Present	—
AMNH-R 52890	*Micrurus spixii obscurus*	Peru	Present	1930
AMNH-R 74813	*M. s. obscurus*	—	Present	—
AMNH-R 92980	*M. surinamensis*	—	Present	—
AMNH-R 142611–5	*Naja melanoleuca*	—	Present	—
AMNH-R 51802, 51803	*N. nigricollis nigricollis*	Angola	Present	1925
Squamata: Elapidae: Hydrophiinae				
AMNH —	*Aipysurus laevis*	—	Absent*	—
AMNH-R 102154	*Aspidelaps lubricus*	—	Present	—
AMNH-R 75733	*Austrelaps superbus*	—	Present	1955
AMNH —	*Hydrophis* sp.	—	Absent*	—
AMNH —	*Oxyuranus* sp.	—	Absent*	—
AMNH-R 76210	*Pseudonaja textilis*	—	Present	—
AMNH-R 75724	*P. textilis*	—	Present	1955
Squamata: Grayiidae				
AMNH-R 12174	*Grayia ornata*	Belgian Congo	Present	1913
Squamata: Homalopsidae				
AMNH —	*Homalopsis buccata*	—	Absent?	—
Squamata: Natricidae				
AMNH-R 57490, 73348	*Nerodia* sp.	—	Faint	—
SR 558	*N. sipedon*	USA: New Jersey	Present	2018
AMNH-R 128200	*N. taxispilota*	USA: South Carolina	Present	1979
SR 693	*Storeria occipitomaculata*	USA: New Jersey	Present	2018
SR 694	*Thamnophis sirtalis*	USA: New Jersey	Present	2018
Squamata: Viperidae: Crotalinae				
SR 490	*Crotalus horridus*	USA: New Jersey	Present	2017
AMNH-R 110177, 114719	*C. scutulatus*	USA: Arizona	Present	1966
AMNH-R 75270	*C. scutulatus*	—	Present	—
AMNH-R 114719	*C. scutulatus*	USA: Arizona	Present	1966
Anura: Bufonidae				
SR 613	*Anaxyrus fowleri*	USA: New Jersey	Present	2018
Testudines: Emydidae				
SR 549	*Chrysemys picta*	USA: New Jersey	Present	2018
SR 626	*Terrapene carolina*	USA: New Jersey	Present	2018

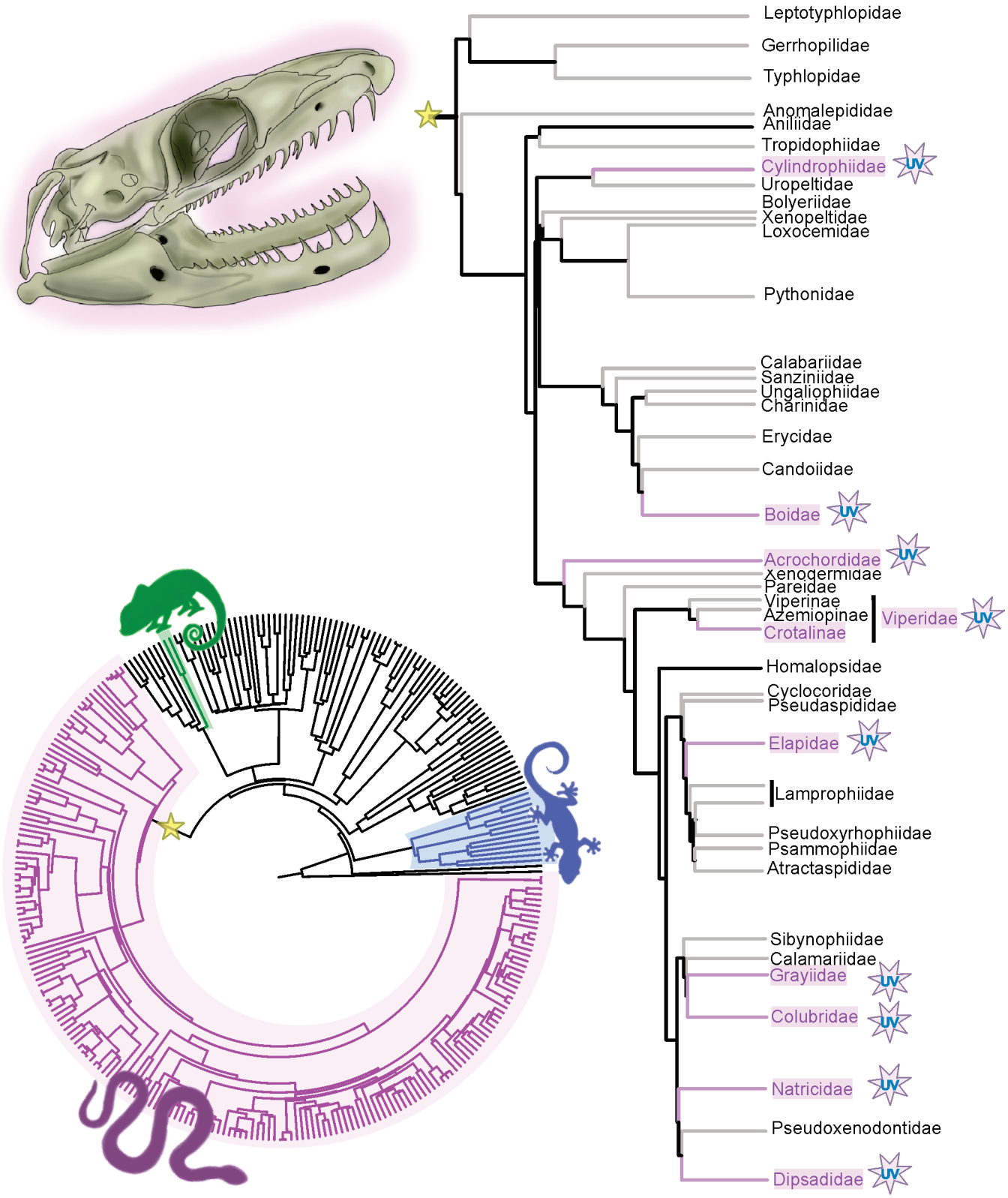

Figure 3. Phylogeny of Squamata (adapted from Burbrink et al. 2020) highlighting lineages in which UV fluorescence has been observed. The circle phylogeny highlights groups with observed skeletal fluorescence: green = chameleons; blue = geckos; purple = snakes). The snake phylogeny shows fluorescence observed in this study: purple = fluorescent families and subfamilies; black = fluorescence not observed; gray = not sampled. Yellow stars indicate the root of extant snakes in both trees. Snake skull graphic art by JMB. Note that groups not highlighted are not necessarily unable to fluoresce, and should be viewed only as an 'absence of fluorescence' in this study.

from outside the animal, this phenomenon could be nothing more than a byproduct of the compounds found in bone (i.e., no ecological or adaptive function). However, the taxa examined in this study have a variety of behaviors and occupy a range of niches, suggesting the possibility of a behavioral or ecological role of bone fluorescence in at least some species. For example, the cobra-like threat display of *Heterodon platirhinos*, during which the interstitial skin on the head and neck are stretched, could be enhanced by fluorescence of the underlying bones. Additionally, although not observed in this study, interstitial skin between scales is often visible during feeding, and some snakes (e.g., *Ahaetulla* spp.) will show colors of this skin during threat displays. Tubercles in chameleons are visible through thin layers of the epidermis (Prötzel et al. 2018), so skin stretching during threat displays or feeding could render fluorescent bones visible, accentuating the display or warding off predators of a vulnerable, feeding snake. Such functional assessments obviously would require understanding how conspecifics and predators (e.g., birds) perceive these wavelengths.

While beyond the scope of this largely opportunistic initial report on fluorescence of snake bones, we emphasize that functional hypotheses should be considered in future studies and will require testing of live snakes and additional taxa and the use of new equipment (long-pass filters, spectrophotometers). Subsequent research should focus on identifying the magnitude and wavelengths of emitted light in fresh snake tissues and including data on age and sex for live and/or preserved skeletal specimens would also be valuable. As mentioned, the observation of 'no fluorescence' in this study is not indicative that the bones of that species do not fluoresce, as bone-based fluorescence is likely widespread if not universal in snakes.

Our study provides the first evidence of skeletal fluorescence in snakes. We acknowledge that this was not unexpected in that these bones contain fluorescent elements. However, despite a few accounts of fluorescent scales in some leptotyphlopid, elapid, colubrid, and viperid species (Odate et al. 1959; Hulse, 1971; Seiko and Terai 2019), observations and studies of fluorescence in snakes as a whole are lacking. This study provides valuable information for how storage of skeletons in natural history collection could impact fluorescence in bones. We show that specimens in natural history collections fluoresced less and of a different spectrum compared to fresh DOR specimens. How those skeletons were treated upon arrival in the collections (e.g., bleaching, dermestid beetle cleaning) is unknown, but given that we were unable to assess any correlation between the time since collection of the specimen and fluorescence, future investigations should identify how different treatments for specimen preservation impact skeletal UV fluorescence. Our observations expand the avenues of research on fluorescence, which has been increasing across vertebrate taxa over the last decade, provide new records of lineages and species demonstrating fluorescence, and note the different intensities of fluorescence in older museum specimens when compared to fresh specimens. The number of invertebrate and vertebrate groups in which fluorescent tissues have been identified is continuously growing, and future organism-specific and comparative studies of biofluorescence will help shed light on its evolution and potential functional and ecological roles.

Acknowledgements

We thank F. Burbrink, D. Kizirian, and L. Vonnahme at the American Museum of Natural History for allowing us to visit the herpetology collection and check skeletal specimens, Raul Diaz (Southeastern Louisiana University) for helpful comments and suggestions regarding this work, and the New Jersey Fish & Wildlife for providing salvage permits (Nos. SW 2017040 and SW 2018011), which led to the observations found in this study. Funding for this work was provided by funds from Rutgers University-Newark to the Ruane Lab.

Literature Cited

Andrews, K., S.M. Reed, and S.E. Masta. 2007. Spiders fluoresce variably across many taxa. *Biology Letters* 3: 265–267. https://doi.org/10.1098/rsbl.2007.0016.

Anthes, N., J. Theobald, T. Gerlach, M.G. Meadows, and N.K. Michiels. 2016. Diversity and ecological correlates of red fluorescence in marine fishes. *Frontiers in Ecology and Evolution* 4: 126. https://doi.org/10.3389/fevo.2016.00126.

Arnold, K.E., I.P. Owens, and N.J. Marshall. 2002. Fluorescent signaling in parrots. *Science* 295: 92. https://doi.org/10.1126/science.295.5552.92.

Bachman, C.H. and E.H. Ellis. 1965. Fluorescence of bone. *Nature* 206: 1328–1331. https://doi.org/10.1038/2061328a0.

Bou-Abdallah, F., N.D. Chasteen, and M.P. Lesser. 2006. Quenching of superoxide radicals by green fluorescent protein. *Biochimica et Biophysica Acta* 1760: 1690–1695. https://doi.org/10.1016/j.bbagen.2006.08.014.

Bruinjé, A.C., F.E. Coelho, T.M. Paiva, and G.C. Costa. 2019. Aggression, color signaling, and performance of the male color morphs of a Brazilian lizard (*Tropidurus semitaeniatus*). *Behavioral Ecology* 73: 72. https://doi.org/10.1007/s00265-019-2673-0.

Burbrink, F.T., F.G. Grazziotin, R.A. Pyron, D. Cundall, S. Donnellan, F. Irish, S. Keogh, F. Kraus, R.W. Murphy, B. Noonan, C.J. Raxworthy, S. Ruane, A.R. Lemmon, E.M. Lemmon, and H. Zaher. 2020. Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology* 69: 502–520. https://doi.org/10.1093/sysbio/syz062.

Field, S.F., M.Y. Bulina, I.V. Kelmanson, J.P. Bielawski, and M.V. Matz. 2006. Adaptive evolution of multicolored fluorescent proteins in reef-building corals. *Journal of Molecular Evolution* 62: 332–339. https://doi.org/10.1007/s00239-005-0129-9.

Fonseca, P.J. 2014. Cicada acoustic communication, pp. 101–121. In: B. Hedwig (ed.), *Insect Hearing and Acoustic Communication*. Springer, Berlin, Germany. https://doi.org/10.1007/s00239-005-0129-9.

Frost, L.M., D.R. Butler, B. O'Dell, and V. Fet. 2001. A coumarin as a fluorescent compound in scorpion cuticle, pp. 365–368. In: V. Fet, P.A. Selden, and J.E. Dalingwater (eds.), *Scorpions 2001 in Memoriam Gary A. Polis*. British Arachnological Society, Burnham Beeches, Bucks, UK.

Fuentes, R.D., J. Ashcroft, H. Quintero-Arrieta, A. de Gracia, V. Gálvez, and A. Batista. 2021. First record of fluorescence in Colombian Long-tailed Snakes (*Enuliophis sclateri*) (Squamata: Dipsadidae) from Panama. *Reptiles & Amphibians* 28: 442–443. https://doi.org/10.17161/randa.v28i3.15595.

Gandía-Herrero, F., F. García-Carmona, and J. Escribano. 2005. Floral fluorescence effect. *Nature* 437: 334. https://doi.org/10.1038/437334a.

Garcia, C.M. and T. de Perera. 2002. Ultraviolet-based female preferences in a viviparous fish. *Behavioral Ecology and Sociobiology* 52: 1–6. https://doi.org/10.1007/s00265-002-0482-2.

Goutte, S., M.J. Mason, J. Christensen-Dalsgaard, F. Montealegre-Z., B.D. Chivers, F.A. Sarria-S., M.M. Antoniazzi, C. Jared, L.A. Sato, and L.F. Toledo. 2017. Evidence of auditory insensitivity to vocalization frequencies in two frogs. *Scientific Reports* 7: 12121. https://doi.org/10.1038/s41598-017-12145-5.

Goutte, S., M.J. Mason, M.M. Antoniazzi, C. Jared, D. Merle, L. Cazes, L.F. Toledo, H. el-Hafci, S. Pallu, H. Portier, S. Schramm, P. Gueriau, and M. Thoury. 2019. Intense bone fluorescence reveals hidden patterns in pumpkin toadlets. *Scientific Reports* 9: 1–8. https://doi.org/10.1038/s41598-019-41959-8.

Gruber, D.F., H.T. Kao, S. Janoschka, J. Tsai, and V.A. Pieribone. 2008. Patterns of fluorescent protein expression in scleractinian corals. *The Biological Bulletin* 215: 143–154. https://doi.org/10.2307/25470695.

Gruber, D.F. and J.S. Sparks. 2015. First observation of fluorescence in marine turtles. *American Museum Novitates* 3845: 1–8. https://doi.org/10.1206/3845.1.

Heinermann, P.H. 1984. Yellow intraocular filters in fishes. *Experimental Biology* 43: 127–147.

Hunt, S., A.T.D. Bennett, I.C. Cuthill, and R. Griffiths. 1998. Blue tits are ultraviolet tits. *Proceedings of the Royal Society of London B. Biological Sciences* 265: 451–455. https://doi.org/10.1098/rspb.1998.0316.

Hulse, A.C. 1971. Fluorescence in *Leptotyphlops humilis* (Serpentes: Leptotyphlopidae). *The Southwestern Naturalist* 16: 123–124. https://doi.org/10.2307/3670106.

Kohler, A.M., E.R. Olson, J.G. Martin, and P.S. Anich. 2019. Ultraviolet fluorescence discovered in New World flying squirrels (*Glaucomys*). *Journal of Mammalogy* 100: 21–30. https://doi.org/10.1093/jmammal/gyy177.

Kumagai, A., R. Ando, H. Miyatake, P. Greimel, T. Kobayashi, Y. Hirabayashi, T. Shimogori, and A. Miyawaki. 2013. A bilirubin-inducible fluorescent protein from eel muscle. *Cell* 153: 1602–1611. https://doi.org/10.1016/j.cell.2013.05.038.

Lamb, J.Y. and M.P. Davis. 2020. Salamanders and other amphibians are aglow with biofluorescence. *Scientific Reports* 10: 1–7. https://doi.org/10.1038/s41598-020-59528-9.

Lawrence, R.F. 1954. Fluorescence in Arthropoda. *Journal of the Entomological Society of Southern Africa* 17: 167–170.

Marshall, J. and S. Johnsen. 2017. Fluorescence as a means of colour signal enhancement. *Philosophical Transactions of the Royal Society B* 372: 20160335. https://doi.org/10.1098/rstb.2016.0335.

Maitland, D.P. and A.G. Hart. 2008. A fluorescent vertebrate: The Iberian wormlizard *Blanus cinereus* (Amphisbaenidae). *Herpetological Review* 39: 50–51.

Michiels, N.K., N. Anthes, N.S. Hart, J. Herler, A.J. Meixner, F. Schleifenbaum, G. Schulte, U. Siebeck, D. Sprenger, and M.F. Wucherer. 2008. Red fluorescence in reef fish: a novel signalling mechanism? *BMC Ecology* 8: 16. https://doi.org/10.1186/1472-6785-8-16.

Narins, P.M. 1990. Seismic communication in anuran amphibians. *Bioscience* 40: 268–274. https://doi.org/10.2307/1311263.

Nowogrodzki, A. 2017. First fluorescent frog found. *Nature* 543: 297. https://doi.org/10.1038/nature.2017.21616.

Odate S., Y. Tatebe, M. Obika, and T. Hama. 1959. Pteridine derivatives in reptilian skin. *Proceedings of the Japan Academy* 35: 567–570.

Olofsson, M., A. Vallin, S. Jakobsson, and C. Wiklund. 2010. Marginal eyespots on butterfly wings deflect bird attacks under low light intensities with UV wavelengths. *PLoS One* 5: e10798. https://doi.org/10.1371/journal.pone.0010798.

Pires, O.R., Jr., A. Sebben, E.F. Schwartz, S.W. Largura, C. Bloch, Jr., R.A.V. Morales, and C.A. Schwartz. 2002. Occurrence of tetrodotoxin and its analogues in the Brazilian frog *Brachycephalus ephippium* (Anura: Brachycephalidae). *Toxicon* 40: 761–766. https://doi.org/10.1016/S0041-0101(01)00279-3.

Prötzel, D., M. Heß, M.D. Scherz, M. Schwager, A. van't Padje, and F. Glaw. 2018. Widespread bone-based fluorescence in chameleons. *Scientific Reports* 8: 698. https://doi.org/10.1038/s41598-017-19070-7.

Paul, L. and R.W. Mendyk. 2021. Glow and behold: Biofluorescence and new insights on the tails of pitvipers (Viperidae: Crotalinae) and other snakes. *Herpetological Review* 52: 221–237.

Roth, M.S. and D.D. Deheyn. 2013. Effects of cold stress and heat stress on coral fluorescence in reef-building corals. *Scientific Reports* 3: 1421. https://doi.org/10.1038/srep01421.

Roth, M.S., M.I., Latz, R. Goericke, and D.D. Deheyn. 2010. Green fluorescent protein regulation in the coral *Acropora yongei* during photoacclimation. *Journal of Experimental Biology* 213: 3644–3655. https://doi.org/10.1242/jeb.040881.

Salih, A., A. Larkum, G. Cox, M. Kühl, and O. Hoegh-Guldberg. 2000. Fluorescent pigments in corals are photoprotective. *Nature* 408: 850–853. https://doi.org/10.1038/35048564.

Schindelin, J., I. Arganda-Carreras, E. Frise, V. Kaynig, M. Longair, T. Pietzsch, S. Preibisch, C. Rueden, S. Saalfeld, B. Schmid, J.-Y. Tinevez, D.J. White, V. Hartenstein, K. Eliceiri, P. Tomancak, and A. Cardona. 2012. Fiji: an open-source platform for biological-image analysis. *Nature Methods* 9: 676–682. https://doi.org/10.1038/nmeth.2019.

Seiko, T. and Y. Terai. 2019. Fluorescence emission in a marine snake. *Galaxea, Journal of Coral Reef Studies* 21: 7–8. https://doi.org/10.3755/galaxea.21.1_7.

Shen, Y., D. Zhu, W. Lu, B. Liu, Y. Li, and S. Cao. 2018. The characteristics of intrinsic fluorescence of type I collagen influenced by collagenase I. *Applied Sciences* 8: 1947. https://doi.org/10.3390/app8101947.

Sloggett, J.J. 2018. Field observations of putative bone-based fluorescence in a gecko. *Current Zoology* 64: 319–320. https://doi.org/10.1093/cz/zoy033.

Sparks, J.S., R.C. Schelly, W.L. Smith, M.P. Davis, D. Tchernov, V.A. Pieribone, and D.F. Gruber. 2014. The covert world of fish biofluorescence: a phylogenetically widespread and phenotypically variable phenomenon. *PLoS One* 9: e83259. https://doi.org/10.1371/journal.pone.0083259.

Stover, D.A. and B.C. Verrelli. 2011. Comparative vertebrate evolutionary analyses of type I collagen: potential of COL1a1 gene structure and intron variation for common bone-related diseases. *Molecular Biology and Evolution* 28: 533–542. https://doi.org/10.1093/molbev/msq221.

Swaraldahab, M.A. and A.M. Christensen. 2016. The effect of time on bone fluorescence: implications for using alternate light sources to search for skeletal remains. *Journal of Forensic Sciences* 61: 442–444. https://doi.org/10.1111/1556-4029.12978.

Surov, A.V. and A.N. Maltsev. 2016. Analysis of chemical communication in mammals: zoological and ecological aspects. *The Biological Bulletin* 43: 1175–1183. https://doi.org/10.1134/S1062359016110157.

Taboada, C., A.E. Brunetti, F.N. Pedron, F.C. Neto, D.A. Estrin, S.E. Bari, L.B. Chemes, N.P. Lopes, M.G. Lagorio, and J. Faivovich. 2017. Naturally occurring fluorescence in frogs. *Proceedings of the National Academy of Sciences of the United States of America* 114: 3672–3677. https://doi.org/10.1073/pnas.1701053114.

Tah, M.M.T.M., C.L. Puan, M.F. Chuang, S.N. Othman, and A. Borzée, A. 2020. First record of ultraviolet fluorescence in Bent-toed Gecko *Cyrtodactylus quadrivirgatus* (Gekkonidae: Sauria). *Herpetology Notes* 13: 211–212.