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Photoluminescence in mammal fur: 111 years of research

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Photoluminescence in the pelage of mammals, a topic that has gained considerable recent research interest, was first documented in the 1700s and reported sporadically in the literature over the last century. The first detailed species accounts were of rabbits and humans, published 111 years ago in 1911. Recent studies have largely overlooked this earlier research into photoluminescent mammalian taxa and their luminophores. Here we provide a comprehensive update on existing research on photoluminescence in mammal fur, with the intention of drawing attention to earlier pioneering research in this field. We provide an overview on appropriate terminology, explain the physics of photoluminescence, and explore pigmentation and the ubiquitous photoluminescence of animal tissues, before touching on the emerging debate regarding visual function. We then provide a chronological account of research into mammalian fur photoluminescence, from the earliest discoveries and identification of luminophores to the most recent studies. While all mammal fur is likely to have a general low-level photoluminescence due to the presence of the protein keratin, fur glows luminously under ultraviolet light if it contains significant concentrations of tryptophan metabolites or porphyrins. Finally, we briefly discuss issues associated with preserved museum specimens in studies of photoluminescence. The study of mammal fur photoluminescence has a substantial history, which provides a broad foundation on which future studies can be grounded.

Key words: fluorescence, hair, luminophore, pelage, phosphorescence, ultraviolet

Photoluminescence in biology results from photons hitting an organic object and causing a change in the energy levels of the electrons within certain molecules, resulting in the reemission of light at a higher wavelength as the electrons return to their ground energy level (Murthy and Virk 2014; Visser and Rolinski 2014). In the oceans, photoluminescence is widespread in corals (Mazel and Fuchs 2003), fish (Sparks et al. 2014), and other organisms (Shimomura et al. 1962; Mazel et al. 2004). On land, photoluminescence occurs in some fungi (Soop 2005), bacteria (Hurley et al. 2019), and ubiquitously in the chlorophyl of plants (Krause and Weis 1991). Photoluminescence has also been recorded in terrestrial invertebrates (Kloock 2005), amphibians (Lamb and Davis 2020), reptiles (Prötzel et al. 2021), birds (Derrien and Turchini 1925), and mammals (Bolliger 1944; Pine et al. 1985; Kohler et al. 2019).

Recent reviews on biological photoluminescence have focused on terrestrial plants, invertebrates, birds, and marine organisms (Lagorio et al. 2015; Macel et al. 2020)–and it appears that what is known about external photoluminescence in mammals is very limited. Only Jeng (2019) and Croce (2021) mention mammals, with examples beginning in 1985, and many of these studies appear to relate specifically to photoluminescence induced by ultraviolet light (termed UV-induced photoluminescence; Toussaint et al. 2023), although this is not always the case. External UV-induced photoluminescence in the pelage of mammals is most well-known from opossums in the Americas (Pine et al. 1985). However, the discovery of mammalian photoluminescence predates the work on opossums, with historical publications documenting photoluminescence in a range of species and the isolation of some of the luminophores involved. Specifically, the term ‘luminophore’ (Kricka

2003) encompasses groups of atoms that luminesce, whether they are specifically fluorophores (colored compounds called chromophores that fluoresce; Tomalia et al. 2019) or phosphors (chromophores that phosphoresce; Valeur and Berberan-Santos 2011), or whether they may exist in both states of excitation. Although most natural substances contain a photoluminescent component, they vary in brightness, and it is the conspicuously bright photoluminescent compounds that are generally thought of as being luminophores (Tomalia et al. 2019).

Although the extent of brightly photoluminescent fur across mammalian taxa has not been comprehensively documented, the phenomenon has been sporadically recorded across 14 of 20 extant mammal orders (Table 1). A timeline of discovery (Fig. 1), divides these orders into the mammal families in which species with luminescent pelage have been documented.

In this review, we convey the historical extent of research on mammalian photoluminescence, filling the gap left by recent reviews (e.g., Lagorio et al. 2015; Jeng 2019; Macel et al. 2020). Photoluminescence is commonly perceived to only be induced by ultraviolet light. However, photoluminescence can also be excited and emitted entirely in the ultraviolet (Millington 2020), entirely in the visible (Lamb and Davis 2020), in the infrared (Huang et al. 2006), or even in the X-ray wavelengths of the electromagnetic radiation spectrum (Rakovan 2021). Most documented biological photoluminescence is triggered by blue or blue/green light (Johnsen 2012; Lagorio et al. 2015; Marshall and Johnsen 2017). Although much photoluminescence in mammal fur has been identified using ultraviolet light, the precise range of excitation wavelengths is unknown for many of the historical observations of photoluminescent fur. Photoluminescence can result from various excitation wavelengths for example, keratin in sheep (*Ovis aries*) wool responds to maximal excitation of 430 nm, in the visible violet–blue light (Melhuish and Smith 1993), while porphyrins are maximally excited at 405 (Croce 2021) or 400 nm, on the cusp of ultraviolet and violet and extending either side, with lesser excitation from 450 to 700 nm, well into the visible range (Goldoni 2002; Hamchand et al. 2021). Therefore, we use the general term 'photoluminescence', rather than 'UV-induced photoluminescence', throughout the text to refer to the phenomena across mammal pelage.

Table 1.—Mammalian orders in which photoluminescent fur has been documented.

Order	Citations
Monotremata	Reinhold 2020; Anich et al. 2021
Didelphimorphia	Pine and Abravaya 1978; Pine et al. 1985; Toussaint et al. 2023
Dasyuromorphia	Reinhold 2020
Peramelemorphia	Reinhold 2020; Reinhold 2021
Diprotodontia	Bolliger 1944; Nicholls and Rienits 1971; Reinhold 2021
Primates	Stübel 1911; Daly et al. 2009; Millington 2020
Lagomorpha	Stübel 1911; Tumlison and Tumlison 2021
Rodentia	Rebell et al. 1956; Kohler et al. 2019; Olson et al. 2021
Eulipotyphla	Derrien and Turchini 1925; Hamchand et al. 2021
Artiodactyla	Hirst 1927; Smith et al. 1994; Millington 2020
Chiroptera	Udall et al. 1964; Reinhold 2022
Perissodactyla	Posudin 2007
Pholidota (scales)	Jeng 2019
Carnivora	Latham 1953; Millington 2020; Tumlison and Tumlison 2021

We first describe photoluminescence and explain the distinction between fluorescence and phosphorescence, and how photoluminescence differs from bioluminescence, then discuss how the physics of photoluminescence might operate in the context of terrestrial illumination. Next, we introduce the chemistry of mammal fur regarding the pigments that give color to fur in white light and the presence of luminophores that effect photoluminescence. Although a possible visual function of luminophores in fur has not been specifically studied, we also briefly discuss hypotheses recently put forward in this emerging debate. We then document the history of mammal photoluminescence research, from earliest discoveries to the present day, attributing photoluminescence predominantly to the two groups of luminophores that are so far known from fur, namely tryptophan metabolites and porphyrin derivatives (Box 1). Finally, we add a cautionary note about over-reliance on museum specimens for the documentation of photoluminescence in fur. Our review brings together a wealth of historical knowledge that remains relevant in the context of ongoing discoveries.

The Physics of Luminescence

Terminology of photoluminescence relating to fur: fluorescence versus phosphorescence.—Luminescence is the blanket term for cold light (Wiedemann 1888), which can be emitted via either chemiluminescence or photoluminescence. In biology, the generation of true glow-in-the-dark light only occurs by chemiluminescence (bioluminescence), a chemical reaction catalyzed by an enzyme (e.g., luciferase) or photoprotein (Abercrombie et al. 1992). Photoluminescence, including phosphorescence and fluorescence, is the reemission of light from matter after excitation by absorption of an external light source (Valeur and Berberan-Santos 2011).

Phosphorescence is a process whereby the electrons of the phosphorescent molecule temporarily reside in an intermediate state before returning to the ground energy level (Valeur and Berberan-Santos 2011). Phosphorescent objects initially need light to glow, and are often defined simply by the length of time the glow lasts after the light source is turned off (Harvey 1957; Johnsen 2012). In phosphorescence, the duration of light emission is typically $>10^{-8}$ s (i.e., tens of nanoseconds to seconds; Murthy and Virk 2014; Visser and Rolinski 2014).

Interestingly, Stokes (1852) coined the term 'fluorescence' to describe the biological property that he identified and reported in white feathers, shells, quills, bristles, skin, nails, horn, bone, and most unpigmented organic materials. However, 'phosphorescence' of such materials had been recorded earlier by de Mairan (1715) and Wilson and Beccari (1775). Giese and Leighton (1937) also found some of these materials 'feathers', 'shells', 'skin', 'nails', 'horn', and 'bone' to *phosphoresce* for 2–25 s. This phosphorescence was attributed to the aromatic amino acids tryptophan and tyrosine in proteins (Warren 1982).

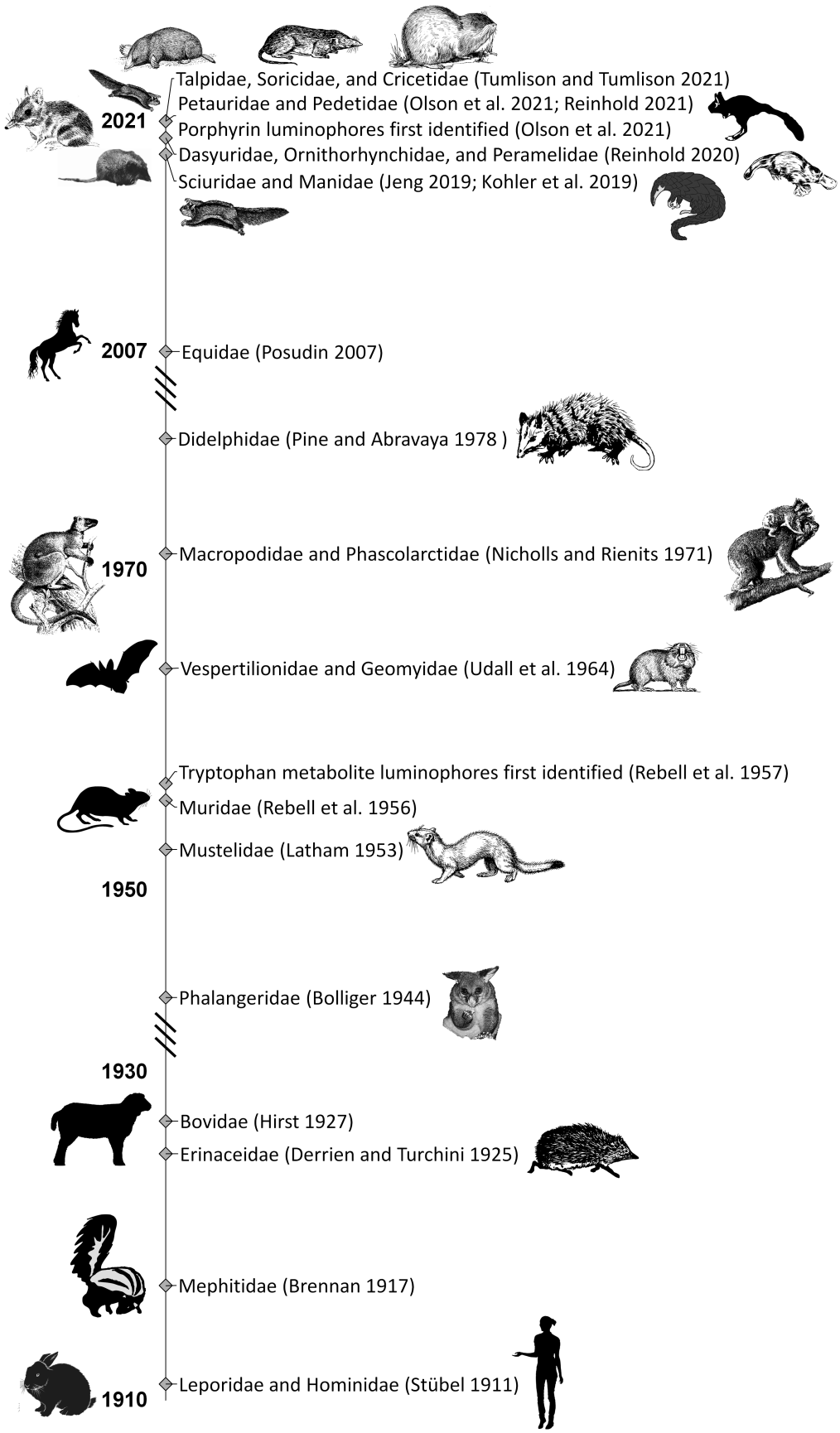

Fig. 1.—Discovery timeline of luminescence in the pelage of mammal families. Antechinus image, David T. Wilson; bandicoot image, Linda M. Reinhold; springhare image, Revolutionrock 1976, https://commons.wikimedia.org/wiki/File:Pedetes_capensis_(South_African_Springhare).jpg; https://creativecommons.org/licenses/by-sa/4.0/deed.en.

BOX 1.—DESCRIPTION OF THE TWO KNOWN LUMINOPHORE GROUPS FOR FUR

Tryptophan metabolites

Tryptophan is an essential amino acid, meaning that mammals are unable to synthesize it endogenously and must obtain it from their diet (Yao et al. 2011). Tryptophan is metabolized in tissues via well-defined steps under enzymatic control (Nicholls and Rienits 1971). When metabolized, tryptophan produces a suite of molecules that photoluminesce in various colors. Pine et al. (1985) suspected different tryptophan metabolites to be mostly responsible for the multi-colored photoluminescence in opossums. Tryptophan metabolism can be affected by steroid hormones or an excess of tryptophan in the diet, so the resulting luminophores have the potential to vary with sex, hormone cycles, and diet (Pine et al. 1985). Various tryptophan metabolites in fur that give rise to visible photoluminescence have absorption peaks of ~320 nm (brushtail possums; Nicholls and Rienits 1971), 358 nm (laboratory rats; Rebell 1966), and 380 nm (mink fur, rabbit fur, cashmere wool, sheep wool, and human hair; Millington 2020). Some tryptophan metabolites present in pelage can emit phosphorescence as well as fluorescence (Leaver 1978; Smith and Melhuish 1985).

Porphyrins

Porphyrins are large heterocyclic organic molecules that act as precursors to hemoglobin and can be synthesized internally by biological organisms (Neves and Galván 2020). In birds, porphyrins can produce red, pink, brown, and green pigmentation (Riedler et al. 2014). Additionally, porphyrins function as chlorophyl intermediates in plant photosynthesis (e.g., protoporphyrin IX; Lee et al. 2018), and dietary chlorophyl can break down into porphyrin-based compounds that transfer into red photoluminescence in the skin of mice (Weagle et al. 1988; Croce 2021).

Spectral analysis of protoporphyrin has identified absorption maxima at 390–398 nm (Kessel and Rossi 1982), with absorption at 400 nm for porphyrins in general (Goldoni 2002). These maximal absorption wavelengths correlate to the 395 nm emission wavelength of the most common modern ultraviolet flashlights (Kohler et al. 2019; Pynne et al. 2021). Lesser absorption bands extend up to 700 nm (Goldoni 2002). This means that the optimal excitation wavelengths for porphyrin photoluminescence are higher than those for tryptophan metabolites. Porphyrins are also weakly phosphorescent, some with afterglows of 70 s and longer being recorded (Gouterman and Khalil 1974). The near-infrared phosphorescence of these porphyrins, however, is excited by wavelengths of 485–633 nm (cyan–yellow–orange; Gouterman and Khalil 1974).

Fluorescence occurs when electrons in fluorescent molecules temporarily jump to an electronically excited higher energy state before they decay back to their original ground state. The outgoing photon is usually emitted at a longer wavelength than the incoming wavelength (Herman et al. 2015). In fluorescence, the duration of light emission is usually $<10^{-8}$ s (nanoseconds), so appears to cease as soon as the excitation light source is stopped (Murthy and Virk 2014).

However, both long-lived fluorescence and short-lived phosphorescence can last for several hundred nanoseconds, meaning the length of light emission alone is not always enough to define the difference between fluorescence and phosphorescence (Valeur and Berberan-Santos 2011). It was not until 1929 that the fluorescence observed in some animals by Stokes (1852) was separated from phosphorescence at the atomic level (Perrin 1929). Even though fluorescence and short-lived phosphorescence differ in their atomic processes, there is little practical difference between them, and in such cases where the processes have not been differentiated, the distinction between the two is sometimes viewed as arbitrary (Harvey 1957). However, the interchangeable use of these two terms in biology can cause confusion.

Historically, phosphorescence was applied to cold light in general (Harvey 1957); however, the newer distinction of fluorescence now seems to have taken its place as the default term unless phosphorescence is demonstrated. In describing any light-induced glowing where the atomic state of the luminophores is unknown, it would be more prudent to use the encompassing term photoluminescence. In a biological context, the prefix ‘bio-’ may be added to any of these words, but would be applicable to live animals more than to specimens examined in museum studies. However, bio- would also imply that the photoluminescence is coming from the organism, whereas photoluminescence is initiated by photons external to the organism.

For clarity, bio- should be reserved for the chemiluminescent process of 'bioluminescence' (Johnsen 2012; Toussaint et al. 2023).

Practicalities of seeing photoluminescence: excitation and visibility.—It is a popular misconception that ultraviolet vision is a prerequisite for seeing the kind of photoluminescence that emits at visible wavelengths (Toussaint et al. 2023). However, the process of photoluminescence transfers photons from the invisible into the visible spectrum (Stokes 1852). Therefore, seeing fluorescence and phosphorescence only requires that the *emitted* wavelengths are within the visible wavelength range of the observer. Consequently, the ability to see photoluminescence is not special. It is not ultraviolet *vision* that is needed to make this phenomenon visible, but rather an external light source, such as ultraviolet light.

When a photoluminescent object absorbs ultraviolet light in an environment that is otherwise dark and reemits light in the visible spectrum, the object will look as if it is glowing. This light appears to come from the object itself because the incident light source is invisible to the naked eye (Baird 2015). The emitted wavelength may also be unusual in the ambient light spectrum illuminating the surroundings, resulting in increased contrast of the object. In the oceans, this means turning the ubiquitous blue light into rare red light (Johnsen 2012; Marshall and Johnsen 2017), a conversion effected by diurnal reef fish (Michiels et al. 2008). A blue glow may blend in to ambient lighting, whereas a red glow would stand out.

In terrestrial environments, photoluminescence (and bioluminescence) may provide the only visible colors during otherwise monochromatic twilight (Pohland 2007). The color contrast of a photoluminescent object against its background would make the light emission more noticeable. Even if an animal is color blind, it could potentially detect the brightness of photoluminescence or its increased contrast against the background. Humans frequently exploit this phenomenon by using photoluminescence to deliberately make objects such as traffic signs appear brighter, particularly in low light conditions (Schnell et al. 2001; Baird 2015). Photoluminescence can also result in a brighter overall appearance without a change in color (Marshall and Johnsen 2017), intensifying the saturation of colors. When photoluminescence occurs in the strong and multiple excitation wavelengths of sunlight, it can add to the appearance of brightness of the visible light reflecting off an object (Baird 2015). Sunlight delivers excitation wavelengths of 330–500 nm at enough intensity to trigger most natural photoluminescence (Marshall and Johnsen 2017). However, the intense ambient light of sunlight may also act to overpower more subtle photoluminescence (Viitala et al. 1995). Without the overpowering yellow rays of the sun, moonlight (Kloock 2005) and the lower wavelength light of twilight (Taboada et al. 2017) have the potential to excite such subtle photoluminescence.

While excitation of photoluminescence in the oceans is widely accepted (Michiels et al. 2008), how photoluminescence is placed in a terrestrial environment is less well understood. While humans regularly employ photoluminescent pigments to make objects 'hi-vis' (Schnell et al. 2001; Baird 2015), our knowledge of how natural photoluminescence may be seen in a terrestrial landscape is relatively limited. Forest structure, low sun angles, and some weather conditions can create terrestrial environments where overpowering middle wavelengths are lessened (Endler 1993). In closed forest shade during the day, light is greenish due to being shone through or reflected from leaves. However, in woodland shade, light also does not come directly from the sun, but holes in the canopy instead let in bluish light from the sky (Endler 1993). Although some habitat and environmental conditions may promote more of the lower wavelengths of light relative to others (Silberglied 1979), no studies have measured whether these levels of ultraviolet, purplish, or blue light actually trigger the excitation of natural photoluminescence at a level that can be detected by animals.

Pigmentation and the Ubiquitous Background Photoluminescence of Mammal Fur

In mammals, the coloration of fur is largely driven by pigments (chromophores; Hubbard and Kropf 1965) that are insoluble in water and absorb light of different wavelengths. Fur in general absorbs ultraviolet radiation due to a characteristic of keratin, a structural protein in hair (Dawson et al. 2014). How light or dark a coat is can change with climate, season, or through the lifetime of an animal (Pawelek and Körner 1982; Mills and Patterson 2009). The dominant coloration in mammal fur is from melanin, a group of natural pigments that animals synthesize in the fur follicles by oxidizing the amino acid tyrosine, and incorporate into the shaft as the fur grows (Pawelek and Körner 1982). Melanin largely limits color patterns to brown, tan, gray, black, white (absence of melanin), red, and yellow (Newman et al. 2005; Penteriani and Delgado 2017). Eumelanin gives fur its characteristic black or brown coloration, while pheomelanin provides yellow and red (Pawelek and Körner 1982). When the black wool of sheep is exposed to light, the black eumelanin is converted into red or yellow pheomelanin (Sumner et al. 1994). Other pigments include cinnabarinic acid, which contributes to the red pigmentation of fur in red kangaroos (*Macropus rufus*; Nicholls and Rienits 1971); and an organic iron pigment, trichosiderin, which is involved in the coloration of human red hair (Flesch and Rothman 1945; Barnicot 1956).

An increasing number of pigments are now known to also photoluminesce (Hudon 2005). Even eumelanin photoluminesces with ultraviolet, visible, and infrared wavelengths (Kozikowski et al. 1984; Mosca et al. 1999; del Rosal et al. 2016). For example, the melanin-rich black fur of a black and white domestic cat (*Felis catus*) photoluminesces in the infrared with greater intensity than the white fur (Huang et al. 2006). However, fur photoluminescence by ultraviolet excitation shows the opposite pattern in striped possums (*Dactylopsila trivirgata*), with the white stripes, and not the black, emitting visible photoluminescence (Reinhold 2021). Because melanin otherwise masks UV-induced photoluminescence, the fur lacking melanin displays the brighter photoluminescence when

exposed to ultraviolet light. The presence of melanin quenches luminophores and their visible photoluminescence (Rebell et al. 1957; Rebell 1966; Daly et al. 2009), so fur containing more melanin absorbs more ultraviolet light, yet reemits less (Posudin 2007).

In addition to masking, melanin can also have a photoprotective effect on photoluminescence (Daly et al. 2009). Fur is susceptible to photobleaching, correlated with the degradation of tryptophan (Lennox and Rowlands 1969), which results in decreased photoluminescence (Smith 1995). Tryptophan-based photoluminescence gradually degrades under light exposure over months (Schäfer et al. 1997; Posudin 2007; Longo et al. 2013). Porphyrin molecules are significantly more prone to photodegradation, and photobleaching of porphyrins can occur within minutes of sunlight exposure (Galván et al. 2016). This extreme lability means that porphyrin photoluminescence will quickly degrade in the fur of animals exposed to sunlight (Toussaint et al. 2023).

Keratin is a high-sulfur, fibrous structural protein comprising a filament-matrix structure embedded in an amorphous keratin matrix (Wang et al. 2016). Forming as a pleated sheet, β-keratin is found in feathers, beaks, and claws. Forming as a helix, α-keratin is found in fur, wool, hair, quills, nails, and horns (Wang et al. 2016). Wool fibers are composed of 82% high-cystine (a sulphur-containing disulfide-bonded dimer of the semiessential amino acid cysteine) keratinous proteins, 17% low-cystine nonkeratinous material, and 1% lipids and polysaccharides (Rippon 2013). Keratin not only functions as a scaffold for luminophores, but the disulfide bonds in the high-cystine content partially quench the tryptophan fluorescence and phosphorescence in wool (Smith 1995). Dietary supplementation of cystine increases the cystine content in the wool (Reis and Schinckel 1963), which would hence result in reduced photoluminescence. Wool keratin itself photoluminesces cyan upon excitation by violet–blue light (Melhuish and Smith 1993).

Pine et al. (1985) reported a yellow–green photoluminescence–which they surmised to be from keratin–coming from all opossum, rodent, and human hair under a fluorescence microscope, even if photoluminescence was not induced in the whole pelt with ultraviolet light. Photoluminescence in keratin is caused by the photoluminescent amino acids tryptophan, tyrosine, and phenylalanine involved in its protein structure (Smith et al. 1980; Longworth 1983). These are also the only three aromatic amino acids known to cause both fluorescence and phosphorescence of proteins in a free state (Konev 1967; Pailthorpe and Nicholls 1972). This background fluorescence and/or phosphorescence of the amino acids in keratin means that fur, in general, photoluminesces to some extent unless it is masked by melanin.

Mammals can also display photoluminescence not just of their own production, but as a host for other organisms. Photoluminescence in fungi is a widespread phenomenon, and photoluminescence in human and other mammal tissues can also be caused by (and used to diagnose) fungal infection (Margarot and Deveze 1925; Rao et al. 2008). An important example is orange–yellow photoluminescence in the microlesioned wings of Holarctic bats with white-nose syndrome, a disease caused by the fungal pathogen *Pseudogymnoascus destructans*, because this photoluminescence can help to rapidly diagnose bats infected with this pathogen (Turner et al. 2014)–the fungal luminophore was identified as lumichrome, a degradation product of riboflavin (Flieger et al. 2016). Bacterial infection by *Staphylococcus aureus* and *Pseudomonas* spp. on human skin is also diagnosable by detection of photoluminescence (Hurley et al. 2019), and *Propionibacterium* spp. produce coproporphyrin III (Cornelius and Ludwig 1967).

Photoluminescence in animal tissues is so ubiquitous it is the norm, not the exception (Stübel 1911). Natural photoluminescence is a characteristic of biological substances such as enamel, chitin, collagen, elastin, lipofuscins, reticulin fibers, and urine (Stübel 1911; Kellie et al. 2004; Viegas et al. 2007). A substantive literature surrounds photoluminescence in bone of humans and other mammals affected by pathologies of congenital erythropoietic porphyria, which apparently occurs normally in eastern fox squirrels (*Sciurus niger*) without ill effects (Turner 1937; Wolff et al. 2005; Rivera and Leung 2008; Neves and Galván 2020).

The molecular trends associated with potential luminophores is a difficult topic to address beyond the basic general description that molecules in which electrons can be elevated to an excited electronic state may fluoresce or phosphoresce if the excited electrons can return to the electronic ground state via radiative decay by spontaneous emission. Sumita et al. (2022) highlight that several intricately intertwined factors, including reactions with oxygen molecules, molecular collisions, intra-/intermolecular electron transfer, and aggregation may deactivate the molecule as it travels in the excited state. This makes it difficult to correlate luminescence with molecular structure and, therefore, there are no clear guidelines for creating or predicting luminescent molecules. In biological luminophores, molecules containing planar conjugated systems, such as aromatic rings, have the potential to luminesce and are regularly observed due to the common occurrence of $\pi^* \leftarrow \pi$ (bonding pi (π) to antibonding pi (π^*) molecular orbital) transitions. However, the potential luminescence of these molecules cannot be easily predicted.

An intrinsic photoluminescence (both fluorescence and phosphorescence) has been described in a range of abiotic and biological molecules, including amino acids (tryptophan, tyrosine, phenylalanine), and peptides and proteins containing these amino acids (Tomalia et al. 2019). This generic blue glow is so pervasive that it can confuse the recognition of synthetic luminophores used in medical imaging (Tomalia et al. 2019). For example, lysozyme- and elastin-derived peptides photoluminesce blue when excited by wavelengths in the 350–400 nm range (Niyangoda et al. 2017; Tomalia et al. 2019). Furthermore, Toussaint et al. (2023) recorded blue photoluminescence in the pelage of all 23 mammal specimens they examined with emission spectroscopy, but they suspected it was at least partially due to keratins.

The ubiquitous background photoluminescence of mammal fur would seem to obscure a distinction between a 'photoluminescent' and a 'non-photoluminescent' mammal, as even mammals regarded as non-photoluminescent may still display this phenomenon when examined microscopically (e.g., Pine et al. 1985). Hirst (1927) saw the difference in photoluminescence of textile fibers as a matter of degree, making only a qualitative distinction between most fibers that yielded ordinary photoluminescence, and those that glowed with brilliant color. Those fibers that contain sufficient concentration of luminophores to be regarded as photoluminescent or not are ill-defined. Therefore, future studies could include spectroscopy to quantitatively measure the intensity of photoluminescence. However, how photoluminescent an animal is under particular excitations would only be relevant if the phenomenon is visually significant in nature. It is the cases of the stunningly bright human-visible photoluminescence that have recently attracted speculation on visual function (Kohler et al. 2019).

Does Fur Photoluminescence Have a Visual Function?

Stübel (1911) doubted that photoluminescence could be biologically significant given that it is so common in both external and internal tissues. A visual function for photoluminescent fur has not been tested, nor have studies explored whether natural twilight or moonlight can excite the luminophores in fur. However, several hypotheses have been proposed, namely that photoluminescence is: (1) adaptive in nocturnal–crepuscular (especially snowy) light environments (Kohler et al. 2019); (2) used in intraspecific communication (Kohler et al. 2019; Pynne et al. 2021); or (3) an antipredator strategy (Kohler et al. 2019; Anich et al. 2021; Olson et al. 2021; Pynne et al. 2021). Several studies have focused on intraspecific communication in other animals, including: budgerigars (*Melopsittacus undulatus*; Arnold et al. 2002); ornate jumping spiders (*Cosmophasis umbratica*; Lim et al. 2007); fairy wrasse (*Cirrhilabrus solorensis*; Gerlach et al. 2014); and crested auklets (*Aethia cristatella*; Douglas et al. 2021). However, these have used either artificial ultraviolet lighting or artificial photoluminescent paint. Studies using natural photoluminescence under natural lighting are rare and results are mixed. One study found that flying insects avoided photoluminescent scorpions (*Vaejovis* spp.) on a full moon (Kloock 2005), whereas another found that house crickets (*Acheta domesticus*) did not react differently to photoluminescent scorpions (*Centruroides granosus*) under a half moon (Gálvez et al. 2020). Until field experiments using real fur and natural lighting are conducted, whether a visual function exists or not remains speculative.

Photoluminescence in Fur: An Historical Account

Some of the earliest documentations of photoluminescence in hair were those of de Mairan (1715), which seemed to confirm the earlier experiments of Wilson and Beccari (1775), and later Stokes (1852). Hair, fur, and wool phosphoresced after excitation by sunlight (Wilson and Beccari 1775). The first mammals for which photoluminescent pelage properties were comprehensively described by species were European rabbits (*Oryctolagus cuniculus*) and humans (*Homo sapiens*; Stübel 1911; Fig. 1). Black rabbit fur did not photoluminesce, but unpigmented fur photoluminesced intense light yellow under excitation by 300–400 nm light. Similarly, in humans, pigmented hair did not photoluminesce, but white hair photoluminesced bright blue and white. Only tissues containing pigment or hemoglobin and its derivatives had their photoluminescence suppressed (Stübel 1911).

In 1917, 'phosphorescence' (bioluminescence in this context) was reported from large black, and black and white skunks (Mephitidae) in deserted mine tunnels in Arizona, United States (Brennan 1917; Fig. 1). Red luminescence emanated from the head, turning blue down the rest of the body and tail (Brennan 1917).

Red photoluminescence, believed to be caused by porphyrins, was then recorded in the quills, but not in the soft fur, of young European hedgehogs (*Erinaceus europaeus*; Derrien and Turchini 1925; Fig. 1). In the same year (1925), a bright green photoluminescence was noted in the hair cortex of some humans and cats, and later in guinea pigs (*Cavia porcellus*), that was ultimately due to a dermatophyte (keratin-eating) fungal infection rather than intrinsic to the fur itself (Margarot and Deveze 1925; Stockdale et al. 1965).

Interest then turned to textile fibers, with ordinary sheep wool noted as having a bright blue photoluminescence (Hirst 1927; Fig. 1). The wool of Australian merino sheep photoluminesced yellow with bluish-white tips. Sheep wool phosphorescence with an afterglow lasting 12 s was described in 1943 (Millson 1943). Fluorescence of wool was yellowish white, whereas phosphorescence was colorless.

Photoluminescence in the fur of a marsupial, the Australian Common Brushtail Possum (*Trichosurus vulpecula*), was first described by Bolliger (1944; Fig. 1). An otherwise colorless substance gave a brilliant sky-blue photoluminescence to the fur shafts (Bolliger 1944). An extraction of this substance photoluminesced in daylight, visible to the human eye. The sky-blue photoluminescence also exuded from the sweat gland walls and coated the skin over the entire animal except for the soles (i.e., the palmar and plantar surfaces) of the paws (Bolliger 1944). Male possums also had vivid salmon red photoluminescence of the fur between the head and middle of the rump, whereas this salmon red photoluminescence was localized to small tufts around the shoulders in females. Newly regrown fur on the dorsal surface or flanks of possums photoluminesced vivid red or purple, whereas fur on the ventral surface photoluminesced pink. Bolliger (1944) also reported fur photoluminescence to be common in other mammals, but with lesser intensity.

In the 1950s, vivid lavender photoluminescence was proposed as a taxonomic character to distinguish the brown summer coats of least weasels (*Mustela nivalis*), recorded as photoluminescent, from two other sympatrically occurring weasel species, ermines (*M. erminea*) and long-tailed weasels

(*Neogale frenata*) that were observed not to photoluminesce (Latham 1953; Fig. 1). Brilliant photoluminescence was also observed in the fur of albino laboratory (Norway) rats (*Rattus norvegicus*; Rebell et al. 1956; Fig. 1). The photoluminescence was confined within the fur itself, with no similar photoluminescence emitted from the skin.

Using paper chromatography, the luminophores extracted from rat fur were identified as the tryptophan metabolites kynurenine, kynurenic acid, and *N*-α-acetyl-L-kynurenine (Rebell et al. 1957; Rebell 1966). Washed fur from albino lab rats had 3.3 mg of kynurenine (including *N*-α-acetyl-L-kynurenine) per 1 g of fur, cinnamon rats had 3.4 mg per 1 g, and black rats had 4.6 mg per 1 g (Rebell 1966). Although the fur of cinnamon and black lab rats contained equivalent amounts of luminophores, the melanin in the fur of rats with black coats quenched the visible photoluminescence. Approximately 1,000 times as much kynurenine was concentrated in the fur of photoluminescent rats than in non-photoluminescent white house mice (*Mus musculus*) or guinea pigs, which still yielded low concentrations of this luminophore (Rebell 1966). Extracts of guinea pig, rabbit, and cat fur also displayed a weak bluish photoluminescence (Rebell et al. 1956).

Udall et al. (1964) reported on photoluminescence studies in a large number of museum specimens of both Old and New World rodents. Both black rats (*R. rattus*) and Norway rats photoluminesced brilliant green–blue. However, members of related genera, such as Malayan spiny rats (*Maxomys rajah*) and African multimammate mice (*Mastomys* spp.) did not photoluminesce. North American pocket gophers of the genus *Geomys* photoluminesced (Fig. 1), whereas pocket gophers of the genus *Thomomys* did not. Udall et al. (1964) also found that photoluminescence was a useful taxonomic character for distinguishing similar species of African gerbils (Gerbillinae) that would otherwise be challenging to discriminate. Museum specimens of least brown bats (*Myotis subulatus*) photoluminesced (Fig. 1), but three other species of *Myotis* did not. Live and freshly dead individuals of various Trinidadian bats also showed variation in photoluminescent colors and intensities (Udall et al. 1964).

Kynurenine was also identified as one of the luminophores in the photoluminescent blue fur of Goodfellow's tree kangaroos (*Dendrolagus goodfellowi*) from New Guinea (Nicholls and Rienits 1971; Fig. 1). Tree kangaroo fur contained an additional tryptophan metabolite, the purple-photoluminescing 3-hydroxyanthranilic acid (Watanabe et al. 1972), which also produced photoluminescence in the fur of common brushtail possums (Nicholls and Rienits 1971). Photoluminescent pigments were exuded from follicles into the internal structure of the fur shafts, and similar secretions were also manufactured in a skin gland in the tree kangaroos. Unpigmented fur of red kangaroos had a moderate blue photoluminescence (Nicholls and Rienits 1971). By this time, photoluminescence was also already known in the fur of other marsupials, such as koalas (*Phascolarctos cinereus*), although Nicholls and Rienits (1971) did not provide specific references for these studies. Nicholls and Rienits (1971) could not completely describe the photoluminescent compounds in the species they investigated, and highlighted that the extent of photoluminescence in marsupials was generally unknown. Australian research into the fur photoluminescence of wildlife species did not progress beyond this study until the 2020s (Reinhold 2020, 2021).

Photoluminescence in mammals was next identified in Brazilian long-nosed short-tailed opossums (*Monodelphis scalops*; Pine and Abravaya 1978; Fig. 1), Virginia opossums (*Didelphis virginiana*; Meisner 1983), and 21 other opossum species from the Americas (Pine et al. 1985). Opossum fur photoluminesced purple, lavender, blue, yellow–green, pink–orange, salmon, pink, rose, and/or red under excitation by 366 nm light. In some specimens, all of the fur exhibited photoluminescence, but more brightly on the ventral surface of the animal, which often photoluminesced a different color to that of the dorsal surface. In other specimens, the pattern of photoluminescence in fur involved spots or a stripe. Photoluminescence characteristics of some taxa were so consistent to genera and species that they could be used as taxonomic characters (Pine et al. 1985). Photoluminescence of specimens did not differ appreciably with age or season, but in one species, the Gray Four-eyed Opossum (*Philander opossum*), females and adult males photoluminesced, whereas juvenile males did not.

Pine et al. (1985) also used thin-layer chromatography of extracts of photoluminescent blue pigment from the fur of the Bare-tailed Woolly Opossum (*Caluromys philander*) to identify the luminophore as 3-hydroxyanthranilic acid, the same tryptophan metabolite found in the fur of both common brushtail possums and Goodfellow's tree kangaroos (Nicholls and Rienits 1971). Fluorescence microscopy revealed that the photoluminescence emanated from inside the medulla and cortex of the hair shaft of little water opossums (*Lutreolina crassicaudata*). Pine et al. (1985) examined Australian marsupials and monotremes, but found they did not photoluminesce to the same extent as opossums. Pine et al. (1985) also studied weasels, but in contrast to Latham (1953), ermines photoluminesced, whereas least weasels did not.

Photoluminescence in the hair of Ukranian sportive and Przewalski horses, and Scotch and Estonian ponies (*Equus ferus*) was examined with microfluorometry spectroscopy in 2007 (Posudin 2007; Fig. 1). The body hair of the horses photoluminesced with more than twice the intensity of their manes and tails. The photoluminescence of pony hair was less intense than that of horse hair, but their tails were the most photoluminescent. Photoluminescence intensity also depended on coat color (Posudin 2007).

Humans and production fur animals have continued to be the focus of much of the ongoing research on mammal pelage photoluminescence. The wool of sheep was again recorded phosphorescing, this time blue–cyan when excited by 330–360 nm ultraviolet light, thought to be from *N*-formylkynurenine (Smith and Melhuish 1985). At least three luminophores are thought to produce phosphorescence in wool, two of which are derived directly or indirectly from tryptophan (Collins 1992). The tryptophan in wool also reacts with α-keto acids, producing

β-carbolines that photoluminesce blue and yellow/green when excited by ultraviolet and blue wavelengths (Smith et al. 1994). However, even with the extensive amount of research conducted on sheep wool, the luminophores have not all been identified with certainty, with even the contribution of *N*-formylkynurenine in doubt (Millington 2006). Millington (2020) warned that intrinsic blue photoluminescence (Niyangoda et al. 2017; Chen et al. 2018) occurring in wool keratin at similar excitation and emission wavelengths as *N*-formylkynurenine could not be ruled out.

Using spectrophotometry to match photoluminescence peaks, the tryptophan metabolites kynurenine, *N*-formylkynurenine, and 3-hydroxykynurenine were identified as luminophores in human hair (Daly et al. 2009). Hair pigmented with melanin did not photoluminescence as strongly as unpigmented hair, agreeing with the initial observation of Stübel (1911) that it was unpigmented human hair that displayed blue and white photoluminescence. However, the 330 nm emission of tryptophan metabolite photoluminescence in human hair was weaker than that of commercial fur animals, such as mink (*Neogale vison*), European rabbit, Cashmere goat (*Capra aegagrus hircus*), and sheep (Millington 2020).

In 2019, there was a resurgence of interest in the fur photoluminescence of wildlife species with the publication of color photographs of New World flying squirrels (*Glaucomys* spp.; Kohler et al. 2019; Tumlison et al. 2019; Fig. 1). The squirrels photoluminesced bright pink under 395 nm illumination, mostly on the ventral body surface and tail. Kohler et al. (2019) ranked the brightness and extent of photoluminescence on each specimen using a qualitative scale based on visual observation of photographs (rather than spectrophotometric analysis of fur) to investigate patterns of photoluminescence among individuals. Although there was variation between individuals, intensity of photoluminescence could not be clearly divided on species, sex, month, year, or latitude. Live animals in the wild photoluminesced comparably to museum specimens, although they were not compared using the same photographic qualitative scale (Kohler et al. 2019). Diurnal nonflying squirrels did not photoluminescence; however, a subsequent study elicited some photoluminescence from both gray squirrel (*Sciurus carolinensis*) and red squirrel (*Tamiasciurus hudsonicus*) fur extracts when excited at 350 nm (Hughes et al. 2022). Twenty unidentified potential luminophores were also found to be present in the fur of non-photoluminescent squirrels (hinting that non-photoluminescent animals carry the potential luminophores, but they are only activated in photoluminescent animals) and were inconsistently present in the fur of all photoluminescent flying squirrels (Hughes et al. 2022). Excitation spectroscopy identified only porphyrin S-411 in the fur of *Glaucomys* spp. (Toussaint et al. 2023). Pink photoluminescence was also found later in the red-cheeked flying squirrel (*Hylopetes spadiceus*) and the smoky flying squirrel (*Pteromyscus pulverulentus*) of southeast Asia (Toussaint et al. 2023).

In addition, photographs of light-blue photoluminescence in the fur of Coxing's white bellied rats (*Niviventer coninga*) and the scales of Chinese pangolins (*Manis pentadactyla*; Fig. 1) came from Taiwan (Jeng 2019). In the following year, photoluminescence was identified in platypuses (*Ornithorhynchus anatinus*; Reinhold 2020; Anich et al. 2021; Fig. 1), antechinus (*Antechinus* spp.), northern brown bandicoots (*Isoodon macrourus*), and long-nosed bandicoots (*Perameles nasuta*) in Australia (Reinhold 2020; Fig. 1). The list was soon extended to include striped possums, Krefft's gliders (*Petaurus notatus*), mosaic-tailed rats (*Melomys* spp.) and bush rats (*R. fuscipes*; Reinhold 2021). Photoluminescence was absent from the skin and whiskers in these species. The live, wild ground-dwelling mammals from these studies photoluminesced either brindled bright pink or bluish white over the entire fur–whereas in arboreal gliders, the mild bluish-white photoluminescence was confined to their ventral surfaces (Reinhold 2020, 2021).

Attention returned to Africa with the discovery of photoluminescence in the fur cuticle of two species of springhares (*Pedetes* spp.; Olson et al. 2021; Fig. 1). Both live and museum animals displayed patchy orange–red photoluminescence, although this photoluminescence had a greater intensity in live animals. There was no sexual dichromatism of photoluminescence, and patterns were consistent over time for an individual. Thin-layer chromatography and high-performance liquid chromatography (HPLC) of photoluminescent red fur extracts of the South African Springhare (*P. capensis*) identified some of the luminophores as porphyrins (uroporphyrin I, uroporphyrin III, heptacarboxylporphyrin, and coproporphyrin I; Olson et al. 2021).

Excitation spectroscopy also identified uroporphyrin I or uroporphyrin III in the pink–red fur of the Guyanan Short-tailed Opossum (*Monodelphis brevicaudata*) and Linnaeus' Mouse Opossum (*Marmosa murina*; Toussaint et al. 2023). HPLC, ultraviolet-visible spectral, and electrospray ionization mass spectrometry analyses confirmed European hedgehog luminophores as coproporphyrin III, uroporphyrin III, and protoporphyrin IX (Hamchand et al. 2021). Hamchand et al. (2021) suspected that Actinobacteria in the spine microbiome of European hedgehogs could be producing the porphyrin photoluminescence. However, the porphyrin photoluminescence in European hedgehog spines is distributed in the walls of the inner lumen, a pattern inconsistent with commensal bacteria (Toussaint et al. 2023).

One of the most recent studies reported fur photoluminescence under ultraviolet light excitation (385–395 nm) in several mammal species from Arkansas, United States (Tumlison and Tumlison 2021). Based on museum specimens, the study examined dry pelts, alcohol-preserved and an untreated frozen specimen of the Eastern Mole (*Scalopus aquaticus*). All specimens of this species across preservation techniques photoluminesced similarly greenish. In dry pelts of southern short-tailed shrews (*Blarina carolinensis*), the tips of the fur photoluminesced greenish, whereas the underfur of muskrats (*Ondatra zibethica*) photoluminesced yellow–green (Tumlison and Tumlison 2021; Fig. 1). Two additional rabbit species, eastern cottontails (*Sylvilagus floridanus*) and swamp rabbits (*S. aquaticus*), displayed small amounts of cyan photoluminescence (Tumlison and Tumlison 2021). However, the fur of the mountain hare (*Lepus timidus*) did not photoluminesce (Toussaint et al. 2023).

The documentation from Tumlison and Tumlison (2021) of mammal species that did not photoluminescence was particularly informative. While not settling the debate on which of least weasels and ermines is the photoluminescent species (Latham 1953; Pine et al. 1985), Tumlison and Tumlison (2021) established that, within long-tailed weasels with brown summer pelage, one specimen photoluminesced greenish, whereas the other specimen did not photoluminescence. Therefore, intraspecies variation may account for the previous conflicting observations, but larger sample sizes in the previous studies should have detected such an anomaly. The observations of Toussaint et al. (2023) of lavender photoluminescence in ermines (white winter pelage) agreed with those of Pine et al. (1985). Latitudinal differences in seasonal coat phases may have played a role in the original discrepancy.

American mink fur did not photoluminescence (Tumlison and Tumlison 2021), whereas mink fur did in Millington (2020); however, that study examined white mink fur, whereas the Tumlison and Tumlison (2021) minks were brown. Raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*) also did not photoluminescence (Tumlison and Tumlison 2021). Furthermore, while Norway rats photoluminesced, 11 other species of rodent did not. Wild-caught brown to grayish (Tumlison R., Henderson State University, Arkadelphia, Arkansas, personal communication, March 2022) house mice did not photoluminesce, giving broader substantiation to the observation of Rebell (1966) of non-photoluminescence in captive-bred albino mice.

The absence of photoluminescence in the eight species of bat examined by Tumlison and Tumlison (2021) is not surprising given that Udall et al. (1964) found photoluminescence in only one of four *Myotis* species preserved as museum specimens. However, Udall et al. (1964) had found bats to be particularly photoluminescent when examining live and freshly dead mammals. Tumlison and Tumlison (2021) likewise found none of the luminescence in museum specimens of striped skunks (*Mephitis mephitis*) or spotted skunks (*Spilogale putorius*) as had Brennan (1917) in live animals.

The observed lack of photoluminescence in the fur of Baird's pocket gopher (*Geomys breviceps*; Tumlison and Tumlison 2021) sets this species apart from records of photoluminescence in other *Geomys* species (Udall et al. 1964; Pynne et al. 2021). Pynne et al. (2021) suggested that the orange–pink photoluminescence in the fur of five species of pocket gophers–including species of *Cratogeomys*, *Geomys*, and *Thomomys*–could be a consequence of bacteria, sequestration from eating photoluminescent blue roots, or a result of orange–pink photoluminescent soil adhering to the fur. The anomaly of *Thomomys* spp. photoluminescence, as observed by Pynne et al. (2021) but not by Udall et al. (1964), indicates that the sporadic observations documented so far are not yet adequate to piece together a taxonomic pattern of photoluminescence in pocket gophers, nor in other mammalian taxa.

A Cautionary Note on Photoluminescence in Museum Specimens

Many of the recent studies on mammalian photoluminescence have been based on preserved museum specimens (e.g., Kohler et al. 2019; Anich et al. 2021; Tumlison and Tumlison 2021; Toussaint et al. 2023). While an invaluable resource, museum specimen photoluminescence should be verified by fresh material where possible. In particular, photoluminescence can fade over time with or without exposure to light (Pine et al. 1985; Olson et al. 2021; Tumlison and Tumlison 2021), and porphyrins in museum specimens are often not detectable (Hill 2010). As a result, absence of (Toussaint et al. 2023), or quantitative comparisons between, porphyrin photoluminescence of specimens cannot be made with certainty. In addition, while the loss of fur photoluminescence that occurs during various chemical preservation procedures has not been quantified, these procedures could drastically affect luminophores and their resulting photoluminescence (Tumlison and Tumlison 2021). Artificial photoluminescent stains, particularly bright greenish or yellowish, are also sometimes inadvertently added to museum specimens during taxidermy (Pohland 2007). X-ray fluorescence toxin-testing by some museums routinely uncovers methyl bromide, and to a lesser extent mercury (Kehoe and Becker 2017), both of which emit green photoluminescence (BOC Sciences 2022; Department of Physics, Imperial College/Science Photo Library 2022). If the photoluminescence of museum specimens is more vivid, or covers different areas than that of fresh animals, contamination should be suspected and tested for.

Summary

Photoluminescence in fur was first observed in the 1700s, by de Mairan (1715) and Wilson and Beccari (1775). Since Stübel (1911), photoluminescence has been described in detail for numerous species from more than two-thirds of all mammal orders. Wool has been documented both fluorescing and phosphorescing (Collins 1992). The most comprehensive work on wildlife species was the description of photoluminescence in opossum fur in 1985 (Pine et al. 1985). Until 2019, vividly photoluminescent pelage was already known from mammals such as rabbits, possums, tree kangaroos, opossums, weasels, rats, bats, humans, and sheep. Since the publication of color photographs of photoluminescent flying squirrels in 2019 (Kohler et al. 2019), the accessibility of the internet and availability of ultraviolet flashlights has led to an increasing number of mammal species being documented with photoluminescent fur.

Animal tissues in general, including keratin proteins (Stübel 1911), exhibit a low-level photoluminescence, but some chemical compounds present in fur generate an additional bright photoluminescence. Photoluminescence differs in degrees of brightness (Hirst 1927), making a definition of how bright mammal fur has to be (over and above that of the generic background glow) to be termed photoluminescent, or when luminescent molecules can be classified as luminophores, difficult.

Luminophores can be incorporated into fur at the follicle (Nicholls and Rienits 1971; Pine et al. 1985) and can reside in different sections of the fur shaft (Pine et al. 1985; Olson et al. 2021). Two classes of luminophore are currently known to cause photoluminescence in mammal fur–tryptophan metabolites, and porphyrin and its derivatives. Tryptophan metabolites photoluminesce in a rainbow of colors (Pine et al. 1985), while porphyrins in mammal fur photoluminesce pink–orange–red (Olson et al. 2021). Few species of mammal have had the chemical composition of their fur analyzed (Nicholls and Rienits 1971; Olson et al. 2021), so more luminophores may be active than are currently known.

The colors and patterns of photoluminescence mostly seem to be species-specific. Intraspecies variation is not correlated with any particular factor (e.g., flying squirrels [Kohler et al. 2019; or springhares [Olson et al. 2021]) apart from some species with sexual dichromatism (e.g., common brushtail possums [Bolliger 1944]; gray and black four-eyed opossums [Pine et al. 1985]). Why the fur of some species contains luminophores at orders of magnitude greater than others, and why equal amounts of luminophores are incorporated into fur whether or not the resulting photoluminescence will be quenched by melanin, is unknown (Rebell 1966). As to why so many species of mammal photoluminesce, and whether the incorporation of luminophores into fur serves a visual purpose (Kohler et al. 2019), is a byproduct of some metabolic process (Toussaint et al. 2023), or is a largely dormant property incidental to functions of fur chemistry (Stübel 1911) awaits investigation.

What we have learned from 111 years of investigations into photoluminescent fur can be used as a basis for the next wave of research. Big picture research can investigate patterns of species-specific levels of luminophores over and above the background levels found in fur in general. Quantification of luminophores per gram of fur (Rebell 1966) will enable comparison between species. Much more needs to be done at the molecular level to determine the causes of photoluminescence and the conditions in which potential luminophores are activated. More detailed research should concentrate on the metabolic pathways that incorporate the property of brilliant photoluminescence into fur. Knowing whether luminophores are energetically expensive to deposit into fur may help to determine whether they have an adaptive function, perhaps correlated with body condition (Galván et al. 2018; Camacho et al. 2019), or whether incorporation into fur is an efficient way to expel metabolic waste products (Toussaint et al. 2023). Studies correlating diet and hormone concentrations to photoluminescent qualities will reveal if photoluminescence can be manipulated. Finally, measurements on whether the photoluminescence of fur can be excited by twilight or moonlight should be conducted to establish the photophysical basis for experimentation on potential visual function.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

Literature Cited

Abercrombie M., Hickman M., Johnson M.L., Thain M. 1992. The new Penguin dictionary of biology. Penguin Books, Ringwood, Australia.

Anich P.S., Anthony S., Carlson M., Gunnelson A., Kohler A.M., Martin J.G., Olson E.R. 2021. Biofluorescence in the platypus (*Ornithorhynchus anatinus*). Mammalia 85:179–181.

Arnold K.E., Owens I.P., Marshall N.J. 2002. Fluorescent signaling in parrots. Science 295:92.

Baird C. 2015. What makes a "fluorescent" highlighter marker so bright? Science questions with surprising answers. West Texas A&M University. https://wtamu.edu/~cbaird/sq/2015/05/15/what-makes-a-fluorescent-highlighter-marker-so-bright/. Accessed 19 April 2021.

Barnicot N.A. 1956. The pigment, trichosiderin, from human red hair. Nature 177:528–529.

BOC Sciences. 2022. BODIPY 493/503 methyl bromide. https://probes.bocsci.com/bodipy-493503-methyl-bromide-item-712.html. Accessed 12 July 2022.

Bolliger A. 1944. On the fluorescence of the skin and the hairs of *Trichosurus vulpecula*. Australian Journal of Science 7:35.

Brennan P. 1917. Will o' the wisp. Scientific American 116:261.

Camacho C., Negro J.J., Redondo I., Palacios S., Sáez-Gómez P. 2019. Correlates of individual variation in the porphyrin-based fluorescence of red-necked nightjars (*Caprimulgus ruficollis*). Scientific Reports 9:19915.

Chen X., Luo W., Ma H., Peng Q., Yuan W.Z., Zhang Y. 2018. Prevalent intrinsic emission from nonaromatic amino acids and poly (amino acids). Science China Chemistry 61:351–359.

Collins S. 1992. Studies on the natural fluorescence of wool and wool grease. Dissertation, City University of London, London, United Kingdom.

Cornelius C.E. III, Ludwig G.D. 1967. Red fluorescence of comedones: production of porphyrins by *Corynebacterium acnes*. Journal of Investigative Dermatology 49:368–370.

Croce A.C. 2021. Light and autofluorescence, multitasking features in living organisms. Photochem 1:67–125.

Daly S., Bianchini R., Polefka T., Jumbelic L., Jachowicz J. 2009. Fluorescence and coloration of grey hair. International Journal of Cosmetic Science 31:347–359.

Dawson T.J., Webster K.N., Maloney S.K. 2014. The fur of mammals in exposed environments; do crypsis and thermal needs necessarily conflict? The polar bear and marsupial koala compared. Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology 184:273–284.

Department of Physics, Imperial College. 2022. SCIENCEphotoLIBRARY. Emission spectrum of mercury. https://www.sciencephoto.com/media/1675/view/emission-spectrum-of-mercury. Accessed 10 July 2022.

Derrien E., Turchini J. 1925. Nouvelles observations de fluorescences rouges chez les animaux. Comptes Rendus Séances Société Biologie 92:1030–1031.

Douglas H.D. III, Ermakov I.V., Gellermann W. 2021. Brighter is better: bill fluorescence increases social attraction in a colonial seabird and reveals a potential link with foraging. Behavioral Ecology and Sociobiology 75:144.

Endler J.A. 1993. The color of light in forests and its implications. Ecological Monographs 63:1–27.

Flesch P., Rothman S. 1945. Isolation of an iron pigment from human red hair. Journal of Investigative Dermatology 6:257–270.

Flieger M., Bandouchova H., Cerny J., Chudíčková M., Kolarik M., Kovacova V., Martínková N., Novák P., Šebesta O., Stodůlková E. 2016. Vitamin B2 as a virulence factor in *Pseudogymnoascus destructans* skin infection. Scientific Reports 6:33200.

Galván I., Camarero P.R., Mateo R., Negro J.J. 2016. Porphyrins produce uniquely ephemeral animal colouration: a possible signal of virginity. Scientific Reports 6:39210.

Galván I., Delgado M.D.M., Camarero P.R., Mateo R., Lourenco R., Penteriani V. 2018. Feather content of porphyrins in Eurasian eagle owl (*Bubo bubo*) fledglings depends on body condition and breeding site quality. Integrative Zoology 13:569–578.

Gálvez D., Nieto C., Samaniego P. 2020. Test of the prey-attraction hypothesis for the scorpion fluorescence. Neotropical Biodiversity 6:172–177.

Gerlach T., Sprenger D., Michiels N.K. 2014. Fairy wrasses perceive and respond to their deep red fluorescent coloration. Proceedings of the Royal Society of London, B: Biological Sciences 281:20140787.

Giese A.C., Leighton P.A. 1937. Phosphorescence of cells and cell products. Science 85:428–429.

Goldoni A. 2002. Porphyrins: fascinating molecules with biological significance. ELETTRA Highlights 2001:64–65.

Gouterman M., Khalil G.E. 1974. Porphyrin free base phosphorescence. Journal of Molecular Spectroscopy 53:88–100.

Hamchand R., Lafountain A.M., Büchel R., Maas K.R., Hird S.M., Warren M., Frank H.A., Brückner C. 2021. Red fluorescence of European hedgehog (*Erinaceus europaeus*) spines results from free-base porphyrins of potential microbial origin. Journal of Chemical Ecology 47:588–596.

Harvey E.N. 1957. A history of luminescence from the earliest times until 1900. Vol. 44. Memoirs of the American Philosophical Society, Philadelphia, Pennsylvania, USA.

Herman B., Frohlich V.E.C., Lakowicz J.R., Murphy D.B., Spring K.R., Davidson M.W. 2015. Fluorescence microscopy. Basic concepts in fluorescence. National High Magnetic Field Laboratory, The Florida State University. https://micro.magnet.fsu.edu/primer/techniques/fluorescence/fluorescenceintro.html. Accessed 12 May 2021.

Hill G. 2010. Bird colouration. National Geographic, Washington, District of Columbia, USA.

Hirst H.R. 1927. Ultra-violet radiation as an aid to textile analysis. Journal of the Textile Institute Transactions 18:T369–T375.

Huang Z., Zeng H., Hamzavi I., Alajlan A., Tan E., McLean D.I., Lui H. 2006. Cutaneous melanin exhibiting fluorescence emission under near-infrared light excitation. Journal of Biomedical Optics 11:034010.

Hubbard R., Kropf A. 1965. On the colors of visual pigment chromophores. The Journal of General Physiology 49:381–385.

Hudon J. 2005. Considerations in the conservation of feathers and hair, particularly their pigments. In: Proceedings of the CAC/ACCR 31st Annual Conference (Fur trade legacy. The preservation of organic materials), Jasper, Alberta, Canada; p. 127–147.

Hughes B., Bowman J., Stock N.L., Burness G. 2022. Using mass spectrometry to investigate fluorescent compounds in squirrel fur. PLoS One 17:e0257156.

Hurley C.M., McClusky P., Sugrue R.M., Clover J.A., Kelly J.E. 2019. Efficacy of a bacterial fluorescence imaging device in an outpatient wound care clinic: a pilot study. Journal of Wound Care 28:438–443.

Jeng M.L. 2019. Biofluorescence in terrestrial animals, with emphasis on fireflies: a review and field observation. In: Suzuki H., editor. Biochemistry. Vol. 4, bioluminescence—analytical applications and basic biology. IntechOpen, London, United Kingdom; p. 87–111.

Johnsen S. 2012. The optics of life: a biologist's guide to light in nature. Princeton University Press, Princeton, New Jersey, USA.

Kehoe A.B., Becker M.J. 2017. Arsenic and old pelts: deadly pesticides in museum collections. History of Anthropology Newsletter 41. http://histanthro.org/notes/arsenic-and-old-pelts/. Accessed 11 July 2022.

Kellie A., Dain S.J., Banks P.B. 2004. Ultraviolet properties of Australian mammal urine. Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 190:429–435.

Kessel D., Rossi E. 1982. Determinants of porphyrin-sensitized photooxidation characterized by fluorescence and absorption spectra. Photochemistry and Photobiology 35:37–41.

Kloock C.T. 2005. Aerial insects avoid fluorescing scorpions. Euscorpius–Occasional Publications in Scorpiology 2005(21):1–7.

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

Konev S.V. 1967. Fluorescence and phosphorescence of proteins and nucleic acids. Udenfriend S., translation editor. Plenum Press, New York City, New York, USA.

Kozikowski S., Wolfram L., Alfano R. 1984. Fluorescence spectroscopy of eumelanins. IEEE Journal of Quantum Electronics 20:1379–1382.

Krause G.H., Weis E. 1991. Chlorophyll fluorescence and photosynthesis: the basics. Annual Review of Plant Biology 42:313–349.

Kricka L.J. 2003 Optical methods: a guide to the "-essences". American Association for Clinical Chemistry, Washington, District of Columbia, USA.

Lagorio M.G., Cordon G.B., Iriel A. 2015. Reviewing the relevance of fluorescence in biological systems. Photochemical & Photobiological Sciences 14:1538–1559.

Lamb J.Y., Davis M.P. 2020. Salamanders and other amphibians are aglow with biofluorescence. Scientific Reports 10:2821.

Latham R.M. 1953. Simple method for identification of least weasel. Journal of Mammalogy 34:385–385.

Leaver I.H. 1978. On the room temperature phosphorescence of wool keratin. Photochemistry and Photobiology 27:439–443.

Lee T.C., Shih T.H., Huang M.Y., Lin K.H., Huang W.D., Yang C.M. 2018. Eliminating interference by anthocyanins when determining the porphyrin ratio of red plant leaves. Journal of Photochemistry and Photobiology, B: Biology 187:106–112.

Lennox F.G., Rowlands R.J. 1969. Photochemical degradation of keratins. Photochemistry and Photobiology 9:359–367.

Lim M.L., Land M.F., Li D. 2007. Sex-specific UV and fluorescence signals in jumping spiders. Science 315:481.

Longo V.M., da Silva Pinheiro A., Sambrano J.R., Agnelli J.A.M., Longo E., Varela J.A. 2013. Towards an insight on photodamage in hair fibre by UV-light: an experimental and theoretical study. International Journal of Cosmetic Science 35:539–545.

Longworth J.W. 1983. Intrinsic fluorescence of proteins. In: Cundall R.B., Dale R.E., editors. Time-resolved fluorescence spectroscopy in biochemistry and biology. Plenum Press, New York City, New York, USA; p. 651–778.

Macel M.L., Ristoratore F., Locascio A., Spagnuolo A., Sordino P., D'Aniello S. 2020. Sea as a color palette: the ecology and evolution of fluorescence. Zoological Letters 6:1–11.

de Mairan J.J.D. 1715. Dissertation sur la cause de la lumiere des phosphores et des noctiluques. Qui a remporté le prix à l'Academie Royale des Belles Lettres. Sciences & Arts de Bordeaux, Pour l'Année, Paris, France.

Margarot J., Deveze P. 1925. Aspect de quelques dermatoses lumiere ultraparaviolette. Note preliminaire. Bulletin de la Société des Sciences Médicales et Biologiques de Montpellier 6:375–378.

Marshall J., Johnsen S. 2017. Fluorescence as a means of colour signal enhancement. Philosophical Transactions of the Royal Society of London, B: Biological Sciences 372:20160335.

Mazel C.H., Cronin T.W., Caldwell R.L., Marshall N.J. 2004. Fluorescent enhancement of signaling in a mantis shrimp. Science 303:51.

Mazel C.H., Fuchs E. 2003. Contribution of fluorescence to the spectral signature and perceived color of corals. Limnology and Oceanography 48:390–401.

Meisner D.H. 1983. Psychedelic opossums: fluorescence of the skin and fur of *Didelphis virginiana* Kerr. Ohio Journal of Science 83:4.

Melhuish W.H., Smith G.J. 1993. Photobleachable fluorescent species in wool keratin. Journal of the Society of Dyers and Colourists 109:163–165.

Michiels N.K., Anthes N., Hart N.S., Herler J., Meixner A.J., Schleifenbaum F., Schulte G., Siebeck U.E., Sprenger D., Wucherer M.F. 2008. Red fluorescence in reef fish: a novel signalling mechanism? BMC Ecology 8:16.

Millington K.R. 2006. Photoyellowing of wool. Part 1: factors affecting photoyellowing and experimental techniques. Coloration Technology 122:169–186.

Millington K.R. 2020. Anomalous fluorescence of white hair compared to other unpigmented keratin fibres. International Journal of Cosmetic Science 42:289–301.

Mills M.G., Patterson L.B. 2009. Not just black and white: pigment pattern development and evolution in vertebrates. Seminars in Cell & Developmental Biology 20:72–81.

Millson H.E. 1943. The phosphorescence of textile fibres and other substances. Textile Colorist 65:495–497, 503–506.

Mosca L., De Marco C., Fontana M., Rosei M.A. 1999. Fluorescence properties of melanins from opioid peptides. Archives of Biochemistry and Biophysics 371:63–69.

Murthy K.V., Virk H.S. 2014. Luminescence phenomena: an introduction. In: Virk H.S., editor. Defect and diffusion forum. Vol. 347. Trans Tech Publications Ltd; p. 1–34.

Neves A.C.O., Galván I. 2020. Models for human porphyrias: have animals in the wild been overlooked? Some birds and mammals accumulate significant amounts of porphyrins in the body without showing the injurious symptoms observed in human porphyrias. Bioessays 42:2000155.

Newman C., Buesching C.D., Wolff J.O. 2005. The function of facial masks in "midguild" carnivores. Oikos 108:623–633.

Nicholls E.M., Rienits K.G. 1971. Tryptophan derivatives and pigment in the hair of some Australian marsupials. International Journal of Biochemistry 2:593–603.

Niyangoda C., Miti T., Breydo L., Uversky V., Muschol M. 2017. Carbonyl-based blue autofluorescence of proteins and amino acids. PLoS One 12:e0176983.

Olson E.R., ET AL. 2021. Vivid biofluorescence discovered in the nocturnal springhare (Pedetidae). Scientific Reports 11:4125.

Pailthorpe M.T., Nicholls C.H. 1972. ESR studies of the low temperature irradiation of keratin and its component amino acids. Photochemistry and Photobiology 15:465–477.

Pawelek J.M., Körner A.M. 1982. The biosynthesis of mammalian melanin: the regulation of pigment formation, the key to disorders such as albinism and piebaldism, may also offer some clues for the treatment of melanoma. American Scientist 70:136–145.

Penteriani V., Delgado M.D.M. 2017. Living in the dark does not mean a blind life: bird and mammal visual communication in dim light. Philosophical Transactions of the Royal Society of London, B: Biological Sciences 372:20160064.

Perrin F. 1929. The fluorescence of solutions – molecular induction. Polarization and duration of emission. Photochemistry. Annals of Physics, EDP Sciences 10:169–275.

Pine R.H., Abravaya J.P. 1978. Notes on the Brazilian opossum *Monodelphis scalops* (Thomas) (Mammalia: Marsupialia: Didelphidae). Mammalia 42:379–382.

Pine R.H., Rice J.E., Bucher J.E., Tank D.J., Greenhall A.M. 1985. Labile pigments and fluorescent pelage in didelphid marsupials. Mammalia 49:249–256.

Pohland G. 2007. Spectral data of avian plumage. Dissertation, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany.

Posudin Y. 2007. Practical spectroscopy in agriculture and food science. Science Publishers, Enfield, Connecticut, USA.

Prötzel D., Heß M., Schwager M., Glaw F., Scherz M.D. 2021. Neon-green fluorescence in the desert gecko *Pachydactylus rangei* caused by iridophores. Scientific Reports 11:297.

Pynne J.T., Castleberry S.B., Conner L.M., Piper C.W., Parsons E.I., Gitzen R.A., Duncan S.I., Austin J.D., McCleery R.A. 2021. Ultraviolet biofluorescence in pocket gophers. The American Midland Naturalist 186:150–155.

Rakovan J. 2021. Coming to terms with fluorescence: a short glossary of common terms in the context of mineral fluorescence. Rocks & Minerals 96:20–23.

Rao S., Rajkumar A., Ehtesham M., Prathiba D. 2008. Autofluorescence: a screening test for mycotic infection in tissues. Indian Journal of Pathology and Microbiology 51:215–217.

Rebell G. 1966. Kynurenine in rat hair. Nature 209:913–914.

Rebell G., Lamb J.H., Mahvi A., Lee H.R. 1957. The identification of L-kynurenine as the cause of the fluorescence of the hair of the laboratory rat. Journal of Investigative Dermatology 29:471–477.

Rebell G., Mahvi A., Lamb J.H. 1956. Paper chromatographic separation of fluorescent materials in normal rat hair. Journal of Investigative Dermatology 27:259–262.

Reinhold L. 2020. Fluorescent forests: of mushrooms and marsupials. The Queensland Mycologist 15:5–12.

Reinhold L. 2021. Mammals with fluorescent fur: observations from the Wet Tropics. North Queensland Naturalist 51:1–8.

Reinhold L. 2022. Photoluminescent yellow wing markings of eastern tube-nosed fruit bats (*Nyctimene robinsoni*). North Queensland Naturalist 52:69–74.

Reis P.J., Schinckel P.G. 1963. Some effects of sulphur-containing amino acids on the growth and composition of wool. Australian Journal of Biological Sciences 16:218–230.

Riedler R., Pesme C., Druzik J., Gleeson M., Pearlstein E. 2014. A review of color-producing mechanisms in feathers and their

influence on preventive conservation strategies. Journal of the American Institute for Conservation 53:44–65.
Rippon J.A. 2013. The structure of wool. In: Lewis D.M., Rippon J.A., editors. The coloration of wool and other keratin fibres. John Wiley & Sons in association with the Society of Dyers and Colourists, Bradford, United Kingdom; p. 1–42.
Rivera D.F., Leung L.K.P. 2008. A rare autosomal recessive condition, congenital erythropoietic porphyria, found in the canefield rat *Rattus sordidus* Gould 1858. Integrative Zoology 3:216–218.
del Rosal B., Villa I., Jaque D., Sanz-Rodríguez F. 2016. *In vivo* autofluorescence in the biological windows: the role of pigmentation. Journal of Biophotonics 9:1059–1067.
Schäfer K., Goddinger D., Höcker H. 1997. Photodegradation of tryptophan in wool. Journal of the Society of Dyers and Colourists 113:350–355.
Schnell T., Bentley K., Hayes E., Rick M. 2001. Legibility distances of fluorescent traffic signs and their normal color counterparts. Transportation Research Record 1754:31–41.
Shimomura O., Johnson F.H., Saiga Y. 1962. Extraction, purification and properties of aequorin, a bioluminescent protein from the luminous hydromedusan, *Aequorea*. Journal of Cellular and Comparative Physiology 59:223–239.
Silberglied R.E. 1979. Communication in the ultraviolet. Annual Review of Ecology and Systematics 10:373–398.
Smith G.J. 1995. New trends in photobiology (invited review) photodegradation of keratin and other structural proteins. Journal of Photochemistry and Photobiology, B: Biology 27:187–198.
Smith G.J., Markham K.R., Melhuish W.H. 1994. The presence of photoreactive β-carboline fluorophores in weathered wool keratin. Photochemistry and Photobiology 60:196–198.
Smith G.J., Melhuish W.H. 1985. Fluorescence and phosphorescence of wool keratin excited by UV-A radiation. Textile Research Journal 55:304–307.
Smith G.J., Thorpe M.R., Melhuish W.H., Beddard G.S. 1980. Fluorescence of tryptophan in keratin. Photochemistry and Photobiology 32:715–718.
Soop K. 2005. A contribution to the study of the cortinarioid mycoflora of New Zealand, III. New Zealand Journal of Botany 43:551–562.
Sparks J.S., Schelly R.C., Smith W.L., Davis M.P., Tchernov D., Pieribone V.A., Gruber D.F. 2014. The covert world of fish biofluorescence: a phylogenetically widespread and phenotypically variable phenomenon. PLoS One 9:e83259.
Stockdale P.M., Mackenzie D.W.R., Austwick P.K.C. 1965. *Arthroderma simii* sp. nov., the perfect state of *Trichophyton simii* (Pinoy) comb. nov. Sabouraudia: Journal of Medical and Veterinary Mycology 4:112–123.
Stokes G.G. 1852. On the change of refrangibility of light. Philosophical Transactions of the Royal Society of London 142:463–562.
Stübel H. 1911. Die fluoreszenz tierischer gewebe in ultraviolettem licht. Pflüger's Archiv für die Gesamte Physiologie des Menschen und der Tiere 142:1–14.
Sumita M., Terayama K., Suzuki N., Ishihara S., Tamura R., Chahal M.K., Payne D.T., Yoshizoe K., Tsuda K. 2022. De novo creation of a naked eye–detectable fluorescent molecule based on quantum chemical computation and machine learning. Science Advances 8:eabj3906.
Sumner R.M.W., Ito S., Wakamatsu, K. 1994. Using objective measurements to understand the biology of wool colour. In: Proceedings of the 4th World Congress of Coloured Sheep, York, United Kingdom.
Taboada C., Brunetti A.E., Pedron F.N., Neto F.C., Estrin D.A., Bari S.E., Chemes L.B., Lopes N.P., Lagorio M.G., Faivovich J. 2017. Naturally occurring fluorescence in frogs. Proceedings of the National Academy of Sciences of the United States of America 114:3672–3677.
Tomalia D.A., Klajnert-Maculewicz B., Johnson K.A.M., Brinkman H.F., Janaszewska A., Hedstrand D.M. 2019. Non-traditional intrinsic luminescence: inexplicable blue fluorescence observed for dendrimers, macromolecules and small molecular structures lacking traditional/conventional luminophores. Progress in Polymer Science 90:35–117.
Toussaint S.L., Ponstein J., Thoury M., Métivier R., Kalthoff D.C., Habermeyer B., Guilard R., Bock S., Mortensen P., Sandberg S. 2023. Fur glowing under ultraviolet: in situ analysis of porphyrin accumulation in the skin appendages of mammals. Integrative Zoology 18:15–26.
Tumlison C.R., McAllister C., Robison H., Connior M., Redman R., Trauth S., Port P. 2019. Vertebrate natural history notes from Arkansas, 2019. Journal of the Arkansas Academy of Science 73:39–45.
Tumlison C.R., Tumlison T.L. 2021. Investigation of fluorescence in selected mammals of Arkansas. Journal of the Arkansas Academy of Science 75:29–35.
Turner G.G., ET AL. 2014. Nonlethal screening of bat-wing skin with the use of ultraviolet fluorescence to detect lesions indicative of white-nose syndrome. Journal of Wildlife Diseases 50:566–573.
Turner W.J. 1937. Studies on porphyria. I. Observations on the fox squirrel, *Sciurus niger*. Journal of Biological Chemistry 118:519–530.
Udall S.L., Briggs F.P., Pautzke C.F., Janzen D.H. 1964. Fluorescence studies. In: Wildlife research: problems programs progress 1963. Activities of the branch of wildlife research in the Bureau of Sport Fisheries and Wildlife for the calendar year 1963. Circular 188. United States Department of the Interior, Fish and Wildlife Service and Bureau of Sport Fisheries and Wildlife, Washington, District of Columbia, USA; p. 64.
Valeur B., Berberan-Santos M.N. 2011. A brief history of fluorescence and phosphorescence before the emergence of quantum theory. Journal of Chemical Education 88:731–738.
Viegas M.S., Martins T.C., Seco F., Do Carmo A. 2007. An improved and cost-effective methodology for the reduction of autofluorescence in direct immunofluorescence studies on formalin-fixed paraffin-embedded tissues. European Journal of Histochemistry 51:59–66.
Viitala J., Korplmäki E., Palokangas P., Koivula M. 1995. Attraction of kestrels to vole scent marks visible in ultraviolet light. Nature 373:425–427.
Visser A.J.W.G, Rolinski O.J. 2014. Basic photophysics. American Society for Photobiology. http://photobiology.info/Visser-Rolinski.html. Accessed 8 April 2021.
Wang B., Yang W., McKittrick J., Meyers M.A. 2016. Keratin: structure, mechanical properties, occurrence in biological organisms, and efforts at bioinspiration. Progress in Materials Science 76:229–318.
Warren M.W. II. 1982. Quantitative analysis by room-temperature phosphorescence. Doctoral dissertation, University of Illinois, Urbana-Champaign, Illinois, USA.
Watanabe M., Ohkubo K., Tamura Z. 1972. Studies on carcinogenic tryptophan metabolites—I: enzymatic formation and hydrolysis of glucuronide of 3-hydroxyanthranilic acid. Biochemical Pharmacology 21:1337–1346.

Weagle G., Paterson P.E., Kennedy J., Pottier R. 1988. The nature of the chromophore responsible for naturally occurring fluorescence in mouse skin. Journal of Photochemistry and Photobiology, B: Biology 2:313–320.

Wiedemann E. 1888. Ueber fluorescenz und phosphorescenz I. Abhandlung. Annalen der Physik 270:446–463.

Wilson B., Beccari J.B. 1775. A series of experiments relating to phosphori and the prismatic colours they are found to exhibit in the dark: by B. Wilson, FRS and member of the Royal Academy at Upsal. Together with a translation of two memoirs from the Bologna Acts upon the same subject by J.B. Beccari, Professor of Philosophy at Bologna. London, United Kingdom: Printed for J. Dodsley in Pall-Mall, T. Becket in the Strand and G. Kearsly in Fleet-Street.

Wolff C., Corradini P., Cortés G. 2005. Congenital erythropoietic porphyria in an African hedgehog (*Atelerix albiventris*). Journal of Zoo and Wildlife Medicine 36:323–325.

Yao K., Fang J., Yin Y.L., Feng Z.M., Tang Z.R., Wu G. 2011. Tryptophan metabolism in animals: important roles in nutrition and health. Frontiers in Bioscience 3:286–297.

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