



Historical Biology

An International Journal of Paleobiology

ISSN: 0891-2963 (Print) 1029-2381 (Online) Journal homepage: <https://www.tandfonline.com/loi/ghbi20>

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To cite this article: D. Cary Woodruff, Darren Naish & Jamie Dunning (2020): Photoluminescent visual displays: an additional function of integumentary structures in extinct archosaurs?, Historical Biology, DOI: [10.1080/08912963.2020.1731806](https://doi.org/10.1080/08912963.2020.1731806)

To link to this article: <https://doi.org/10.1080/08912963.2020.1731806>



Published online: 01 Mar 2020.



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ARTICLE



Photoluminescent visual displays: an additional function of integumentary structures in extinct archosaurs?

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ABSTRACT

Many extant invertebrate and vertebrate taxa possess osteological, keratinous, or chitinous structures that are photoluminescent: that is, variably coloured and patterned when observed under ultraviolet light. These features are frequently associated with inter- and/or intraspecific display. Among terrestrial vertebrates, keratinous photoluminescent capabilities are especially well documented in birds. Inspired by recent discoveries, we consider whether non-bird dinosaurs, the evolutionary precursors to birds, might also have possessed photoluminescent display structures. Dinosaurs and other bird-line archosaurs (collectively ornithodirans) often possess extravagant structures that likely functioned in visual display. From a phylogenetic bracketing perspective, UV-sensitive visual capabilities in extant reptiles – including Aves – support the likelihood of tetrachromatic vision in extinct ornithodirans. The ability to perceive the ultraviolet, or near-ultraviolet, range of the visible light spectrum, combined with the presence of extravagant, keratinous-covered display structures, supports proposals that these features may have played an important role in inter- and intraspecific visual displays and communication in extinct Mesozoic bird-line archosaurs.

ARTICLE HISTORY

Received 22 December 2019
Accepted 16 February 2020

KEYWORDS

Photoluminescence; keratin; archosaur; dinosaur; pterosaur; ultraviolet

Introduction

The ability to see across the visible light spectrum is widespread in vertebrates. Less well known is that many animals that see in colour also detect ultraviolet (UV) or near UV wavelengths (Cronin and Bok 2016). Among such animals, many studies have shown that integumentary structures and even, in cases, the skeleton is photoluminescent such that it exhibits enhanced contrast and colour relative to other tissues. Among extant terrestrial vertebrates, photoluminescence has been demonstrated for lizards (teiids [Bajer et al. 2011; Lisboa et al. 2017], cordylids [Stapley and Whiting 2006; Whiting et al. 2006] chameleons [Prötzel et al. 2018]), turtles (deirochelyines [Steffen et al. 2015]), birds (see Burkhardt 1982, 1989; Bennett and Cuthill 1994; Cuthill et al. 2000 for avian UV overviews), mammals (flying squirrels [Kohler et al. 2019]), and amphibians (pumpkin toadlets [Goutte et al. 2019]; Figure 1(a)).

Within these extant cases, the ultraviolet tissues and structures with unusual visual properties in UV mostly involve eyespot-like markings, prominent stripes or other patterned areas, a distribution which has led photoluminescence to be linked with intraspecific signalling. However, an ability to see into the UV part of the spectrum is not only useful with respect to this putative function but may also serve an ecological role. Tedore and Nilsson (2019), for example, found UV-sensitive vision in birds to enhance leaf surface contrast and hence plausibly provide an advantage during foraging in forest environments. In addition to habitat ‘visual enhancement’, UV flora/fauna association is also a well-documented life history and food acquisition strategy. Papiorek et al. (2016) demonstrated a direct correlation between spectral reflectance patterns (UV absorbing or reflecting) within yellow flowers and the visual capabilities of pollinating bees and birds. Only the UV patterned flowers (UV absorbing or reflecting) attracted pollinators of either type, potentially indicating that UV properties may in some cases be more visually enticing than normal non-UV colouration.

Recently described fossils demonstrate that non-bird maniraptoran theropods possessed feathers similar or identical to those of Aves. Melanosomes – melanin-containing organelles – are preserved on some of these feathers, their shapes and structures revealing pigments and structural colouration (i.e. iridescence; Li et al. 2010, 2012; Zhang et al. 2010). Photoluminescent colouration/patterning in the feathers of extant birds has been well documented (see Burkhardt 1989; Mullen and Pohland 2008), although this association in fossil feathers has yet to be ascertained.

Of note here is the correlation between eye anatomy and photo-reception: most extant birds are tetrachromats, and can biologically invest in the incorporation of feathers into complex displays, in some cases including ultraviolet colouration. Interestingly, an enantiornithine bird from the Early Cretaceous of China preserves cone cells (Tanaka et al. 2017), indicating the presence in this extinct group (and likely other avialan lineages outside the crown) of colour vision comparable to that of modern birds.

Two studies have recently documented non-feather photoluminescence within the keratinous bill sheaths and/or ceres of extant birds, although neither found evidence of ecological function. Dunning et al. (2018) reported both non-UV and UV colouration/patterning in the Atlantic puffin *Fratercula arctica* while Wilkinson et al. (2019) described photoluminescence in the keratinous horn of the Rhinoceros auklet *Cerorhinca monocerata* (Figure 2(a) & (b)). These cases demonstrate the existence of photoluminescence in large, visually striking and seasonally developed, keratin-covered structures in extant animals; structures which superficially recall the prominent keratinous integumentary structures of many pterosaurs and non-bird dinosaurs. These are mostly located on the head and include horns, crests, frills, spikes and domes. Given that many avian traits are now known to have originated deep within Theropoda, Dinosauria or

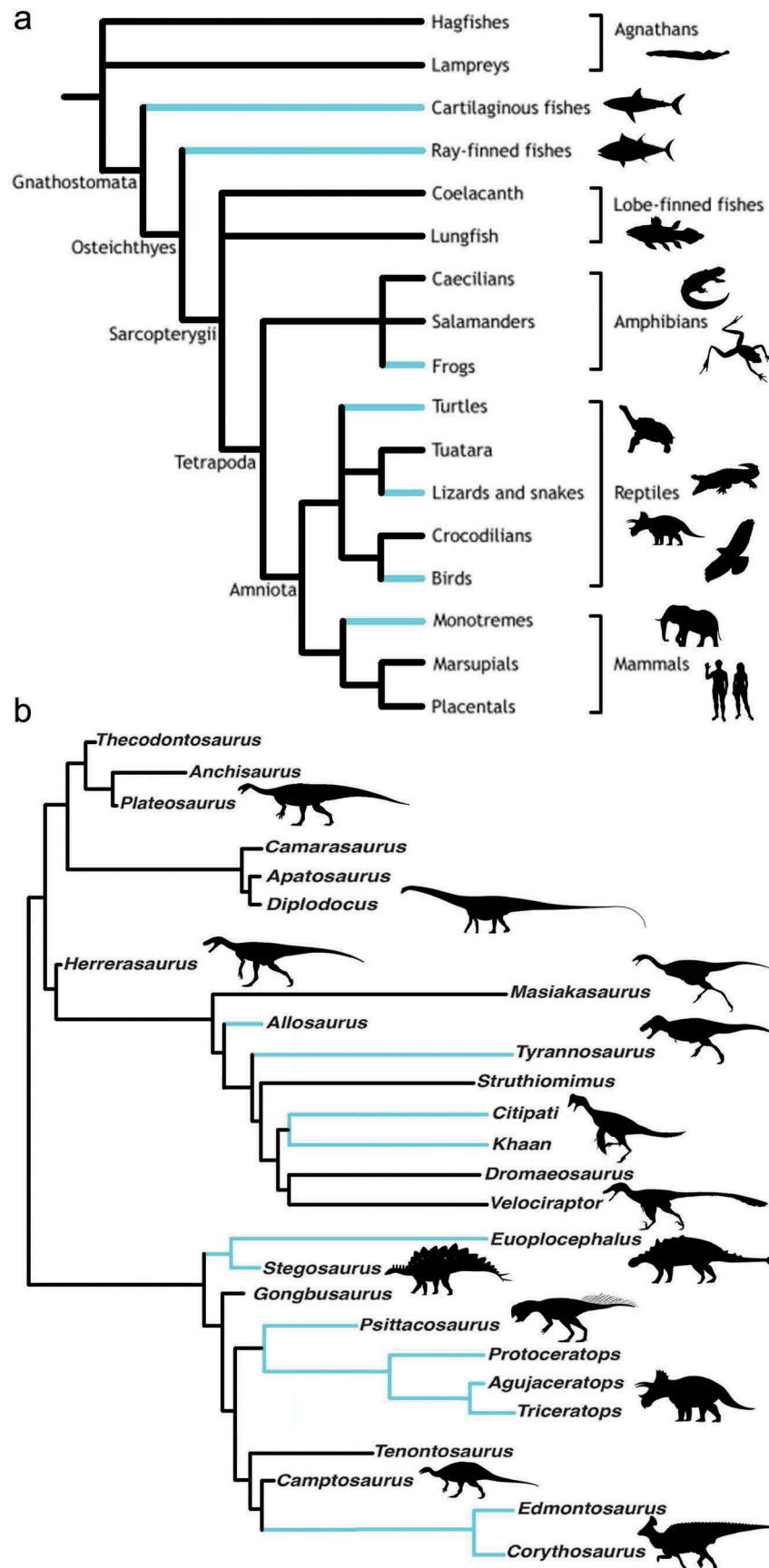


Figure 1. Phylogenetic distribution of functional and potential vertebrate photoluminescence. (a) Phylogeny of Vertebrata with clades that photoluminesce in neon blue. Note that vertebrate UV research is in its infancy, and the clades highlighted herein are the ones thus far documented. Modified from the UCL grant museum; www.ucl.ac.uk/museums-static/obl4he/vertebratediversity/index.html. (b) Phylogeny of Dinosauria with clades that exhibit exaggerated structures highlighted in neon blue. modified from Georgi et al. (2013). Silhouettes in A and B from phyloPic.

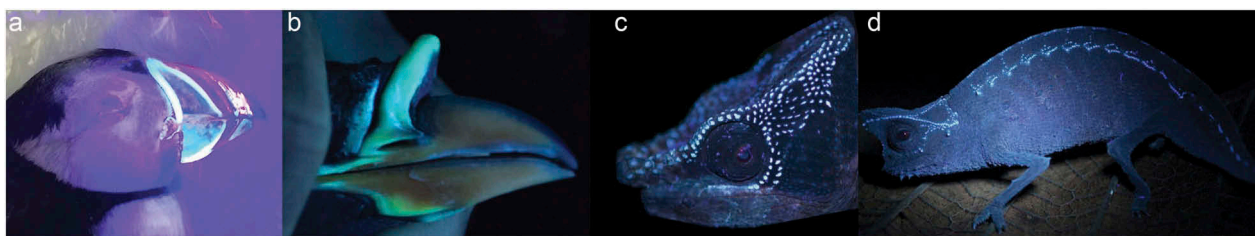


Figure 2. Examples of keratin (A and B) and bone-based (C and D) photoluminescence in extant vertebrates. (a) Atlantic puffin (*Fratercula arctica*). (b) Rhinoceros auklet (*Cerorhinca monocerata*). Modified from Wilkinson et al. (2019). (c) Globe-horned chameleon (*Calumma globifer*). (d) Brown leaf chameleon (*Brookesia superciliosa*). C and D modified from Prötzel et al. (2018). All images are specimens under UV light.

Ornithodira (including the furcula, semilunate carpals, pneumaticity, unidirectional respiration, medullary tissue, and feathers), we speculate that the presence of photoluminescent structures may also pre-date the origin of Aves.

Terminology

We use the term photoluminescence in preference to the more frequently used ‘fluorescence’, since the latter is too specific within this context. Fluorescence is a specific form of photoluminescence, as is phosphorescence; both relate to particular extinction times relevant to the mechanism whereby a molecule returns to its ground state following excitation stimulus. This is especially inappropriate for the extinct species that form our focus here given that we cannot test the precise molecular mechanisms that might have occurred during light-emitting events.

The term ‘bird-line archosaur’ and ‘ornithodiran’ are used here for Ornithodira, the crown-archosaur lineage that includes pterosaurs, dinosaurs and their close kin. Within Dinosauria, those taxa that are not part of the bird clade – termed Avialae by some authors and Aves by others – are referred to as ‘non-bird dinosaurs’ herein, such that we can avoid the unwieldy and unfamiliar ‘non-avian dinosaurs’. Similarly, theropods that are not part of the bird clade are referred to as ‘non-bird theropods’.

Discussion of visual display hypothesis

Large orbits and well-developed optic lobes demonstrate that non-bird dinosaurs and pterosaurs had large eyes and good eyesight. The proportionally large eyes of some non-bird dinosaurs and pterosaurs have even been used to infer a crepuscular lifestyle (e.g. Longrich 2010; Schmitz and Motani 2011). However, neither relative eye size nor visual acuity demonstrates an ability to perceive colour. Therefore, phylogenetic bracketing – even if only, at maximum, a second-order inference (Witmer and Thomason 1995) – is our only recourse.

Traditionally, dinosaurian attributes are assessed via bracketing between extant archosaurs – Crocodylia and Aves (Extant Phylogenetic Bracket [EPB]; Witmer and Thomason 1995). While crocodylians are trichromats, most birds are tetrachromats. From a bracketing standing, this may appear problematic; however, some turtles (archosaurian kin, see below) are tetrachromats, and crocodylians may be secondarily trichromatic (Kelber et al. 2003). A similar pattern in cone loss and regeneration is observed in mammals (Kelber et al. 2003), implying that some archosaurs may have been ancestrally tetrachromatic.

Beyond Archosauria, the presence of what appears to be colour vision in turtles is relevant (Twyman et al. 2016) given molecular data indicating that turtles are close kin of archosaurs, the two being sister-groups within the clade Archelosauria according to some data

(Chiari et al. 2012; Crawford et al. 2015). We speculate that extinct archosaurs likely did see in colour and that sensitivity to UV, while not demonstrable, is plausible or even likely for these animals, given its presence in their extant relatives.

Regarding photoluminescence further from Archosauria, Prötzel et al. (2018) documented photoluminescence in chameleons where bony protuberances on the skull and ribs display apparent fluorescence visible through the thin dermis and epidermis (Prötzel et al. 2018; Figure 2(c) & (d)). This novel, ‘bone-based’ photoluminescence, was also recently documented in the extant anuran *Brachycephalus* (Goutte et al. 2019). Although, it is difficult to link an ecological function to this trait.

On the subject of squamates and UV vision capabilities, Simões and Gower (2001) noted that many groups – Lacertoidea, Anguimorpha, Iguania, Serpentes, Scincoidea, and Gekkota – possess short-wavelength sensitive visual pigments (specifically SWS1) which are in the range of UV sensitivity. Furthermore, such lizards as anoles and some lacertids (*Podarcis muralis* and *Zootoca vivipara*; Simões and Gower 2001) incorporate UV-sensitive pigments into their throat displays, indicating a correlation between UV visual capabilities and UV displays in at least some taxa. Surprisingly, some diurnal colubrids (*Ahaetulla nasuta* and *Chrysopelea ornata*; Simões and Gower 2001) possess UV sensitive pigments but have secondarily evolved UV-blocking lenses.

In view of the predominance of UV visual capabilities in diapsids, we consider it highly parsimonious that non-bird dinosaurs were likely tetrachromatic and could have exhibited some degree of UV visual displays. Based on the phylogenetic support derived from birds and chameleons, we hypothesise that non-bird dinosaurs may have in part exhibited photoluminescent integumentary structures in the form of keratinous displays (and perhaps photoluminescent feathers were present as well).

Which structures could have been photoluminescent?

Essentially all structures associated with visual display in pterosaurs and non-bird dinosaurs are thought to have been sheathed in keratin. Cranial crests are widespread in pterosaurs (Hone et al. 2011) and the distal vanes and other caudal appendages of long-tailed taxa like *Rhamphorhynchus* and *Pterorhynchus* may also have been display structures. The horns, bosses, domes, crests, plates, casques, protuberances, frills and dorsal sails of various theropods (ceratosaurians, spinosaurids, allosauroids, tyrannosauroids, oviraptorosaurs) and ornithischians (thyreophorans, ceratopsians, hadrosaurs, marginocephalians) are mostly regarded as visual display structures (Figure 1(b) & 3), though other functions (like heat dissipation) could have played ancillary roles. Sauropodomorpha is conventionally regarded as the only dinosaurian clade that did not evolve any form of display structure, but the dermal spines of some diplodocoids, raised internarial structures of some macronarians

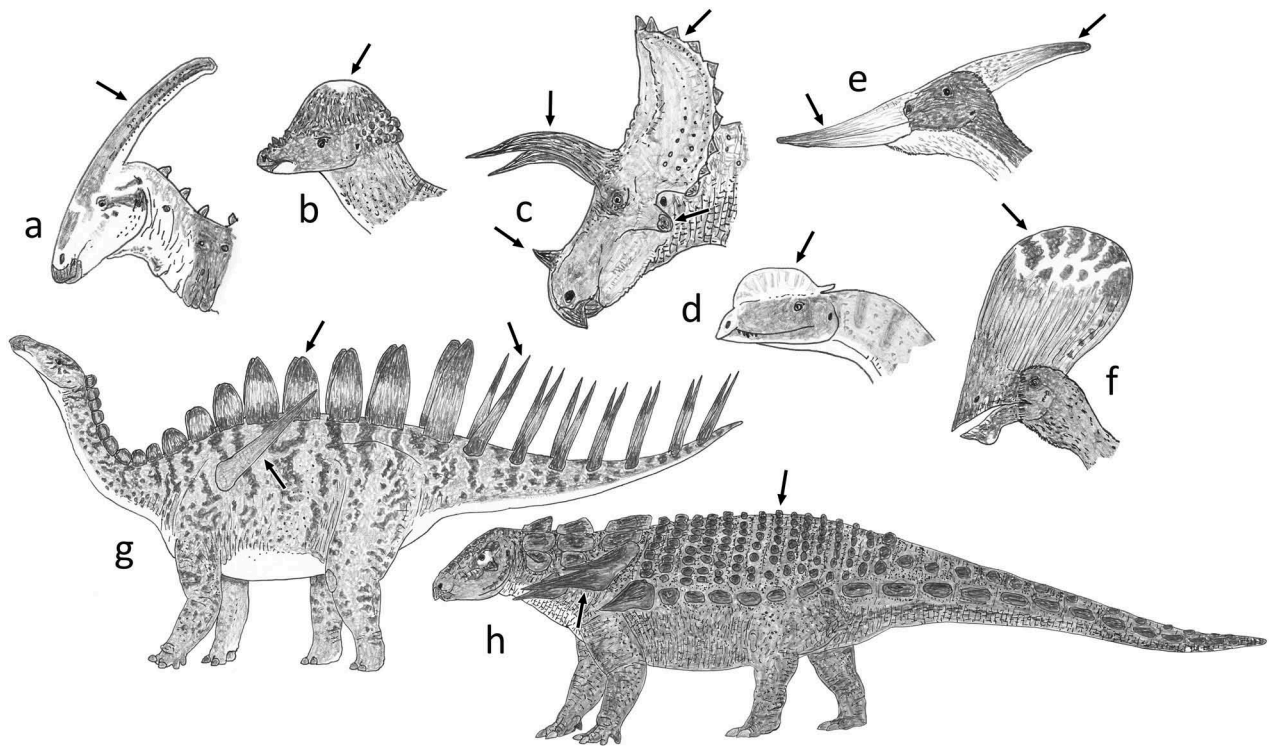


Figure 3. Reconstructions of the extravagant structures in extinct archosaurs. Black arrows pointing to relevant structures. (a) The cranial crest of *Parasaurolophus*, (b) The frontoparietal dome of *Pachycephalosaurius*, (c) The nasal and orbital horns, laterally flared jugals, and the elongated ‘frill’ of *Triceratops*, (d) The cranial crest of *Dilophosaurus*, (e & f) The cranial crests of the pterosaurs *Pteranodon* and *Tupandactylus*; (g & h) the highly modified bone supported scutes, spikes, and plates in the thyreophorans *Miragaia* and *Edmontonia*. Images by DN.

(Hone et al. 2011), as well as the keratin covered osteoderms of some titanosaurs could have functioned in these display roles.

In a few cases, preservation of the overlying keratin is known for such integumentary structures. Where present, this sometimes shows that the organic structures were larger and/or differently shaped than their underlying bony core. Melanosomes associated with ankylosaurian spines and plates provide support for a visual display role: in the Early Cretaceous Canadian nodosaurid *Borealopelta*, the long parascapular spines appear to have been strikingly different in colour from the rest of the animal (Brown et al. 2017).

The discovery of bone-based photoluminescence in chameleons and frogs invites additional speculation with regard to the horned, frill-bearing skulls of ceratopsians and the thickened skulls of pachycephalosaurs in particular, which are often decorated with bony nodes and hornlets. However, the much greater size of these taxa relative to chameleons and frogs requires the existence of a proportionally thicker epidermis and hence less or no likelihood of the bones being visible through the skin. Indeed, preserved skin from ceratopsians have epidermal scales as much as 20 mm in thickness (P. Larson pers. comm. 2019), which is almost definitely too thick for the emission of bone-based photoluminescence.

Vaned feathers, similar to those of extant birds, appear to have been widespread in non-bird maniraptoran theropods. Bristle- or hair-like structures are also known from many non-bird theropod lineages within Coelurosauria, and might have been more widespread within Theropoda (Rauhut et al. 2012). Ornithischians of some lineages possessed bristles or more complex, multi-branched, feather-like structures (i.e. *Kulindadromeus*; Godefroit et al. 2014). Pterosaurs also possessed integumentary filaments recently shown to be, in some lineages at least, multi-branched and feather-like (Yang et al. 2019). Any or all of these integumentary structures could have functioned in

visual display and hence, depending on the visual capabilities of the animal, could have had photoluminescent properties.

Non-bird dinosaurs and pterosaurs and their extravagant structures

The function of extravagant structures is, broadly speaking, not controversial since they are widely agreed to have functioned in visual signalling rather than having an offensive or defensive role exclusively. It remains controversial whether their evolution was driven by sexual selection (Hone et al. 2011; Knell and Sampson 2011; Knell et al. 2012; Hone and Naish 2013) or species identification and social selection (Padian and Horner 2011a; 2011b).

Pterosaurs and non-bird dinosaurs are unusual compared to their extant analogues in that their extravagant structures do not appear to exhibit sexual dimorphism (Mallon 2017). One proposed explanation for this pattern is that mutual sexual selection was in play (Hone et al. 2011). As many birds exhibit sexual dichromatism in feather displays and colouration (e.g. peafowl), UV-reflectance and photoluminescent plumage have been shown to be significant in courtship displays (Hausmann et al. 2003). The incorporation of photoluminescence into courtship displays and mate recognition in one form of keratinous structure (feathers) raises the possibility of its presence and usage in others (i.e. beaks, casques, etc.).

The possibility of photoluminescence in these keratin-covered features suggests that they were sheathed in integument that photofluoresced to different degrees between sexes. In morphologically monomorphic chameleon species (that is, where males and females both possess the same cranial protuberances), osteological features photofluoresce to differing degrees between sexes (Prötzel et al. 2018). Likewise, while further analysis is needed, Goutte et al. (2019) noted

uniform normal light colouration and photofluoresce between the *Brachycephalus* sexes, but did note that photofluorescent patterning was absent in non-sexually mature specimens and developed with sexual maturity. It is tempting to compare these ontogenetic changes to those that occur across the ontogeny of some non-bird dinosaur taxa (Horner and Goodwin 2006).

It is, therefore, possible that monomorphic elaborate structures in pterosaurs and non-bird dinosaurs were not monomorphic in life, but sheathed by sexually dichromatic integument that possessed colouration and patterning visible in UV and/or non-UV light (that is, any colour present in one sex and absent in the other). While these structures were, in superficial form, the same between sexes, they were perhaps visually the opposite, negating the need for 'traditional' dimorphic structures.

Testing for photoluminescence and avenues for future research

The fact that UV sensitivity in extant birds may be linked with life in forests (Tedore and Nilsson 2019) raises the possibility that fossil taxa could similarly have benefited from UV-sensitivity in well vegetated and arboreal habitats. In turn, this sensitivity to UV light could mean that they were especially likely to employ photoluminescence in their own visual display structures. The exploitation of forested environments by bird-line archosaurs could, therefore, conceivably have been a catalyst for the evolution of UV ornamentation; a limitation to our understanding here, however, is that our knowledge of habitat preference and adaptation in extinct bird-line archosaurs is not sufficiently finely tuned to determine whether a given lineage or taxon was specialised for forest-dwelling life. However, a tantalising possible line of evidence is the remarkably preserved counter shaded *Psittacosaurus* (Vinther et al. 2016). Though no UV-related colouration is yet evident in this specimen, the countershading across the body (as seen in extant taxa) supports that *Psittacosaurus* lived in a forested habitat with a dense, light-inhibiting canopy (Vinther et al. 2016).

Finally, how might the presence of photoluminescent structures be tested for in fossil vertebrates? Several tissue types, including keratin, bone and chitin, fluoresce under UV light, and our abilities to detect ever more subtly fluorescing forms of these tissues have improved within recent years (*Scaphognathus* [Jäger et al. 2018]; *Archaeopteryx* [Rauhut et al. 2018]). Of relevance here is the debate over the presence of original keratin versus chemically altered replacements (Moyer et al. 2016; Saitta et al. 2017), since the process of fossilisation could affect the visual properties of display structures through degradation or chemical modification - potentially meaning that their current appearance is not representative of their in-life condition.

Another factor to consider is the natural, non-diagenetic, degradation of keratin and potentially UV-emitting structures. Personal observation (by both DCW and JD) shows that historic taxidermied specimens 'lose' much of this UV colouration, indicating that there is likely a structural or chemical component that degrades over time.

An added possible mineralogical complication is the fact that countless minerals (both organic and non-organic) fluoresce. Mineral replacement or alteration occurring during the fossilisation processes could mean that some fossils become a 'reservoir' for photoluminescing minerals. The same could potentially hold true for fossilised keratinous structures. In addition to this 'reservoir' scenario, many fossil preservatives fluoresce and could thus produce false-positive results. Remarkably preserved fossils with large tracts of keratinous structures, and where the record of preservative application has been recorded, could, therefore, function as worthwhile inaugural examinations. Potential examples include the

recently discovered ankylosaurs *Borealopelta markmitchelli* (TMP 2011.033.0001; Brown et al. 2017) and *Zuul crurivastator* (ROM 75860; Arbour and Evans 2017).

These two ankylosaurs (*Borealopelta markmitchelli* [TMP 2011.033.0001; Brown et al. 2017] and *Zuul crurivastator* [ROM 75860; Arbour and Evans 2017]) may present interesting 'first cases'. As Brown et al. (2017) demonstrated, the keratinous sheaths of *Borealopelta markmitchelli* (TMP 2011.033.0001) - particularly the parascapular spine - photofluoresce under UV light. Interestingly, the lateral ~half of the parascapular spine is differently patterned and has a distinct fluorescence pattern when exposed to UV. In normal light, some of this region - such as the anterolateral edge of the parascapular spine - is lighter in colouration. Additionally, many of the raised keratinous sheath ridges of cervical osteoderms are visible in normal light and UV. In the life reconstruction produced for their study, Brown et al. (2017) depicted nearly the entire length of the parascapular spine as uniform white in colouration. While this normal light and UV photofluorescence could be due to geochemical (calcium phosphate salts) or biological (the natural thinning of the keratinous sheath in these regions) factors, and not visual in nature (C. Brown pers. comm. 2020), the location and degree of photofluorescence in this specimen warrants further study.

Conversely, the ankylosaur *Zuul crurivastator* (ROM 75860; Arbour and Evans 2017) offers the opportunity to examine the overlying keratinous sheaths and the underlying osteoderms. In many of the osteoderms, regions of both the sheath and bone are visible for the same osteoderm. In normal light, the preserved osteoderm keratin is a visible dark grey to black, in stark contrast to the reddish-orange bone (Arbour and Evans 2017). Exposure to different UV wavelengths (A, B, and C) reveals that the keratin-covered caudal osteoderms fluoresce differently than the bone exposed in the same osteoderms (Figure 4) and throughout the rest of the exposed caudal series. Differing colours should denote different elements reacting to the UV wavelength (and the same for *Borealopelta markmitchelli*); and this differing fluorescence could be due to any of the features mentioned above. It was not possible to conduct x-ray fluorescence (XRF) tests for our study; however, a basic identification of those elements present could contribute to our fundamental understanding of fossilised keratin (i.e. different elements present between keratin and bone could support the 'reservoir' hypothesis, while uniform elements could support the organic-based hypotheses herein).

Additionally, a biological factor to consider is the visual perceptibility of photofluorescence. Some organic minerals incorporated into the vertebrate body - including fluorapatite and hydroxyapatite - are photoluminescent, yet this property has not been acted upon by sexual selection (so far as we know). Many other keratinous or chitinous structures have photofluorescent capabilities, yet are not sexually selected for, nor may the organisms in possession of these materials be visually aware of this spectral ability (Bok et al. 2014).

We are also limited in our understanding of the structure and function of photoluminescent traits in extant species; although observations are well documented, the molecular or physical processes behind such traits are seldom explored. We openly admit that many of the propositions we propose herein regarding photoluminescence testing are open ended and not yet empirically supported. The aforementioned issues merely serve as cautionary possibilities and factors to consider in the future examinations of fossilised UV keratinous displays. The discipline currently has no information regarding the taphonomy of UV keratinous displays. If such microscopic and delicate structures as melanosomes can remain structurally intact throughout the permineralization process in one keratinous structure (i.e. feathers), can other keratinous-based features likewise be preserved? And what of iridescence and photoluminescence; do highly iridescent feathers equally photoluminesce, and if not, is there

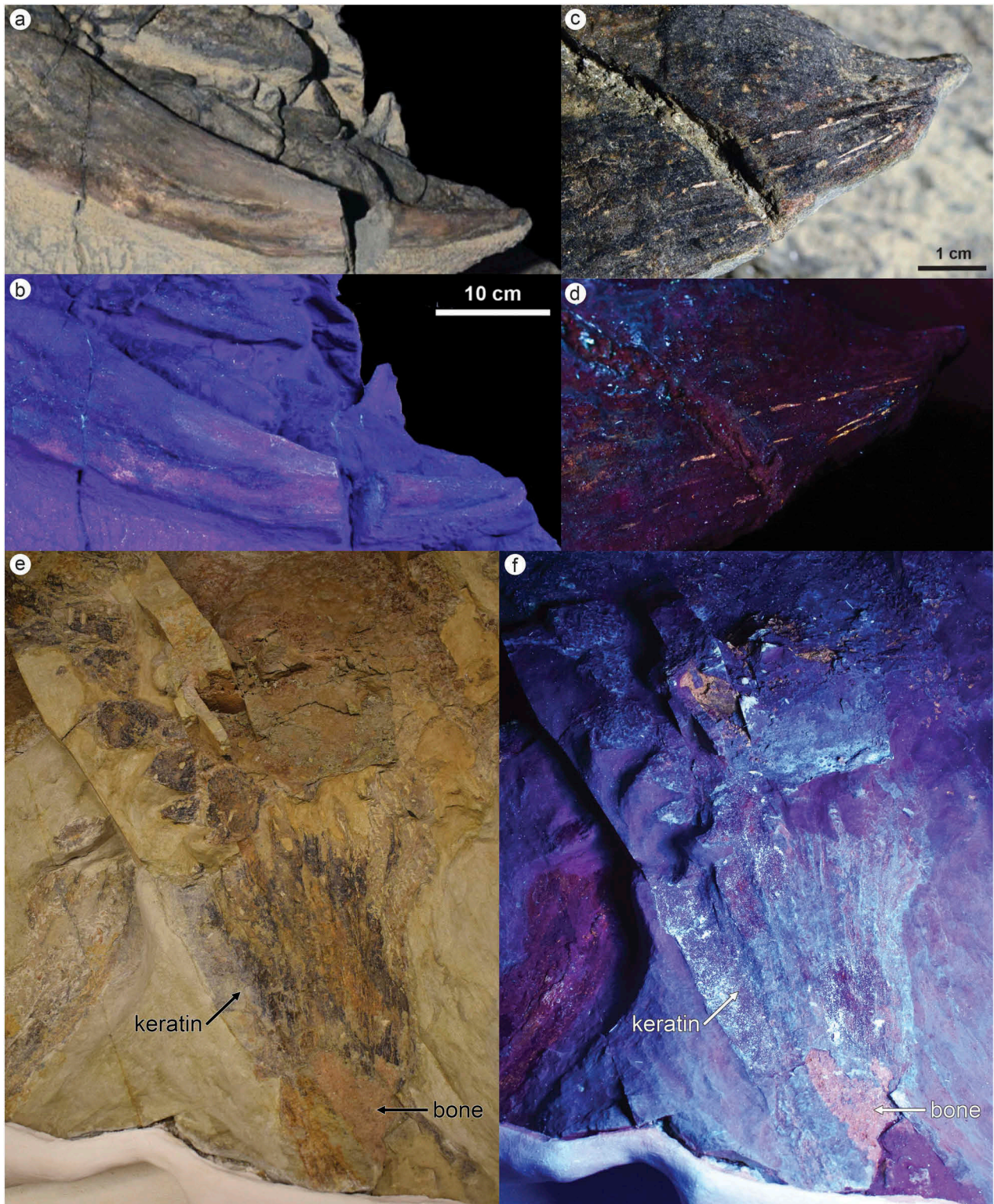


Figure 4. Osteoderms with preserved keratin sheaths of the ankylosaurs *Borealopelta markmitchelli* (tmp 2011.033.0001) and *Zuul crurivastator* (ROM 75,860). *Borealopelta* osteoderms under normal light (a and c), compared to UV light (b and d). A-D modified from Brown et al. (2017). *Zuul* osteoderm under normal light (e), compared to UV light (f). Arrows in E and F point to and denote the exposed bone of the osteoderm and the overlying keratinous sheath. Note the difference in fluorescence between the bone and keratin (which could indicate different elements present).

a display trade-off? Is that why large keratin covered bills and casques are largely absent from highly iridescent birds? Additionally, the ongoing debate over original or altered fossil keratin (Moyer et al. 2016 vs. Saitta et al. 2017) means that our 'hunt' for UV keratinous displays may depend on what form of keratin survives the

fossilisation process. Does permineralization of keratin biologically and mineralogically follow that of osseous tissues? Actualistic experiments exploring such topics would make for wonderful contributions, and some studies exploring said topics are underway (laudably such as Slater et al. 2019), and we hope others will continue in order



Figure 5. Speculative life reconstruction of a heterodontosaur (left image) showing the possibility of UV fluorescing integumentary structures (right image). As discussed herein, the inclusion of fluorescing integumentary structures could have been incorporated into the visual displays of extinct archosaurs. And potentially in some cases, a normal/UV dichromatic visual component could be used as evidence towards the lack of sexually dimorphic structures. Illustration by Brian Engh - dontmesswithdinosaurs.com.

to answer these questions. We welcome continued research into this area, and accept that our speculations here will likely be further informed and shaped by future developments in the fields of taphonomy, biology, bio- and geochemistry, biogeochemistry, visual signalling, and animal perception.

Finally, although much of the speculation proposed herein is based on observational data and phylogenetic bracketing, rarely have the cited studies reported on an ecological function for the traits described. Marshall and Johnsen (2017) reviewed the function of fluorescent signals in the context of visual communication in extant animals. Their review sought to separate ecological function from the artefact of pigment or other molecules present and found that most observations lack sufficient evidence to suggest that they are used in visually driven behaviours. We, therefore, urge any future exploration into the occurrence of photoluminescent structures to attempt to be grounded not just in the anatomy of the structure, but also within the visual capabilities of the taxa.

Conclusions

Those fossil bird-line archosaurs – pterosaurs and non-bird dinosaurs – possessing elaborate yet sexually monomorphic display structures may, we speculate, have been dichromatic in life with respect to both non-UV and UV-emitting colouration and patterning, their visual properties perhaps even changing on a seasonal basis (as described in extant auks). The monomorphic appearance of the relevant elaborate structures may therefore belie the possibility of a more diverse repertoire in signalling opportunities. The structures may thus have been billboard-like: the shape and size may be similar, but the messages they broadcast could be radically different.

The diversity of extant avian behaviour involves the use of a vast array and combination of displays incorporating vocalisations, courtship dances, feather and skin morphology, and UV and non-UV colouration and patterning. While birds have likely taken many of these traits to extremes, such traits are unlikely to have originated in the avian crown. The fact that keratin-sheathed bony structures in extant birds can be photoluminescent – an area still in its research infancy – offers an intriguing possibility for non-bird dinosaurs and other bird-line archosaurs. If these animals were indeed tetrachromatic, UV-related colouration and patterning could represent an important way to emphasise the visual impact of their keratinous-

covered display structures. It may be that these extravagant organs played pivotal roles in inter- and intraspecific communication and display analogous to that provided by elaborate feathers in extant Aves.

Acknowledgments

Thanks to D. Evans, S. Claramunt, M. Peck, V. DiCecco, and K. Seymour of the Royal Ontario Museum for access to vertebrate palaeontology, avian, and osteology collections as well as the use of research-grade UV lights. C. Brown provided insightful conversation about *Boreolopelta markmitchelli* and research. B. Engh provided the amazing artwork used in Figure 5 (dontmesswithdinosaurs.com). Thanks to T. Holtz, an anonymous reviewer, and a previous anonymous reviewer for valued feedback, insightful comments, and constructive discussions. Additionally, this project stemmed from the power of social media – sharing discoveries and connecting researchers around the globe to discuss new research, ask new questions, and spark new ideas.

Disclosure statement

No potential conflict of interest was reported by the authors.

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