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A unique hollow melanosome morphology in the hairs of the platypus *Ornithorhynchus anatinus*

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Melanin pigments are ubiquitous and serve diverse functions, including UV protection and colour production. In vertebrates, they are housed in organelles called melanosomes that typically vary in shape from spherical to rod-like, but can also adopt unusual morphologies, such as flatness or hollowness. For over 50 years, it was thought that melanosome hollowness occurred only in birds and always alongside elongation, where hollow rods or platelets form organized nanostructures that produce brilliant iridescent colours. Here, we present the first description of hollow, spherical melanosomes in mammals, from the hairs of the platypus (Monotremata: *Ornithorhynchus anatinus*). By contrast, we found no evidence of hollow melanosomes in the other two monotreme genera or in any other mammal so far examined (from a combined dataset of 126 species encompassing 103 genera). These spherical, hollow platypus melanosomes are unique among vertebrates and, surprisingly, only produce brown coloration, suggesting a potential function unrelated to colour or a non-adaptive origin. This finding provides exciting new avenues of research into mammal melanogenesis and the evolution of melanosomes.

1. Introduction

Melanins are dark pigments ubiquitous in the natural world. They are found widely across the plant, fungi and animal kingdoms and have multiple biological functions [1–3]. In vertebrates, the functional diversity of melanin is broad and multifaceted, playing roles in thermoregulation [4,5], photoprotection [6], physical strengthening [7] and colour production for camouflage and sexual displays in mammals, birds, reptiles and fish [8–13].

Across vertebrates, melanins produce and underpin diverse colours. Eumelanin, one of two major melanin subtypes, produces blacks, greys and dark browns, whereas phaeomelanin usually generates rufous, reds and some orange/yellows [8,14]. Typically, these two chemical forms occur in combination with each other [1], housed within specialized organelles (melanosomes) where they are synthesized, stored and transported. In some birds [15] and mammals [11,16], the shape of melanosomes is highly correlated with colour. Eumelanin is typically housed in melanosomes with a greater aspect ratio, i.e. long, cylindrical melanosomes, while melanosomes associated with phaeomelanin are somewhat spherical [11,16]. In mammals, melanosome morphologies are a gradient between round and elongated [11], but they are always

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solid (figure 1) [11,17]. In birds, they come in a wide range of morphologies, including hollow and/or flattened, which enhances their colour-producing ability (figure 1) [18]. More specifically, these unusual melanosomes in birds are often organized into nanostructures that produce iridescent structural colours in feather barbules, vastly increasing the attainable colour space [19]. All hollow melanosomes described thus far are long, either rod-like or flattened [20], and increase the brightness of iridescent colours compared to solid rods. Since the classic work of Durrer [18] and Durrer & Villiger [21,22] in the 1970s, such hollowness has still only been documented in birds [23–25].

While compiling a database of mammalian melanosomes [11], we found melanosomes with an unusual morphology in platypus hairs. Using transmission- and scanning electron microscopy (TEM and SEM, respectively), along with Fourier transform infrared spectroscopy (FTIR), we investigated the morphology and chemical signature of these melanosomes and discovered a hollow, spherical melanosome morphology not previously reported in any animal.

2. Methods

(a) Sample collection

We collected individual guard hairs from the head, flank and dorsum of three species of monotreme: platypus *Ornithorhynchus anatinus*, western long-beaked echidna *Zaglossus bruijnii* and short-beaked echidna *Tachyglossus aculeatus*, ventral hairs for *O. anatinus* and *Z. bruijnii* and tail hairs for *O. anatinus* (all Naturalis Biodiversity Centre (NL)). We then collected guard hairs from the dorsal area of a further 10 specimens of *O. anatinus* from the American Natural History Museum (USA) for melanin extraction. We also collected dorsal hairs from six Metatheria (Australian National Wildlife Collection (AUS)) (electronic supplementary material, table S1) to see if hollowness is found elsewhere and compared them to existing literature on mammal melanosomes [11,17], totalling 126 species.

(b) Transmission electron microscopy

We progressively infiltrated individual guard hairs for each species (electronic supplementary material, table S1) with the following ratios of acetone : epon; 85 : 15, 50 : 50, 30 : 70 and 100% Epon® for 24 h each [26]. We placed samples in block moulds and polymerized them at 60°C for 16 h before cutting ultrathin sections at a thickness of 100 nm using a Leica UC-6 ultramicrotome in both the horizontal and longitudinal planes and transferred them to Formvar-coated copper grids. We stained grids with 1% uranyl acetate and lead citrate, then imaged them using TEM on a JEOL JEM 1010 TEM (JEOL, Japan) equipped with a CCD side-mounted Veleta camera (figure 2Ai,ii, electronic supplementary material, figures S1–S4, image acquisition parameters: accelerating voltage = 60 kV, magnification = ×2000–100 000).

(c) Melanin extraction

To maximize melanin yield, we pooled samples from 10 platypus specimens (American Natural History Museum, USA) for melanin extraction and FTIR analysis. We transferred the hairs into a round-bottom flask fitted with a condenser, with 15 ml 37% hydrochloric acid (HCl), and heated it to 50°C for 3.5 h with continuous stirring, then to 100°C for 45 min. We centrifuged the cooled solution in an Eppendorf tube at 15 200 rpm for 2 min at room temperature, discarded the supernatant, then resuspended the precipitate in 1 ml deionized water. We vortexed the solution for 10 s, before repeating the centrifuge and wash cycle another three times, to achieve a neutral supernatant as informed by a pH indicator. After the final centrifuge step, we discarded the supernatant and resuspended the precipitate in 100% ethanol, with sonication for 30 s to aid dispersion. To check the extraction results, we dropped 20 µl of the melanin/ethanol solution directly onto a copper grid, allowed the ethanol to evaporate and then viewed the grid using a JEOL JEM 1010 TEM (JEOL, Japan). TEM images (figure 2, electronic supplementary material, figure S5) were then used to calculate the dimensions of the individual extracted melanosomes in ImageJ [27]. We then dried the extracted melanin at 60°C for 3 h.

In addition, as a reference eumelanin standard, we extracted melanin from cuttlefish *Sepia officinalis* ink by dispersing 0.9 g ink in 120 ml of 37% HCl in a round-bottom flask fitted with a condenser. We heated the mixture to 100°C for 3 h before collecting the melanin via centrifuging. We washed the precipitate with deionized water for several cycles as above, until the supernatant became neutral, and then dried the extract at 60°C.

(d) Scanning electron microscopy

We placed individual hairs in block moulds with 100% Epon® and polymerized them at 60°C for 24 h before cutting sections at a thickness of 1 µm using a Leica UC-6 ultramicrotome. We transferred sections to aluminium stubs with carbon tape and sputter-coated them with gold/palladium to a thickness of 10 nm, then viewed and imaged them using a FlexSEM 1000 (Hitachi, Japan) (figure 2C,D, image acquisition parameters: accelerating voltage = 20 kV, magnification = ×37 000–45 000, working distance = 5.5–5.7 mm).

(e) Fourier transform infrared spectroscopy analysis

To confirm that the hollow organelles were melanin, we obtained infrared absorption spectra of the dried extract from the platypus hairs and compared it to extracted reference melanin (figure 3), supplementing this with additional published spectra

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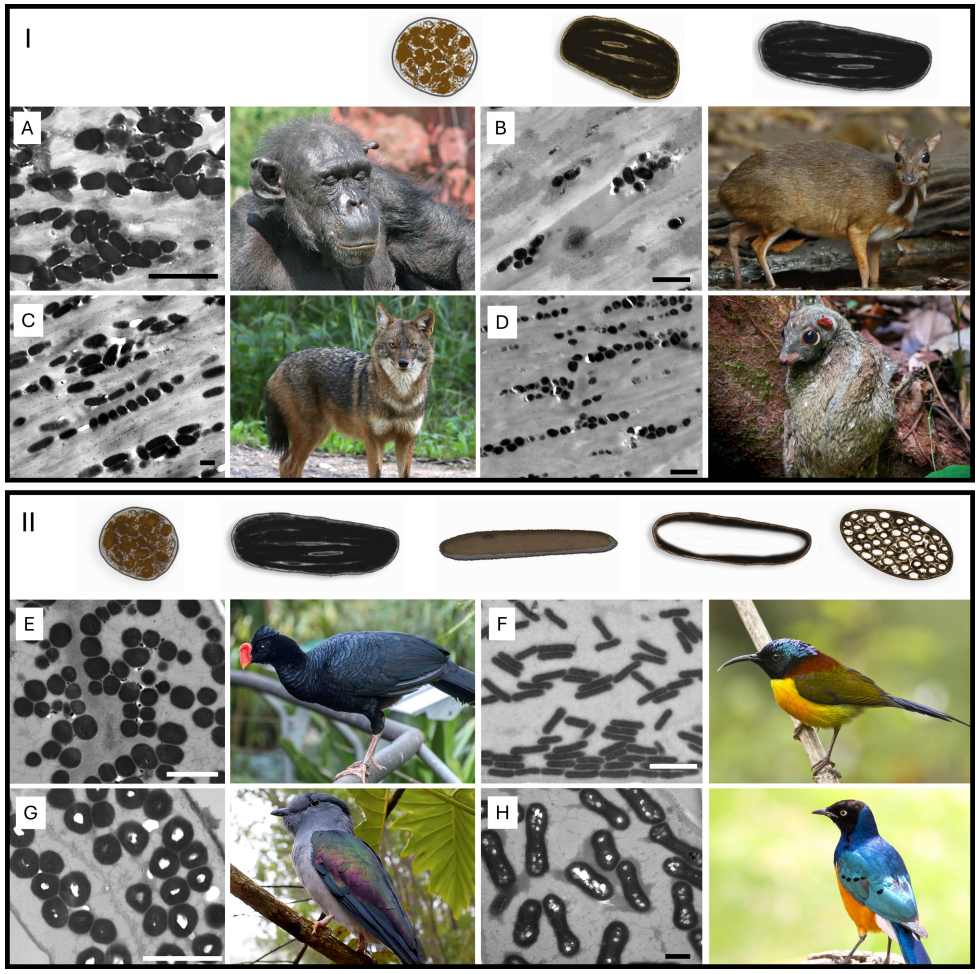

Figure 1. Melanosome diversity in (i) mammals and (ii) birds. Illustrations are representative of the melanosome shapes found in (i) mammals and (ii) birds. Transmission electron micrograph cross sections of melanosomes found in (A) chimpanzee *Pan troglodytes* (photo: Gerd W. Schmölter), TEM scale bar = 2 µm, (B) water chevrotain *Hyemoschus aquaticus* (photo: Dave Curtis), TEM scale bar = 1 µm, (C) golden jackal *Canis aureus* (photo: Jan Ebr & Ivana Ebrová), TEM scale bar = 500 nm, (D) Sunda flying lemur *Galeopterus variegatus* (photo: Petre Kimbely), TEM scale bar = 1 µm, (E) razor-billed curassow *Mitu tuberosum* (photo: Animalia CC BY-SA 3.0), TEM scale bar = 500 nm, (F) green-tailed sunbird *Aethopyga nipalensis* (photo: Animalia CC BY-SA 4.0), TEM scale bar = 500 nm, (G) cuckoo-roller *Leptosomus discolor* (photo: Oleg Rozhko), TEM scale bar = 1 µm, (H) superb starling *Lamprotornis superbus* (photo: Tong Mu), TEM scale bar = 200 nm.

of eumelanin and synthetic phaeomelanin curves [28–33] for peak identification. We recorded the infrared spectra for both samples using a Nicolet iS50 FTIR spectrometer equipped with a universal attenuated total reflectance (ATR) attachment, from 4000 cm $^{-1}$ to 400 cm $^{-1}$, at a resolution of 4 cm $^{-1}$ and 32 scans per sample measurement.

3. Results

(a) Electron microscopy

We found abundant hollow melanosomes in the hair cortex of all brown platypus guard hairs, but not white stomach hairs which contain only solid melanosomes within the medulla, with no melanosomes in the cortex (figure 2Ai,ii, electronic supplementary material, figure S1). Across the head, tail and dorsal side of the torso, hollow melanosomes are clearly visible in both TEM and SEM sections, with some solid melanosomes randomly distributed throughout (figure 2, electronic supplementary material, figure S1). This interpretation is supported by the TEMs of the extracted melanosomes (figure 2B, electronic supplementary material, figure S5), which show a mix of solid and hollow morphologies.

From the SEM micrographs (figure 2C,D) and TEM images of the extracted melanosomes (figure 2B, electronic supplementary material, figure S5), hollow melanosomes of the platypus are spherical, differing little between longitudinal and horizontal sections (electronic supplementary material, figure S3), with average dimensions for length and width of 319 nm and 285 nm, respectively (n = 397, electronic supplementary material, table S2), giving an average aspect ratio of 1.13. Solid melanosomes are slightly more elongate (average length, width and aspect ratio of 370 nm, 284 nm and 1.32 respectively, n = 82, electronic supplementary material, table S2). By contrast, longitudinal TEM sections of both echidna species contain only elongate melanosomes (electronic supplementary material, figure S3).

We did not find hollow melanosomes in any of the hairs of either echidna species tested (electronic supplementary material, figure S2A–D, F–I). In a few rare cases, we observed individual melanosomes with a semi-hollow appearance, i.e. the central cavity is partially filled with melanin of a granular or loose appearance, in *T. aculeatus* sections (electronic supplementary

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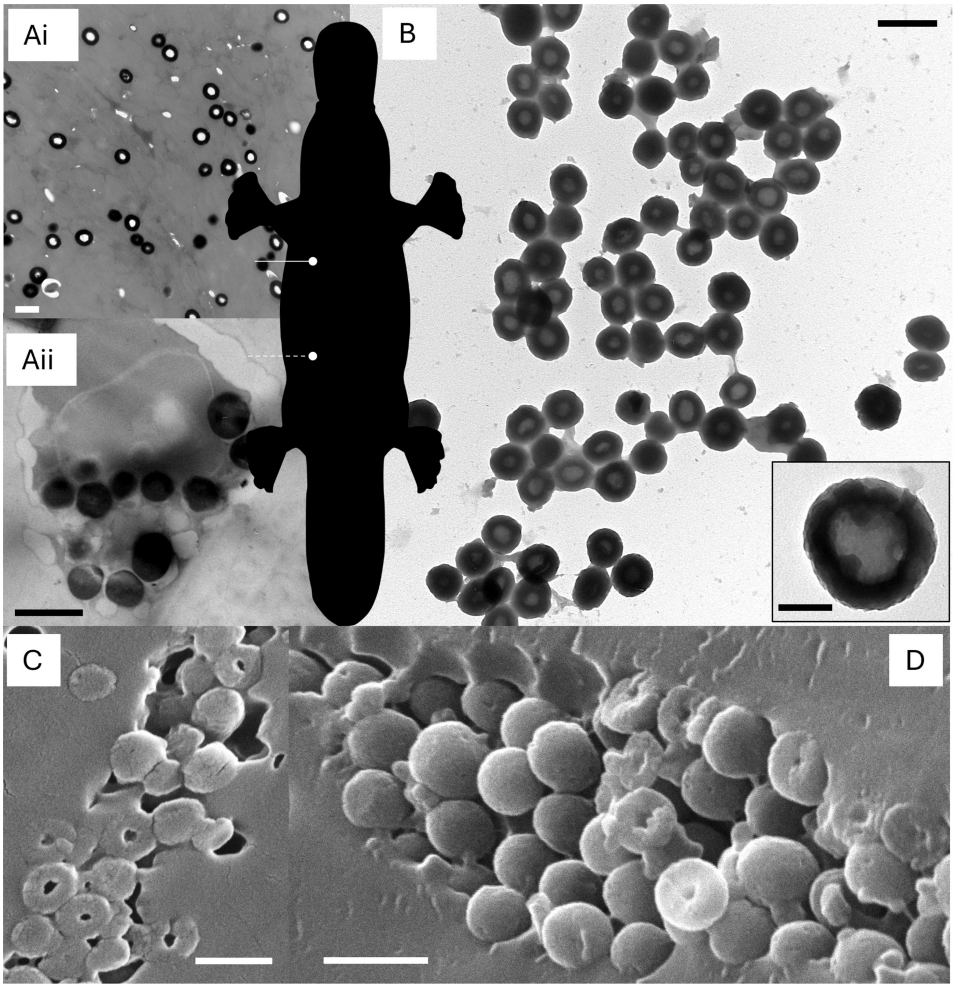

Figure 2. Morphology of melanosomes in the hairs of the platypus *Ornithorhynchus anatinus.* (A) Transmission electron micrographs of hair cross sections taken from (i) dorsum, scale bar = 500 nm, (ii) stomach, scale bar = 1 µm. (B) Transmission electron micrograph of multiple melanosomes extracted from dorsal hairs, showing a mixture of hollow and full melanosomes, scale bar = 500 nm. Insert shows a magnified view of an individual extracted hollow melanosome, scale bar = 100 nm. (C) Scanning electron micrograph of cross section of a dorsal hair, scale bar = 1 µm. (D) Scanning electron micrograph of longitudinal section of a dorsal hair, scale bar = 1 µm. Platypus silhouette from Phylopics.

material, figure S2I). The rarity of these organelles, however, means they could be artefacts and are therefore not considered hollow. Additionally, hollow melanosomes were not observed in any of the six marsupial hairs tested here (electronic supplementary material, figure S4), or in any other mammals for which we have published melanosome morphology data (n = 120 [11,17] species).

(b) Fourier transform infrared spectroscopy analysis

The FTIR analysis for the extracted platypus hair melanosomes is consistent with that of the extracted eumelanin reference sample (figure 3) and published literature [29–31,33], with some additional peaks seen in the FTIR analysis that could correspond to phaeomelanin [32], or small amounts of residual hair proteins [30] (see supplementary methods for band assignment). While the extracted melanin likely contains large amounts of eumelanin, we are unable at present to confirm with certainty the presence of phaeomelanin, as proteins can produce similar FTIR peaks [30].

4. Discussion

Here, we present a novel hollow and spherical melanosome morphology, likely composed of eumelanin, in platypus hairs. Spherical but not hollow melanosomes are found in other mammals, while hollow melanosomes in birds are (to date) never spherical [18]. Thus, to our knowledge, this is the first example of hollow, spherical melanosomes in any vertebrate.

Melanosome shape in mammals is tightly associated with colour [11,15] and typically related to melanin chemistry: red and orange hairs contain more spherical (likely phaeomelanin-rich [15]) melanosomes than eumelanin-rich black and dark brown hairs. It is therefore unexpected that the more spherical (electronic supplementary material, table S2) melanosomes in platypus produce dark brown hair colours. Are they richer in phaeomelanin (consistent with their shape) or eumelanin (consistent with their colour)? FTIR analysis suggests the latter, but with potential trace amounts of phaeomelanin (figure 3). These two melanins are often found together [25], and many if not most melanosomes may have a mixed chemical composition [35]; thus, this

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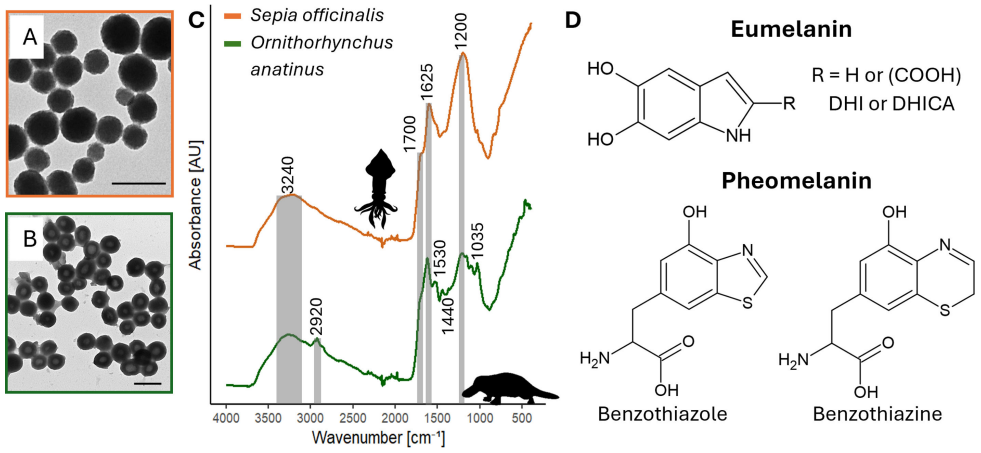

Figure 3. FTIR spectra of extracted melanins. (A) Micrograph of extracted standard cuttlefish *Sepia officinalis* melanin, scale bar = 200 nm. (B) Micrograph of extracted platypus *Ornithorhynchus anatinus* melanin, scale bar = 500 nm. (C) FTIR spectra of extracted standard cuttlefish *Sepia officinalis* melanin (top) and platypus *Ornithorhynchus anatinus* melanin (bottom), with highlighted peaks. Peaks were determined using [28–33]. Spectra have been offset against each other. Additional peaks can be seen in the spectrum collected from the platypus melanin, potentially indicative of phaeomelanin (e.g. 2920 cm^{-1}, 1527 and 1035 cm^{-1}, see supplementary methods for peak assignment); however, this could also be residual proteins. (D) Basic units of eumelanin and phaeomelanin, adapted from [34]. Silhouettes from Phylopics.

mixture in itself is not surprising. That dominant amounts of eumelanin are found in a spherical melanosome is unexpected and requires further work in the future. Indeed, the mechanism for the link between shape and colour of melanosomes in mammals is still unclear [25]. Melanin chemistry and shape are not associated in animals other than birds and mammals, suggesting that this is the ancestral condition [35]. This 'exception to the rule', in which a mammal shows no relationship between shape and colour, may provide an excellent study system to investigate this further.

In mature hairs, approximately 20% of melanosomes are solid, with the rest showing varying amounts of hollowness (figure 2B, electronic supplementary material, figure S5, electronic supplementary material, table S2). This variation could be partly attributed to the cutting plane during electron microscopy preparation (figure 2Ai,C,D, electronic supplementary material, figure S6) and the irregular distribution of the melanosomes throughout the hair cortex (figure 2Ai,C,D). However, the micrographs of extracted melanosomes (figure 2B, electronic supplementary material, figure S5) show that their central core also varies in size, suggesting that shell thickness variation is not solely attributable to sample preparation artefacts. In birds, hollow melanosomes can form optically active organized layers at the feather surface. This effect requires the thickness of melanin (i.e. the shells of hollow melanosomes) to be within a certain thickness [19,20,23,36]. In the platypus, hollow melanosomes are scattered throughout the hair cortex. When melanosomes do not align into coherent layers, melanin shell thickness becomes optically irrelevant, reducing selection on shell thickness consistency.

Because they are the only mammal known to have hollow melanosomes, platypus may be an excellent study system for uncovering the mechanism(s) of hollow melanosome production. Interestingly, melanotic melanoma (i.e. cancerous) cell lines (MNT-1) contain toroid-shaped melanosomes [37,38] which may be important in the process of melanosome biogenesis in dysregulated melanoma cells [37]. Similarly, a single nucleotide polymorphism within the *LYST* gene in corn snakes (*Pantherophis guttatus*) produces a lavender phenotype, with some dermal melanosomes not fully melanized and appearing hollow [39]. Exploring a possible developmental/genetic link between melanosomes in cancerous mammalian cells, mutant vertebrates and platypus hairs is a very intriguing avenue for future research.

Within birds, hollow melanosomes increase the brightness of iridescent colours via enhanced differences in refractive indices between keratin and melanin, as well as between melanin and the air within the central cavity of the melanosome [19,40]. Conversely, the mutation in corn snakes leading to hollow melanosomes results in the opposite: a dramatic loss of melanin-based colour. A similar refractive index contrast likely exists in the platypus; however, the lack of organized melanosome arrangement precludes an increase in brightness or the production of angle-dependent colour. Why the non-iridescent platypus has abundant hollow melanosomes with no clear effect on their brown coat colour is therefore uncertain and raises the broader question of why they have them at all. Since monotremes are the most basal mammal split, hollowness might appear ancestral, shared by the common ancestor of mammals and birds. Its absence in other monotremes and likely derivation in birds [19,41], however, suggests a single evolutionary origin with limited distribution, although loss in echidnas cannot be ruled out [42].

Platypus and echidna ancestors were likely aquatic foragers [42], and hollow melanosomes might have been an adaptation to an aquatic lifestyle, speculatively aiding in insulation, for example, similarly to how the air-filled central medulla cavity in hair may have insulator capacities [43]. The loss of such a lifestyle in modern echidnas may have resulted in the loss of hollow melanosomes but been retained in aquatic platypus. This interpretation, however, raises the additional question of why it is not more widespread among aquatic mammals, and future research could investigate the potential adaptive significance (if any) of this finding. In addition to hollow melanosomes, the platypus also shares other traits with birds, including egg-laying and sex chromosomes [44]. Whether this similarity extends to the genes relating to melanin production, specifically those involved in the formation of hollow melanosomes in birds, is unclear. Indeed, the genetics and development of hollow melanosomes in birds remain unknown, potentially requiring upregulation of TYRP1 [45–47], although this requires more research. Excitingly, over 200 years after its description as something in between birds and mammals [48–50], we find additional convergence

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between the platypus and birds. The discovery of a unique melanosome morphology opens up exciting new avenues of research into melanin genetics, melanosome development and the evolution of melanosomes.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data are available within the manuscript and as supplementary material [51].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.L.D.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; F.B.: data curation, investigation, methodology, visualization, writing—review and editing; W.X.: data curation, formal analysis, investigation, methodology, writing—review and editing; M.P.J.N.: data curation, formal analysis, investigation, methodology, visualization, writing—review and editing; G.D.: data curation, formal analysis, investigation, methodology, writing—review and editing; K.D.C.: resources, writing—review and editing; M.D.S.: funding acquisition, resources, supervision, writing—review and editing; L.D.: conceptualization, funding acquisition, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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