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Editorial: Biological and physical basis of the development of integument and associated structures

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Editorial on the Research Topic
Biological and physical basis of the development of integument and associated structures

> *"Everything about microscopic life is terribly upsetting. How can things so small be so important?"*
> Isaac Asimov

The integument of organisms differs greatly in nature and shape, including the cell wall in bacteria, fungi, algae and plants, the cuticle in arthropods, and the skin in vertebrates. The integumentary surface offers a range of micro- and nano-structures that serve a variety of purposes like environmental sensing, light scattering, substrate adhesion, (super) hydrophobicity, (super)hydrophilicity, and thermoregulation (Barthlott et al., 2016; Watson et al., 2017; Seale et al., 2018; Akat et al., 2022). It is worth noting that these structures are often multifunctional. Water striders, for instance, have leg bristles that give both mechanosensation and water repellency (Finet et al., 2018, 2022), whilst clearwing butterflies have transparent wings with anti-reflective and hydrophobic nipple arrays (Finet et al., 2023).

While integuments and their accompanying structures are extremely diverse, their material composition is the result of developmental and evolutionary tinkering of a small set of biopolymers like chitin, keratin, and cellulose, as well as various proteins, lipids, and pigments (Pasquina-Lemonche et al., 2020; Akat et al., 2022; Muthukrishnan et al., 2022; Gow and Lenardon, 2023; Cosgrove, 2024). Structural colors for example, can be created by combinations of these biomaterials (McPhedran et al., 2001; Seago et al., 2009; Sun and Bhushan, 2012; Airoldi et al., 2019; Hsiung et al., 2019; Middleton et al., 2020; Saranathan and Finet, 2021; Thayer and Patel, 2023). Furthermore, these biomaterials are optimized and often hierarchically structured, indicating precise cellular/tissue control over biomaterial assembly across space and time (Miserez et al., 2008; Carroll et al., 2022).

The morphogenesis of integumentary surfaces and nanostructures remains a vast and underexplored field. However, the emergence of recent reviews (Airoldi et al., 2019; Lloyd and Nadeau, 2021; Saranathan and Finet, 2021; Finet, 2024) and research papers on this topic highlights an active field of research. Our understanding of the spatial control of chitin assembly at the subcellular level has progressed (Pesch et al., 2017; Adler, 2019; Sviben et al., 2020; De Giorgio et al., 2023; Ghosh and Treisman, 2024; Ikeda et al., 2024; Inagaki et al., 2024; Itakura et al., 2024). Single-cell gene expression atlases of developing scales in butterflies (Prakash et al., 2024; Loh et al., 2025) and bristles in *Drosophila* (Hopkins et al., 2023) have identified gene networks involved in hair-like structure morphogenesis. Progress has been made to understand the formation of different nanostructures in butterfly wing scales such as the laminae (Thayer et al., 2020; Prakash et al., 2022; Chatterjee et al., 2023; Balakrishnan et al., 2024), the ridges (Brien et al., 2022; Ficarrotta et al., 2022; Lloyd et al., 2024; Totz et al., 2024), the luminal gyroid (Wilts et al., 2017), and the trabeculae (Ru et al., 2024). Work on cuticular proteins has identified their roles and spatial distributions in the development of beetle elytra (Noh et al., 2014; Murata et al., 2022; Bao et al., 2024) and butterfly scales (Liu et al., 2021).

In particular, many studies feed into the biomimetic and bioengineering fields of research. For example, the natural world has inspired multiple solutions for material adhesion (Li et al., 2024). The morphology of shark scales has led to various applications from membrane antifouling to hydrodynamics (Ghimire et al., 2024), and chameleons and cephalopods have inspired color-changing hydrogels for multiple functions including sensors (Lu et al., 2022; Zhang et al., 2023). However, beyond extracting design principles from biological materials, the ultimate goal would be to develop bio-inspired manufacturing processes, which require an in-depth understanding of the biological processes themselves.

This topic explores the genetics and cellular mechanisms underlying the development of integument and associated structures in animals and plants. With this Research Topic, we wish to direct readers to the emerging field of bio-inspired manufacturing and hope to acknowledge the need for more studies in understanding biological processes that can produce precise and compositionally driven micro- and nano-structures.

Plant cell walls are made up of cellulose microfibrils embedded in a matrix of glycoproteins, and pectic and hemicellulosic polysaccharides. Glycosylphosphatidylinositol (GPI) is a common eukaryotic lipid modification that helps proteins adhere to the membrane lipid bilayer. Zhou reviews our knowledge on GPI-anchored proteins involved in cell wall regulation in the plant model *Arabidopsis*. The author proposes that these proteins might act as structural components of the cell wall by organizing cellulose microfibrils at the cell surface.

In reptiles, a mutation in the *TFEC* gene leads to a piebald phenotype with white patches in the ball python while it causes reduced coloration in the brown anole lizard due to the loss of iridophores (Garcia-Elfring et al., 2023). Using comparative histology, Tzika demonstrates that *TFEC* mutants produce similar phenotypes of reduced coloration via different mechanisms. In the anole, TFEC is necessary for the development of iridophores, whereas in the ball python, which lacks iridophores, TFEC is important for the development of melanophores and xanthophores. By pointing out that the same transcription factor can function differently within the same taxon, this study emphasizes that the phenotypic mutant approach is insufficient for elucidating the underlying molecular mechanisms.

Like reptiles, the ribbontail stingray exhibits structurally colored blue spots produced by dermal iridophores. These iridophores are unique by having numerous fingerlike protuberances (Surapaneni et al., 2024) and contain spherical iridosomes enclosing guanine nanocrystals. Blumer et al. provide a detailed ultrastructural description of the ribbontail ray's novel iridophore. They found that intermediate filaments form an intracellular scaffold that spaces the iridosomes within the iridophores.

In crickets and grasshoppers, males have evolved cuticular structures on their forewings to produce sound via stridulation. Turchyn and Popadić identify the POU homeodomain gene *nubbin* as a regulator of the development of sound resonators on the wings of the house cricket. They propose that *nubbin*, a key player in the wing development network, has been recruited in the course of evolution of Orthoptera to evolve these new cuticular nanostructures.

Banerjee et al. investigate the interplay between nanomorphology and pigmentation during the development of butterfly scales. They show that the loss-of-function mutations in *Optix* result in both pigmentation and nanomorphology defects. By comparing these effects with mutants in melanin and/or ommochrome pathways, they propose that Optix regulates nanomorphology via its effects on pigmentation, complementing earlier studies on melanized (Matsuoka and Monteiro, 2018) and silver scales (Prakash et al., 2022).

Author contributions

CF: Writing – original draft, Writing – review & editing. AP: Writing – original draft, Writing – review & editing.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

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