frontiers | Frontiers in Ecology and Evolution

TYPE Editorial
PUBLISHED 06 May 2025
DOI 10.3389/fevo.2025.1609597

Check for updates

OPEN ACCESS

EDITED AND REVIEWED BY
Maria Ina Arnone,
Stazione Zoologica Anton Dohrn, Italy

*CORRESPONDENCE
Cédric Finet
cedric.finet@ens-lyon.org
Anupama Prakash
a.sarojini-prakash@imperial.ac.uk

†PRESENT ADDRESS
Anupama Prakash,
Department of Bioengineering, Imperial College, London, United Kingdom

RECEIVED 10 April 2025
ACCEPTED 22 April 2025
PUBLISHED 06 May 2025

CITATION
Finet C and Prakash A (2025) Editorial: Biological and physical basis of the development of integument and associated structures.
Front. Ecol. Evol. 13:1609597.
doi: 10.3389/fevo.2025.1609597

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

Cédric Finet[1*] and Anupama Prakash[2*†]

[1]Department of Biological Sciences, National University of Singapore, Singapore, Singapore, [2]Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield, United Kingdom

KEYWORDS

integument, micro- and nano-structures, morphogenesis, biomaterials, bioinspiration and biomimetics

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

References

Adler, P. N. (2019). The localization of chitin synthase mediates the patterned deposition of chitin in developing *Drosophila* bristles. *bioRxiv* [Preprint]. doi: 10.1101/718841

Airoldi, C. A., Ferria, J., and Glover, B. J. (2019). The cellular and genetic basis of structural colour in plants. *Curr. Opin. Plant Biol.* 47, 81–87. doi: 10.1016/j.pbi.2018.10.002

Akat, E., Yenmiş, M., Pombal, M. A., Molist, P., Megías, M., Arman, S., et al. (2022). Comparison of vertebrate skin structure at class level: A review. *Anat. Rec.* 305, 3543–3608. doi: 10.1002/ar.24908

Balakrishnan, D., Prakash, A., Daurer, B. J., Finet, C., Chen Lim, Y., Shen, Z., et al. (2024). Nanoscale cuticle mass density variations influenced by pigmentation in butterfly wing scales. *arXiv* [Preprint]. doi: 10.48550/arXiv.2305.16628

Bao, H., Liu, Y., Duan, Y., Chen, L., and Yang, Q. (2024). The beetle's structural protein CPCFC making elytra tough and rigid. *Insect Sci* [Preprint]. doi: 10.1111/1744-7917.13443. Online ahead of print.

Barthlott, W., Mail, M., and Neinhuis, C. (2016). Superhydrophobic hierarchically structured surfaces in biology: Evolution, structural principles and biomimetic applications. *Philos. Trans. R. Soc A Math. Phys. Eng. Sci.* 374, 20160191. doi: 10.1098/rsta.2016.0191

Brien, M. N., Enciso-Romero, J., Lloyd, V. J., Curran, E. V., Parnell, A. J., Morochz, C., et al. (2022). The genetic basis of structural colour variation in mimetic *Heliconius* butterflies. *Philos. Trans. R. Soc B Biol. Sci.* 377, 20200505. doi: 10.1098/rstb.2020.0505

Carroll, S., Amsbury, S., Durney, C. H., Smith, R. S., Morris, R. J., Gray, J. E., et al. (2022). Altering arabinans increases *Arabidopsis* guard cell flexibility and stomatal opening. *Curr. Biol.* 32, 3170–3179.e4. doi: 10.1016/j.cub.2022.05.042

Chatterjee, M., Siegel, K. J., Loh, L. S., McDonald, J. M. C., and Reed, R. D. (2023). Butterfly wing iridescence is regulated by *araucan*, a direct target of optix and spalt. *bioRxiv* [Preprint]. doi: 10.1101/2023.11.21.568172

Cosgrove, D. J. (2024). Structure and growth of plant cell walls. *Nat. Rev. Mol. Cell Biol.* 25, 340–358. doi: 10.1038/s41580-023-00691-y

De Giorgio, E., Giannios, P., Espinàs, M. L., and Llimargas, M. (2023). A dynamic interplay between chitin synthase and the proteins Expansion/Rebuf reveals that chitin polymerisation and translocation are uncoupled in *Drosophila*. *PloS Biol.* 21, e3001978. doi: 10.1371/journal.pbio.3001978

Ficarrotta, V., Hanly, J. J., Loh, L. S., Francescutti, C. M., Ren, A., Tunström, K., et al. (2022). A genetic switch for male UV iridescence in an incipient species pair of sulphur butterflies. *Proc. Natl. Acad. Sci. U. S. A.* 119, e2109255118. doi: 10.1073/pnas.2109255118

Finet, C. (2024). Developmental genetics of cuticular micro- and nano-structures in insects. *Curr. Opin. Insect Sci.* 65, 101254. doi: 10.1016/j.cois.2024.101254

Finet, C., Decaras, A., Armisén, D., and Khila, A. (2018). The achaete–scute complex contains a single gene that controls bristle development in the semi-aquatic bugs. *Proc. R. Soc B Biol. Sci.* 285, 20182387. doi: 10.1098/rspb.2018.2387

Finet, C., Decaras, A., Rutkowska, M., Roux, P., Collaudin, S., Joncour, P., et al. (2022). Leg length and bristle density, both necessary for water surface locomotion, are genetically correlated in water striders. *Proc. Natl. Acad. Sci. U. S. A.* 119, e2119210119. doi: 10.1073/pnas.2119210119

Finet, C., Ruan, Q., Bei, Y. Y., You En Chan, J., Saranathan, V., Yang, J. K. W., et al. (2023). Multi-scale dissection of wing transparency in the clearwing butterfly *Phanus vitreus*. *J. R. Soc Interface* 20, 20230135. doi: 10.1098/rsif.2023.0135

Garcia-Elfring, A., Sabin, C. E., Iouchmanov, A. L., Roffey, H. L., Samudra, S. P., Alcala, A. J., et al. (2023). Piebaldism and chromatophore development in reptiles are linked to the tfec gene. *Curr. Biol.* 33, 755–763.e3. doi: 10.1016/j.cub.2023.01.004

Ghimire, A., Dahl, R. B., Shen, S. F., and Chen, P. Y. (2024). Shark skin denticles: from morphological diversity to multi-functional adaptations and applications. *Adv. Funct. Mater.* 34, 2307121. doi: 10.1002/adfm.202307121

Ghosh, N., and Treisman, J. E. (2024). Apical cell expansion maintained by Dusky-like establishes a scaffold for corneal lens morphogenesis. *Sci. Adv.* 10, eado4167. doi: 10.1126/sciadv.ado4167

Gow, N. A. R., and Lenardon, M. D. (2023). Architecture of the dynamic fungal cell wall. *Nat. Rev. Microbiol.* 21, 248–259. doi: 10.1038/s41579-022-00796-9

Hopkins, B. R., Barmina, O., and Kopp, A. (2023). A single-cell atlas of the sexually dimorphic *Drosophila* foreleg and its sensory organs during development. *PloS Biol.* 21, e3002148. doi: 10.1371/journal.pbio.3002148

Hsiung, B. K., Shawkey, M. D., and Blackledge, T. A. (2019). Color production mechanisms in spiders. *J. Arachnol.* 47, 165–180. doi: 10.1636/JoA-S-18-022

Ikeda, K. N., Belevich, I., Zelaya-Lainez, L., Orel, L., Fussl, J., Gumulec, J., et al. (2024). Dynamic microvilli sculpt bristles at nanometric scale. *Nat. Commun.* 15, 3733. doi: 10.1038/s41467-024-48044-3

Inagaki, S., Wada, H., Itabashi, T., Itakura, Y., Nakagawa, R., Chen, L., et al. (2024). Endoplasmic reticulum patterns insect cuticle nanostructure. *bioRxiv* [Preprint]. doi: 10.1101/2024.08.20.608717

Itakura, Y., Wada, H., Inagaki, S., and Hayashi, S. (2024). Mechanical control of the insect extracellular matrix nanostructure. *bioRxiv* [Preprint]. doi: 10.1101/2024.08.20.608778

Li, W., Zhou, R., Ouyang, Y., Guan, Q., Shen, Y., Saiz, E., et al. (2024). Harnessing biomimicry for controlled adhesion on material surfaces. *Small* 20, 2401859. doi: 10.1002/smll.202401859

Liu, J., Chen, Z., Xiao, Y., Asano, T., Li, S., Peng, L., et al. (2021). Lepidopteran wing scales contain abundant cross-linked film-forming histidine-rich cuticular proteins. *Commun. Biol.* 4, 491. doi: 10.1038/s42003-021-01996-4

Lloyd, V. J., Burg, S. L., Harizanova, J., Garcia, E., Hill, O., Enciso-Romero, J., et al. (2024). The actin cytoskeleton plays multiple roles in structural color formation in butterfly wing scales. *Nat. Commun.* 15, 4073. doi: 10.1038/s41467-024-48060-3

Lloyd, V. J., and Nadeau, N. J. (2021). The evolution of structural colour in butterflies. *Curr. Opin. Genet. Dev.* 69, 28–34. doi: 10.1016/j.gde.2021.01.004

Loh, L. S., DeMarr, K. A., Tsimba, M., Heryanto, C., Berrio, A., Patel, N. H., et al. (2025). Lepidopteran scale cells derive from sensory organ precursors through a canonical lineage. *Development* 152, DEV204501. doi: 10.1242/dev.204501

Lu, W., Si, M., Le, X., and Chen, T. (2022). Mimicking color-changing organisms to enable the multicolors and multifunctions of smart fluorescent polymeric hydrogels. *Acc. Chem. Res.* 55, 2291–2303. doi: 10.1021/acs.accounts.2c00320

Matsuoka, Y., and Monteiro, A. (2018). Melanin pathway genes regulate color and morphology of butterfly wing scales. *Cell Rep.* 24, 56–65. doi: 10.1016/j.celrep.2018.05.092

McPhedran, R. C., Nicorovici, N. A., McKenzie, D. R., Botten, L. C., Parker, A. R., and Rouse, G. W. (2001). The sea mouse and the photonic crystal. *Aust. J. Chem.* 54, 241–244. doi: 10.1071/CH01054

Middleton, R., Sinnott-Armstrong, M., Ogawa, Y., Jacucci, G., Moyroud, E., Rudall, P. J., et al. (2020). *Viburnum tinus* fruits use lipids to produce metallic blue structural color. *Curr. Biol.* 30, 3804–3810.e2. doi: 10.1016/j.cub.2020.07.005

Miserez, A., Schneberk, T., Sun, C., Zok, F. W., and Waite, J. H. (2008). The transition from stiff to compliant materials in squid beaks. *Science* 319, 1816–1819. doi: 10.1126/science.1154117

Murata, S., Rivera, J., Noh, M. Y., Hiyoshi, N., Yang, W., Parkinson, D. Y., et al. (2022). Unveiling characteristic proteins for the structural development of beetle elytra. *Acta Biomater.* 140, 467–480. doi: 10.1016/j.actbio.2021.12.021

Muthukrishnan, S., Arakane, Y., Noh, M. Y., Mun, S., Merzendorfer, H., Boehringer, C., et al. (2022). Chitin in insect cuticle. *Adv. Insect Physiol.* 62, 1–110. doi: 10.1016/bs.aiip.2022.03.001

Noh, M. Y., Kramer, K. J., Muthukrishnan, S., Kanost, M. R., Beeman, R. W., and Arakane, Y. (2014). Two major cuticular proteins are required for assembly of horizontal laminae and vertical pore canals in rigid cuticle of *Tribolium castaneum*. *Insect Biochem. Mol. Biol.* 53, 22–29. doi: 10.1016/j.ibmb.2014.07.005

Pasquina-Lemonche, L., Burns, J., Turner, R. D., Kumar, S., Tank, R., Mullin, N., et al. (2020). The architecture of the Gram-positive bacterial cell wall. *Nature* 582, 294–297. doi: 10.1038/s41586-020-2236-6

Pesch, Y. Y., Riedel, D., and Behr, M. (2017). *Drosophila* Chitinase 2 is expressed in chitin producing organs for cuticle formation. *Arthropod Struct. Dev.* 46, 4–12. doi: 10.1016/j.asd.2016.11.002

Prakash, A., Dion, E., Banerjee, T. D., and Monteiro, A. (2024). The molecular basis of scale development highlighted by a single-cell atlas of *Bicyclus anynana* butterfly pupal forewings. *Cell Rep.* 43, 114147. doi: 10.1016/j.celrep.2024.114147

Prakash, A., Finet, C., Banerjee, T. D., Saranathan, V., and Monteiro, A. (2022). *Antennapedia* and *optix* regulate metallic silver wing scale development and cell shape in *Bicyclus anynana* butterflies. *Cell Rep.* 40, 111052. doi: 10.1016/j.celrep.2022.111052

Ru, H., Finet, C., and Monteiro, A. (2024). Calreticulin is required for cuticle deposition and trabeculae formation inside butterfly wing scale cells. *bioRxiv* [Preprint]. doi: 10.1101/2024.09.12.612608

Saranathan, V., and Finet, C. (2021). Cellular and developmental basis of avian structural coloration. *Curr. Opin. Genet. Dev.* 69, 56–64. doi: 10.1016/j.gde.2021.02.004

Seago, A. E., Brady, P., Vigneron, J. P., and Schultz, T. D. (2009). Gold bugs and beyond: A review of iridescence and structural colour mechanisms in beetles (Coleoptera). *J. R. Soc Interface* 6, S165–S184. doi: 10.1098/rsif.2008.0354.focus

Seale, M., Cummins, C., Viola, I. M., Mastropaolo, E., and Nakayama, N. (2018). Design principles of hair-like structures as biological machines. *J. R. Soc Interface* 15, 20180206. doi: 10.1098/rsif.2018.0206

Sun, J., and Bhushan, B. (2012). Hierarchical structure and mechanical properties of nacre: A review. *RSC Adv.* 2, 7617–7632. doi: 10.1039/c2ra20218b

Surapaneni, V. A., Blumer, M. J., Tadayon, K., McIvor, A. J., Redl, S., Honis, H. R., et al. (2024). Ribbontail stingray skin employs a core–shell photonic glass ultrastructure to make blue structural color. *Adv. Opt. Mater.* 12, 2301909. doi: 10.1002/adom.202301909

Sviben, S., Spaeker, O., Bennet, M., Albéric, M., Albéric, M., Dirks, J. H., et al. (2020). Epidermal cell surface structure and chitin-protein co-assembly determine fiber architecture in the locust cuticle. *ACS Appl. Mater. Interfaces* 12, 25581–25590. doi: 10.1021/acsami.0c04572

Thayer, R., Allen, F., and Patel, N. H. (2020). Structural color in *Junonia* butterflies evolves by tuning scale lamina thickness. *Elife* 9, e52187. doi: 10.7554/eLife.52187

Thayer, R., and Patel, N. H. (2023). A meta-analysis of butterfly structural colors: their color range, distribution and biological production. *J. Exp. Biol.* 226, jeb245940. doi: 10.1242/jeb.245940

Totz, J. F., McDougal, A. D., WAgner, L., Kang, S., So, P. T. C., Dunkel, J., et al. (2024). Cell membrane buckling governs early-stage ridge formation in butterfly wing scales. *Cell Rep. Phys. Sci.* 5, 102063. doi: 10.1016/j.xcrp.2024.102063

Watson, G. S., Watson, J. A., and Cribb, B. W. (2017). Diversity of cuticular micro- and nanostructures on insects: properties, functions, and potential applications. *Annu. Rev. Entomol.* 62, 185–205. doi: 10.1146/annurev-ento-031616-035020

Wilts, B. D., Zubiri, B. A., Klatt, M. A., Butz, B., Fischer, M. G., Kelly, S. T., et al. (2017). Butterfly gyroid nanostructures as a time-frozen glimpse of intracellular membrane development. *Sci. Adv.* 3, e1603119. doi: 10.1126/sciadv.1603119

Zhang, W., Tian, H., Liu, T., Liu, H., Zhao, F., Li, X., et al. (2023). Chameleon-inspired active tunable structural color based on smart skin with multi-functions of structural color, sensing and actuation. *Mater. Horizons* 10, 2024–2034. doi: 10.1039/d3mh00070b