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Morphological investigations on the wing scales of four species of common Indian butterflies

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ABSTRACT: Wing scales of butterflies exhibit extreme diversity in shape, size, colour, and number of spines. They are sub microscopic with a length of 300 to 600 µm and a breadth of 150 to 400 µm. A typical scale possessed a flat body with basal pedicel and apical crown which is provided with a varying number of pointed edges called spines. Investigations were carried out on the morphology of wing scales in four species of common butterflies viz., *Pachilopta hector* (Linnaeus 1758), *Troides minos* (Cramer 1779), *Jamides celeno* (Cramer 1775) and *Eurema andersonii* (Linnaeus 1758). Wings of *P. hector* possessed nine types of scales, the crown of all are with pointed spines of varying numbers, ranging from one to five. The southern birdwing *T. minos*, possessed nine types of scales. A major portion of wings with black colour is due to black coloured scales but white bands of the forewings are due to transparent and colourless scales. The prominent yellow colour on the hind wings of this butterfly is due to the presence of a single type of scale with a round crown that is devoid of spines and is fully packed with yellow pigment. *Jamides celeno* possessed twenty different types of scales, most of them are devoid of spines and the ridges within the scales are not clear. Scales on the upper surface of the wing with ashy blue colour and scales of white bands on the lower surface of the wings are identical and are transparent and colourless. The common grass yellow *E. andersonii* possessed twenty five different types of scales, of which thirteen are on the black margins of wings and twelve are in the yellow portions of wings. Almost half of the total number of scales in the yellow portions of the wing is transparent and colourless and in coloured scales distribution of pigment is not uniform. This is the first report on the different types of wings scales in the selected butterflies. © 2022 Association for Advancement of Entomology

KEY WORDS: Morphology, scales, types, spines, distribution of pigment, bands

INTRODUCTION

Lepidopteran insects produce their wing colours in two fundamentally distinct ways; via scale pigmentation (chemical colour) and through scale morphology (physical colour) (Vértesy *et al*., 2004). Butterflies and moths belong to the order Lepidoptera. The order is classified into 46 super families (Imms *et al*., 2013; Heppner, 2010) which are subdivided into 126 families (Heppner, 2022), each one with characteristic unique features. Butterflies are adored for their striking metallic colours and varied wing patterns. Presence of thousands of microscopic scales on their wings is the reason behind the diverse coloration in the animal kingdom. The periodic nanostructures of chitin and air in the scales of the wings produce the structural colours of butterflies (Ghiradella, 1991; Vukusic *et al*., 2002). Scales possess various types

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of pigments such as melanin with varying shades of colour from brown to black, derivatives of uric acid, and flavones of larval food, which provide different shades of yellow (Nijihout and Koch, 1991; Scoble, 1995). The structural colours of butterflies and moths have been attributed to a wide range of physical processes, including multilayer interference, diffraction, Bragg scattering, Tyndall scattering and Rayleigh scattering.

The upper surface of the wing contains two types of scales called cover and basal scales; which are alternately arranged in an overlapping manner. Scales are embedded in the scale sockets of the wing membrane. Therefore, the colours are believed to be due to the functional difference among the scales and actually they are modified hairs. Scale contains photonic nanostructures that are mainly constructed with chitinous matrix, including air holes (Scoble, 1995; Kristensen *et al.*, 2007). These microscopic scales attract more and more attention because they constitute a transition between random and crystalline order (Shawkey *et al.*, 2009 a, b; Liu *et al.,* 2011; Munisha Murali and Sheeba, 2022). Scales have different functions like pattern formation, pheromone dispersal, thermoregulation, mimicry, visual signalling and protection from enemies (Archana *et al.*, 2022). The most relevant studies about butterfly scales and photonics were done by Ghiradella (1998) and dealt mainly with the biological aspect of the subject. Despite this, butterfly wing scales represents a less studied area and demand the immediate attention of researchers to unravel the hidden truth behind these beautiful organisms. There are no detailed studies reported from India based on butterfly wing scales (Imms *et al*., 2013; Heppner, 2022). A study was undertakenon the morphology of wing scales in four species of common butterflies viz., *Pachilopta hector* (Linnaeus 1758)*, Troides minos* (Cramer 1779), *Jamides celeno* (Cramer1775) and *Eurema andersonii* (Linnaeus 1758).

MATERIALS AND METHODS

Selection of butterfly samples

Butterfly species that are commonly present in the premises of the University College, Thiruvananthapuram, Kerala were selected for the study. The selected butterfly families are Papilioniodae, Pieridae and Lycaenidae, from which four species, *P. hector, T. minos*, *J. celeno* and *E. andersonii,* were chosen for the study. Butterflies were identified using the taxonomic keys (Lowalker and Kunte, 2020; Heppner, 2022). Common grass yellow (*E. andersonii*) belonging to family Pieridae, has a yellow coloured body with a brown border. The yellow coloured regions and black border of the wing were analysed. Common cerulean (*J. celeno*) is a member of family Lycaenidae. The upper side of the butterfly has pale ashy white colour and the lower side of the butterfly have a greyish brown colour with transverse white bands. Both sides of the wings were selected for the study. Southern bird wing (*T. minos*) and crimson rose (*P. hector*) are members of super family Papilionoidea. The southern bird wing has a black coloured forewing with white streaks; the hind wing has a yellow colour with black margins. The yellow spot on the hind wing, white streaks on the forewing, and black colour of the wing were selected for collecting scales. Crimson rose is a swallow-tailed butterfly with black-coloured forewing with white patches. The hind wing has red or crimson coloured spots with tail-like extension. The areas selected for the study include red spots, white patches, and black colour on the wing. Butterflies collected for taxonomic studies were preserved as dry specimens and such samples were used for scale morphology.

Extraction of scales

Scales were collected from the upper and lower sides of the wing of the *J. celeno* butterfly. The upper surface of the wing is ashy blue and the lower surface is brown with white streaks and black eye spots possessing pseudo antennae at the posterior margin of the hind wing. Three regions were selected from the lower side of the wing and they are black spots on the hind wing, a brown border, and white wavy lines. Three regions of the *P. hector* were selected for closer observation. They are white-coloured streaks on the forewing, red-coloured spots on the hind wing, and black colour on certain parts of the wing. The selected regions from *T. minos* include black-coloured regions and white shades on the wing. Yellow coloured regions of the hind wing were also selected for the study. In *E. andersonii,* the yellow coloured region and black border of the wings were selected for the study. Scales were gently separated from the wings by using soaked cotton attached to the pinhead and transferred to a microscopic slide, with a drop of water and covered with a coverslip. A microscope (Labomed, USA) with a camera was used to save the images, and measurements were recorded with help of micrometry software within the microscope.

RESULTS AND DISCUSSION

A typical scale has three-parts, a crown with spines, a flat body or blade, and a pedicel or stalk for the attachment to the scale socket. The body has upper and lower lamina. Longitudinally running parallel ridges are present in the lamina (Fig. 1). Wings of *P. hector* (Fig. 2) are black coloured with white bands or streaks on the forewings and prominent crimson spots on the hindwings. Nine different types of scales were identified from this butterfly (Fig. 3). Scale crown with a variable number of spines such as one, three, four or five could be identified in the study. Scale with a single spine appeared as a transparent lancet with a length of 480µm and width of 110 µm was identified from the black region (Fig. 3b4). The other three types of scales in the black region are black coloured but their spines in the crown varied from three to five and the intensity of black shade was different in individual scales. (Fig. 3b1- b3). Four types of crimsoncoloured scales were identified from crimson spots (Fig. 3a1- a4), with differences in size, number of crown spines, distribution of crimson pigments, and on possession of parallel lines. The length of these scales ranged from 460 to 490 µm and the width ranged from 160 to 310 µm. Only one type of scale was observed from the white bands of the forewings and were transparent, colourless with four spines (Fig. 3c).

Wing colour of the *T. minos* is a mixing of black shades with white prominence at the immediate vicinity of wing veins in forewings and bright yellow coloured with prominent black margins in hind wings. Nine different types of scales were identified from *T. minos* (Fig. 4). Some of the black coloured scales in their wings are very large and their length was up to 600 µm. White patches of forewing showed five types of scales, differing in shape, size and number of spines on the crown. The number of spines ranged from three to five and all of them were transparent and colourless. Scales of the white patches exhibited a length of 400 to 460 µm and width of 170 to 280 µm and they are the smallest scales in these butterflies (Fig. 5a1-a5). The yellow region exhibited only one type of scale which has a different morphology when compared with other scales. The yellow scale is devoid of spines and the scale appeared like a spatula (Fig. 5b). The black region of the hind wings and forewings showed three types of scales (Fig. 5c1- c3). One type of black scale has three spines and the others are broad with six spines on the crown.

The ashy blue colour on the upper surface of wings in *J. celeno* (Fig. 6) possessed six different types of scales (Fig.7). All these scales are transparent and colourless. The crown of all these scales is either devoid of spines or spines with smooth undifferentiated spines (Fig. 7a1 - a6). The length of the transparent scales ranged between 370 and 580µm and the breadth is between 180 and 200µm. Scales under the surface of the wings with brown shades of colour exhibited nine different types of scales (Fig. 8) and their pigmentation is not uniform. Some of the scales in the brown region possessed granulated ridges (Fig. 8b1), others are devoid of such granules. Crown of all these scales are smooth and spines are undifferentiated. Some of the scales in the brown regions are lancet like with length ranges between 560 and 580 µm and width ranges between 40 and 50 µm (Fig. 8b5). Black eye spot on the lower surface of the wing *J. celeno* possessed four different types of scales (Fig. 8c1 to c4). Unlike the scales in other regions of the wing, scales of the black eye spot possessed well-differentiated spines on the crown, the number of which varied from three to six (Fig. 8c1, c4). Among these four different types of scales one group of scales are narrow and long with length up to 600 µm and breadth up to 120 µm (Fig. 8c1 and c2), and the other group of scales are broad with length up to 500 μm and breadth up to 400 μm (Fig. 8c3, c4). All the seven white bands seen as traversed by the underside of the forewing exhibited only one type of transparent and colourless scale (Fig. 8 d1). Due to their extremely transparent nature, the scales were nearly invisible under the microscopic field. In total, 20 different types of scales are identified in *J. celeno*. Compared to the scales of *T. minos* and *P. hector* scales of *J. celeno* are thin and scale ridges are not visible.

Common grass yellow *E. andersonii* is very common butterfly with a wingspan of 40-50mm. It is recognized by their bright yellow wings with a black margin on the upper side of the wings. Both pairs of wings (Fig. 9) are yellow with black margins. Twelve different types of scales were identified from the black margins and they exhibited significant variation in size, shape, colour and the number of spines (Fig.10). Majority of scales were with three or four spines and all of them are small with 320 to 350 μm length and 300 to 320 μm width. Another small proportion of black scales with two spines and among them one type of long narrow and broad triangular with the tapering basal end (Fig. 10a6) were detected.Yellow portions of wings in *E. andersonii* exhibited thirteen different types of scales (Fig. 11). Among them almost half the proportion exhibited yellow pigmentation (Fig. 11 b1- b6) but the body is not filled with pigment. Crown of these scales exhibited variation in shapes such as flat, round, and round spines. The other half proportion of scales are completely transparent and colourless (Fig. 11 b7 - b13). A total of 25 different types of scales were identified from the wings of *E. andersonii.*

Ghiradella (1991, 1998) has extensively studied the structure of the Lepidopteran wing using TEM micrographs and reported that the chitinous wing scale has different parts, and they are organized into the upper and lower lamina. The lamina has numerous rows of parallel ridges with cross ribs in between them, are called as trabeculae. It has now been proposed that all structurally coloured butterfly scale nanostructures, regardless of anatomical position (on the surface or within the scale) or spatial organization (multilayer or crystal-like), share the same physical process for producing colour. The mechanism is called as coherent scattering, which means the differential reinforcement and interference of visible wavelengths by light scattered within the nanostructureswhich differed in refractive index (Prum *et al.,* 2006). Transparent scales were obtained from all the white regions, irrespective of the butterfly taken. Transparent scales reflect all the incident light resulting in white colour as seen in the case of southern bird wing and crimson rose. Papilionids exhibit more structurally coloured scales than other families. This group represents all the structurally coloured scale types reported so far in all other families (Ghiradella, 1985). Transparent, yellow, red and dark-coloured scales are observed in the papilionid butterflies examined.

Pachliopta hector is one of the spectacular species of swallow tails, with a red body and wing span of 90-120 mm. The upper side of the fore wings is bluish-black and fore wings carry interrupted, and irregular discal and apical white bands, and the hind wings bear nearly round and marginal rows of bright crimson crescent spots (Ramana *et al*., 2004). Nine different types of scales could be identified in this butterfly. Eventhough the background colour of wings is black the colour of scales in this region of wings ranged with different shades of brown and the colour variation is due to variation in the melanin pigment deposited in them. Among the four species of the studied butterflies, *P. hector* possessed wing scales with clear and sharp ridges in the scale lamina.

Commonly known as southern birdwing *T. minos* is one of the largest Indian butterflies with a wing span ranging between 140-190 mm, is considered as least concern on IUCN red list (Sharmila and Thatheyus, 2014; Jiji *et al*., 2015). Now, it is described as the state butterfly of Karnataka state in India, and this species is endemic to the Western Ghats of south India (Jiji *et al*., 2015; Shawkey *et al*., 2009a, b). The forewings of are black coloured with white shades along their cellular disc regions. The hind wings have a bright yellow colour with black coloured veins and black markings at their

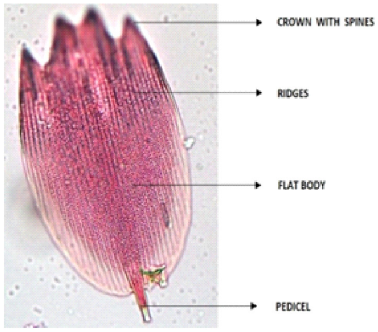

Fig. 1

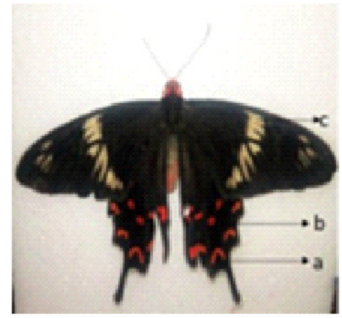

Fig. 2

Fig. 1 Structure of a typical wing scale

Fig. 2 *Pachliopta hector* L.- Three regions of the butterfly selected for the study are marked as a, b & c

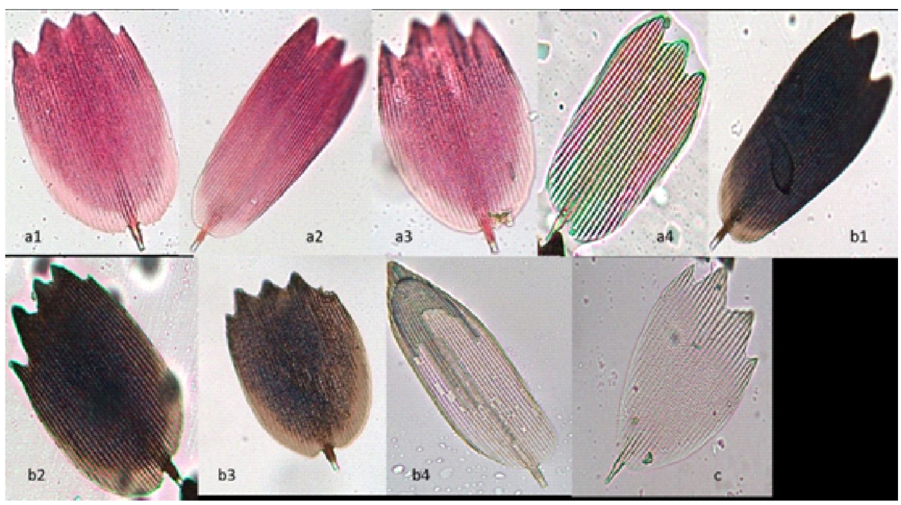

Fig. 3 Wing scale diversity of *Pachliopta hector* L. obtained from regions which are marked as a, b and c.Length ranged from 460 to 490 µm and width ranged from 160 to 310 µm

Fig. 4

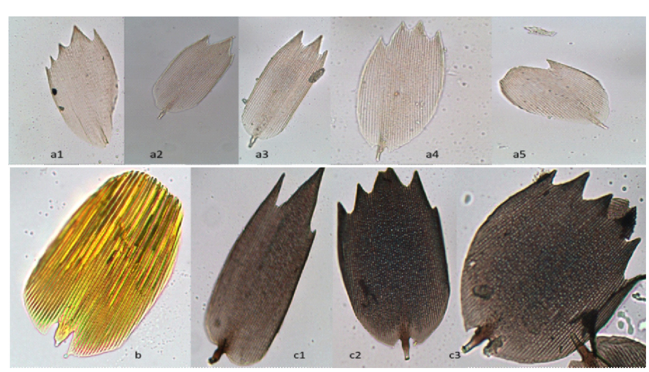

Fig. 5

Fig. 4 *Troides minos* -Three regions of the butterfly selected for the study are marked as a,b & c Fig. 5 Wing scale diversity of scales obtained from *Troides minos* -Scales of the white patches exhibited length of 400 to 460 µm and width of 170 to 280 µm and are the smallest scales in these butterflies

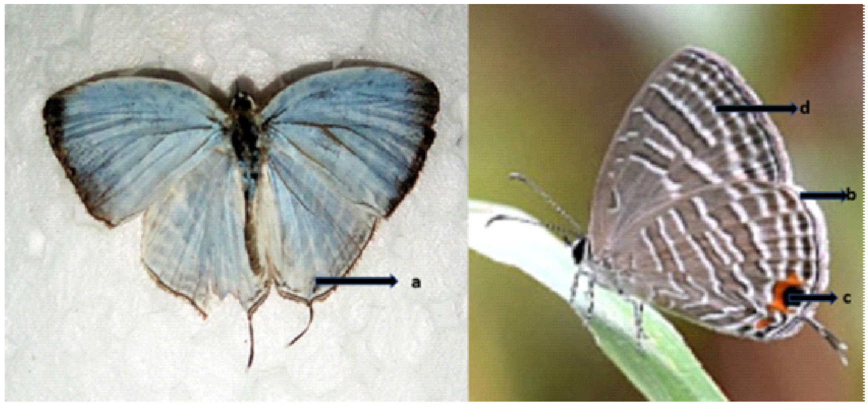

Fig. 6 *Jamedes celeno*-Upper and lower sides of the butterfly scales removed from the marked regions are indicated as a,b,c and d

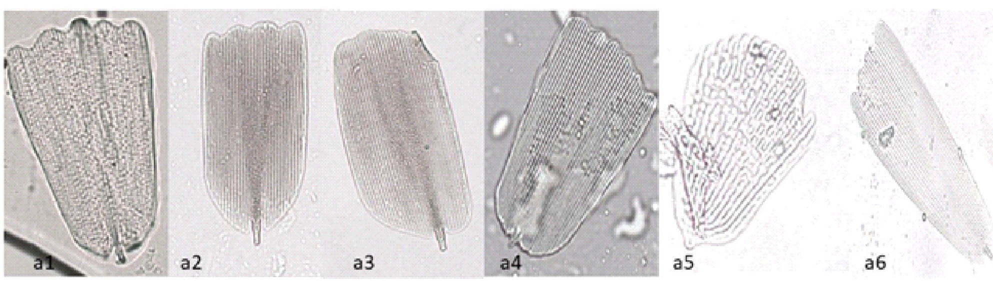

Fig. 7 Scales of ashy blue colour in *Jamedes celeno*- Six different types of scales are identified from ashy blue side of wing (Fig. 7a1 to a6). Length ranged between 370 and 580 µm and breadth between 180 and 200 µm

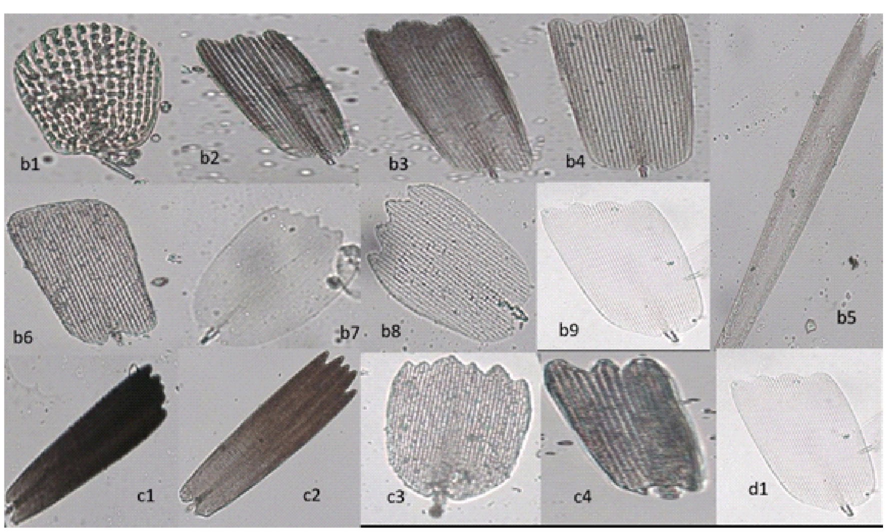

Fig. 8 Scales of brown region, black eye spot and white lines in *Jamedes celeno* (rod like with length between 560 and 580 µm and width between 40 and 50 µm (Fig. 8 b5). Two types of scales in the eye spot are black, narrow and long with length upto 600 µm and breadth upto 120 µm (Fig. 8 c1 and c2), the other two group of scales are broad with length upto 500 µm and breadth upto 400 µm (Fig. 8c3 and c4). Scales of the white bands are transparent (Fig. 8 d1)

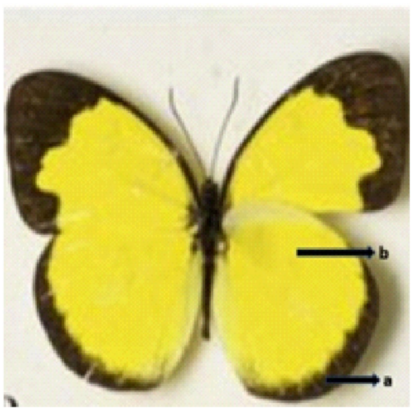

Fig. 9

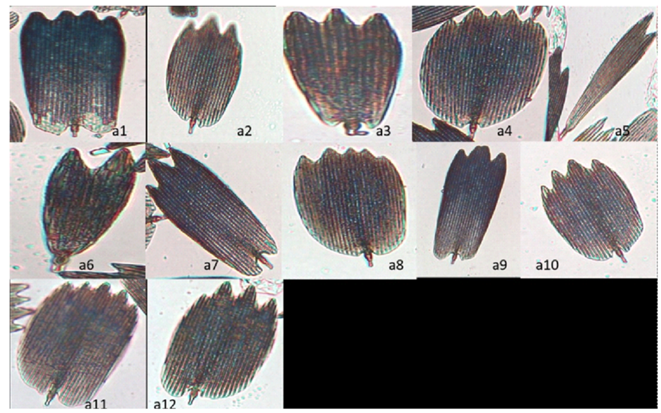

Fig. 10

Fig. 9 *Eurema hecabe* Fig. 10 Scales on the black margins of wings in *Eurema hecabe* - Majority of scales are with three or four spines with 320 to 350 μm in length and 300 to 320 μm width

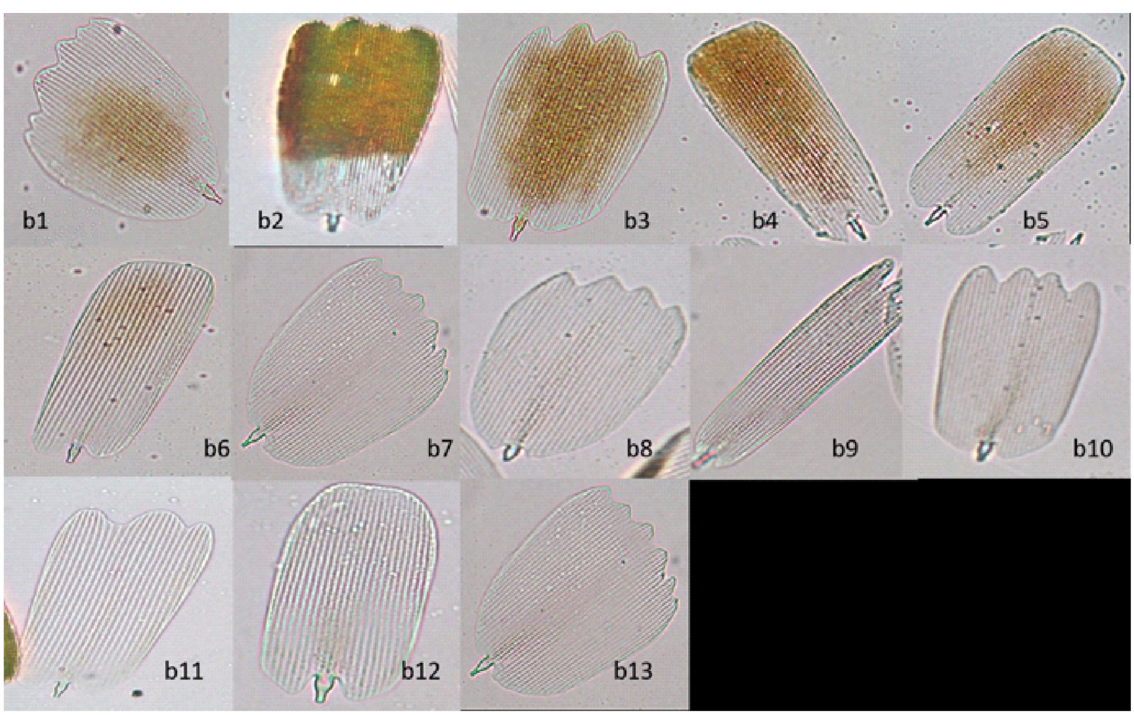

Fig. 11 Scales on the yellow regions of wings in *Eurema hecabe* - Among the scales, almost half the population exhibited yellow pigmentation (b1 to b6) but the body is not completely filled with pigment. Crown of the scales exhibited variation in shape such as flat, round and with round spines. Other scales are completely transparent and colourless (b7 to b13)

margins. A black spot was observed between the hind wing's 5th and 6th disc cellular veins (Ghiradella, 1991). Among the four species of the studied butterflies, *T. minos* exhibited largest of all scales with length upto 600 µm.

In *J. celeno* mostly transparent and brown-coloured scales observed. The vivid colours on the upper surface of wings in the lycaenids, normally ranges between the blues and violets but extends to the ultraviolet and greens, arise from microstructural components of the undifferentiated structures embedded withinthe transparent scales. This will enable the white light falling upon the scales to interfere one with another; the resulting a species specific colour which is a cumulative action of physical effects and not due to pigmentation (Onslow, 1921; Mason, 1926). Extensive anatomical studies of lycaenid wing scales have revealed three different spatial organizations that give rise to structural colours. Lycaenid butterflies produce iridescent colours via a multilayer elaboration within the lumen of the scale into a Urania-type microstructure (Tilley and Eliot, 2002). Wilts *et al.* (2009, 2011) suggested that lycaenids apparently can modulate their coloration by subtle changes in their scale structures. *J.celeno* is a sexually dimorphic species with wide distribution in the south and East Asia (Eastwood *et al*., 2005) and is a tailed bluish-white butterfly with the terminal margin of the forewing having a narrow border. When the wings are kept extended, the upper surface appeared as ashy blue but in the folded state, it has a whitish appearance. The lower surface of the wings is greyish brown traversed by seven white lines. At the folded state hind wings possessed a pair of pseudo antennae and prominent black eye spots. The characteristic feature observed in this butterfly is the difference on the arrangement of transparent and colourless scales on either side of wings. Scales arranged on the upper surface of wingsare in such a way to cause diffraction of light, leading to ashy blue colour and identical scales on the lower surface of wings which differ on the pattern of arrangement, resulting reflection of lightleads to white colour.

Transparent and yellow coloured scales were obtained from pierid butterflies. Previous work demonstrated that the pigments of pierid wings belong to the class of pterins (Wilts *et al*., 2009, 2011; Archana *et al*., 2022). Various pterins have different absorption spectra, which can be restricted to the ultraviolet or can extend into the yellow or green wave length range. Another study reports that the scales of pierid butterflies have usually numerous pigmented beads, which absorb light at short wavelengths and enhance light scattering at long wavelengths. Males of many species of the pierid subfamily Coliadinae have ultraviolet-iridescent wings because the scale ridges are structured into a multilayer reflector. The iridescence is combined with a yellow or orange-brown coloration, causing the common name of the subfamily, the yellows or sulfurs (Stavengaen and Leertouwer, 2007). In the present study E. *andersonii* showed 25 different types of scales. Conspicuous yellow colour in both pairs of wings in *E. andersonii*is due to packed arrangement of completely colourless and transparent scales and another group of scales with their distal end is yellow but proximal end is colourless.The study demonstrates that the structure of the scale is different in different species of butterflies and the butterflies under the same family also showed different types of scales. There were transparent and colourless scales with differences in scale morphology from the all-white regions examined, irrespective of the butterfly species selected. From this, it is evident that scales play a fundamental role in the colour production and pattern formation of butterfly wings.

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REFERENCES

Archana B., Joy Sharmila E., Snegapriya M., Rangesh K. and Susaritha S. (2022) Fourier transform infra-red spectrochemical analyses of Pieridae butterfly wings. Entomon 47(2): 103-112. doi.org/10.33307/entomon.v47i2.709

Eastwood R.G., Kitching R.L. and Manh H.B. (2005) Behavioral observations on the early stages of *Jamides celeno* (Cramer) (Lycaenidae) at Cat Tien National Park, Vietnam:an obligate myrmecophile? Journal of the Lepidopterists' Society 59: 219-222.

Ghiradella H. (1985) Structure and development of iridescent butterfly scales: the Papilionidae as a showcase family. Annals of the Entomological Society of America 78: 252-264.

Ghiradella H. (1991) Light and colour on the wing-structural colours in butterflies and moths. Applied Optics 30: 3492-3500.

Ghiradella H. (1998) Hairs bristles, and scales. In: Microscopic anatomy of invertebrates (ed. M. Locke). Insecta 11A: 257-287.

Heppner J.B. (2010) Manual of Lepidoptera : Butterflies and Moths In : Encyclopedia of Entomology, Springer, Dordrecht. doi.org.10.1007/ 0- 306 – 48380 – 7 – 633.

Heppner J.B. (2022) Manual of Lepidoptera: Butterflies and Moths of the World, CRC Press. ISBN 9780849321610.

Imms A.D., Richard O.W. and Davies R.G. (2013) Imms' General Textbook of Entomology. Eleventh Edition, Springer, India.

Jiji J.V., Mashkoor K. and Lazar V.K. (2015) Molecular phylogeny of the southern birdwing butterfly, *Troides minos*, indicates its origin before the rise of Himalayas. International Journal of Recent Scientific Research 6: 6662-6665.

Kristensen N.P., Scoble M.J. and Karsholt O. (2007) Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. Zootaxa 1668: e747.

Liu F., Dong B., Zhao F., Hu X., Liu X. and Zi J. (2011) Ultranegative angular dispersion of diffraction in quasiorderedbiophotonic structures. Optics Express 19: 7750 -7755.

Lovalekar R. and Kunte K. (2020) List of identification keys on Butterflies of India–*ifound butterflies. org*. In: Kunte, K. Sondhi, S.S. and Roy, P. (Eds.) Butterflies of India. v3: 03. India Foundation of Butterflies.

Mason C.W. (1926) Structural colors in insects. I. Journal of Physical Chemistry 30(3): 383-395.doi.org/10.1021/j150261a009.

Munisha Murali S. and Sheeba S. (2022) Wing scale patterns of *Hypolimnas bolina* (Linnaeus, 1758) (Lepidoptera: Nymphalidae). Entomon 47(2): 157-164. doi.org/10.33307/entomon.v47i2.716

Nijhout H. F. and Koch P. B. (1991) The distribution of radio labelled pigment precursors in the wing patterns of nymphalid butterflies. Journal of Research in Lepidoptera 30: 1-13.

Onslow H. (1923) I - On a periodic structure in many insect scales, and the cause of their iridescent colours. Philosophical Transactions of the Royal Society of London Series B 211: 382-390, 1-74.

Prum R.O., Quinn T. and Torres R.H. (2006) Anatomically diverse butterfly scales all produce structural colours by coherent scattering. Journal of Experimental Biology 209(4): 748-765.

Ramana S.P.V., Atluri J.B. and Reddy C.S. (2004) Autecology of the endemic Crimson rose butterfly *Pachilopta hectar* (Lepidoptera – Papilionidae), Journal of the Indian Institute of Science 84: 21-24.

Scoble M.J. (1995) The Lepidoptera: form, function, and diversity. Oxford University Press.

Sharmila E. and Thatheyus A. (2014) A first report of southern birdwing *Troides minos* (Cramer) in Alagar Hills, Tamil Nadu India. Research Journal of Agriculture and Environment Management 3: 74-76.

Shawkey M.D., Morehouse N.I. and Vukusic P. (2009a) A protein palette: colour materials and mixing in birds and butterflies. Journal of the Royal Society Interface 6: S221–231.

Shawkey M.D., Saranathan V., Palsdottir H., Crum J., Ellisman M.H., Auer M. and Prum R.O. (2009b) Electron tomography, three dimensional Fourier analysis and colour prediction of a three-dimensional amorphous biophotonic nano structure. Journal of the Royal Society Interface 6: S213-220.

Stavenga D.G. and Leertouwer H.L. (2007) Colourful butterfly wings: scale stacks, iridescence and sexual dichromatism of Pieridae. Entomologische Berichten (Dutch) 67(5): 158-164.

Tilley R.J.D. and Eliot J.N. (2002) Scale microstructure and its phylogenetic implications in lycaenid butterflies (Lepidoptera, Lycaenidae).

Transactions of the Lepidopterological Society of Japan 53: 153-180.

Vértesy Z., Bálint Z., Kertesz K., Mehn D., Kiricsi I., Lousse V., Vigneron J.-P. and Biró L.P. (2004) Modifications to wing scale microstructures in lycaenid butterflies. Microscopy and Analysis 18: 25-27.

Vukusic P. S. J.R., Lawrence C.R. and Wootton R.J. (2002) Limited – view of iridescence in the butterfly *Ancyluris meliboeus.* Proceedings of the Royal Society B: Biological Sciences 269(1486): 7–14. doi: 10.1098/rspb.2001.1836

Wilts B.D., Leertouwer H.L. and Stavenga D.G. (2009) Imaging scatterometry and microspectroph otometry of lycaenid butterfly wing scales with perforated multilayers. Journal of the Royal Society Interface 6 (suppl_2): S185-192.

Wilts B.D., Pirih P. and Stavenga D.G. (2011) Spectral reflectance properties of iridescent pierid butterfly wings. Journal of Comparative Physiology A 197(6): 693-702.

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