

Wing Surface of Lepidopteran Insects (Butterflies and Moths): Layered Structure Composed of Two Kinds of Scales

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Wing surfaces of most lepidopteran insects (butterflies and moths) are covered with abundant scales. Most scales are classified into two kinds, called cover and basal scales, which are overlapped each other to make the layered structure on the wing surface. The detailed morphology, functions, and development of this layered structure are reviewed and discussed.

Key words: Lepidopteran Insects, Wing, Scale, Surface, Layered Structure

1. Introduction

The wing surfaces of lepidopteran insects (butterflies and moths) are covered with abundant scales. It is suggested that the scales present various functions in communication, defence, flight, thermoregulation, feeding, and waterproof, which are reasonably attributed to the functions of a single scale (Ghiradella, 1998; Goodwyn *et al.*, 2009).

In most species of lepidopteran insects, wings have two kinds of scales, called cover and basal (or ground) scales, except for some specialized scales such as scent ones (Barth, 1949; Downey and Allyn, 1975; Yoshida and Aoki, 1989; Yoshida *et al.*, 2000). Since the cover scales literally cover the basal ones, all the cover scales are visible while all the basal ones are almost invisible in the intact wing. Accordingly, the butterfly wing surface is virtually composed of a double layer of scales. This feature of the butterfly wing surface, however, has been poorly addressed, since a number of the wing surface functions have been attributed to those of a single scale. In this article, I review and discuss the detailed morphology, the functions, and the development of the wing surface composed of two kinds of scales, mainly of the small white cabbage butterfly, *Pieris rapae*.

2. Arrangement of Two Kinds of Scales

Figure 1 shows the small cabbage butterfly, *Pieris rapae*. In most lepidopteran species, including *Pieris*, wings are covered with abundant scales. These scales are arranged in the anteroposterior direction of the wing, and those anteroposterior rows of scales are arranged in the proximodistal direction at regular intervals (Fig. 2). Most of the two kinds of scales are alternately arranged within each anteroposterior row of scales, and accordingly right and left halves of the basal scales are covered with their adjacent cover scales (Figs. 3A–C). Yoshida and Aoki (1989) reported that two cover or basal scales are rarely adjacent, which occurs with

the low rate of about 4% (Fig. 3D). Since the alternation of two kinds of scales is fairly precise, the scales form a virtual double-layered row composed of the upper layer of cover scales and the lower layer of basal scales.

Basal parts of the scales are narrow, and their tips are plunged into the sockets which project on the wing surface (Fig. 3). Thus, the narrow basal parts of the scales are unable to completely cover the whole wing surface around them. In the intact wing, however, the wing surface areas around them are completely covered with the wide apical parts of the proximally adjacent scales. This partial overlapping of the anteroposterior scale rows is proximodistally repeated to completely cover the whole wing surface. Thus, the partial overlapping of the scale rows and the precise alternation of two kinds of scales within those rows complementarily contribute to the complete covering of the whole wing surface with scales.

3. Roles of the Layered Structure Composed of Two Kinds of Scales

It is suggested that some “structural colors” (Kinoshita and Yoshioka, 2005) are generated or modified through the layered structure, as described below. It is preliminarily reported (Yoshida *et al.*, 1989; Yoshida, 1992) that the blue color on the wing of the Chinese swallowtail, *Papilio xuthus*, is likely generated through this layered structure composed of cover and basal scales (Fig. 4). The cover scale with blue color in the intact wing was almost invisible when it was detached from the wing and put on the white paper, while this scale presented blue color when it was put on the black paper. When the cover scale was observed through the transmitted natural light, it presented brownish yellow. These results suggest that the blue color of the cover scales on the intact wing of *Papilio* is likely the color not of blue pigments but of scattered light, and that the other light transmitted through the cover scale is absorbed by the black basal scales, which may contribute to emphasize the blue color of the cover scales. Yoshioka and Kinoshita (2004) reported that the structural blue color of the *Morpho* butter-



Fig. 1. *Pieris rapae* (female) (Yoshida, 2002). The distance between the apical tips of the right and left forewings about 4.7 cm.

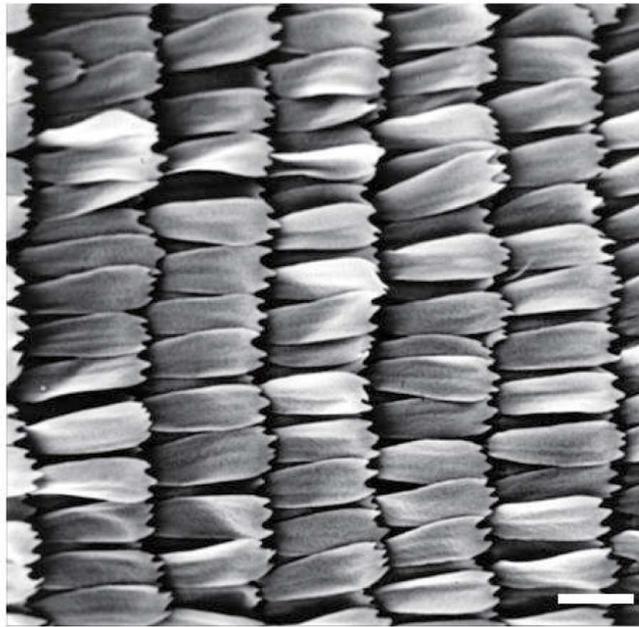


Fig. 2. Scanning electron micrograph of scales in the right wing of *Pieris* (female) (Yoshida and Aoki, 1989). Distal is to the right. This direction is the same as in Figs. 3–5 and 7.

fly, *Morpho didius*, is modified through the layered structure composed of cover and basal scales; the cover scales diffuse the structural blue color. The *Morpho* wing presents the blue or purple color depending on the vision angle, and they indicated that the cover scales contribute to making the blue color region more widely visible. Furthermore, the basal scales absorb the transmitted light to emphasize the blue color of the cover scales.

Yoshida (1992) proposed another role of the layered structure composed of cover and basal scales, taking the scale-wing attachment force into account. Rubbing the wing surface moderately with a piece of sticky tape, cover scales were easily removed and basal ones were exposed (Fig. 3B). The exposed basal scales could not so easily removed as cover scales, which indicates that basal scales are

attached to the wing more firmly than cover scales.

It is indicated that the scale-detaching is responsible for protecting the lepidopterans from being stuck to the spider web (Eisner *et al.*, 1964); the lepidopteran eludes out of the spider web by leaving only its scales on it as if it took off its “clothes”. Thus, the scale-detaching contributes to the lepidopteran life. On the other hand, it appears that the scale-detaching may not be beneficial to it, since the scales have a number of functions which also contribute to it. It seems that the scale-detaching may give the two apparently inconsistent effects on the lepidopteran life. It is possible that the layered structure composed of the two kinds of scales may solve this apparent inconsistency of the scale-detaching effects, as described below. In eluding out of the spider web, it is assumed that most of the detached scales may be the

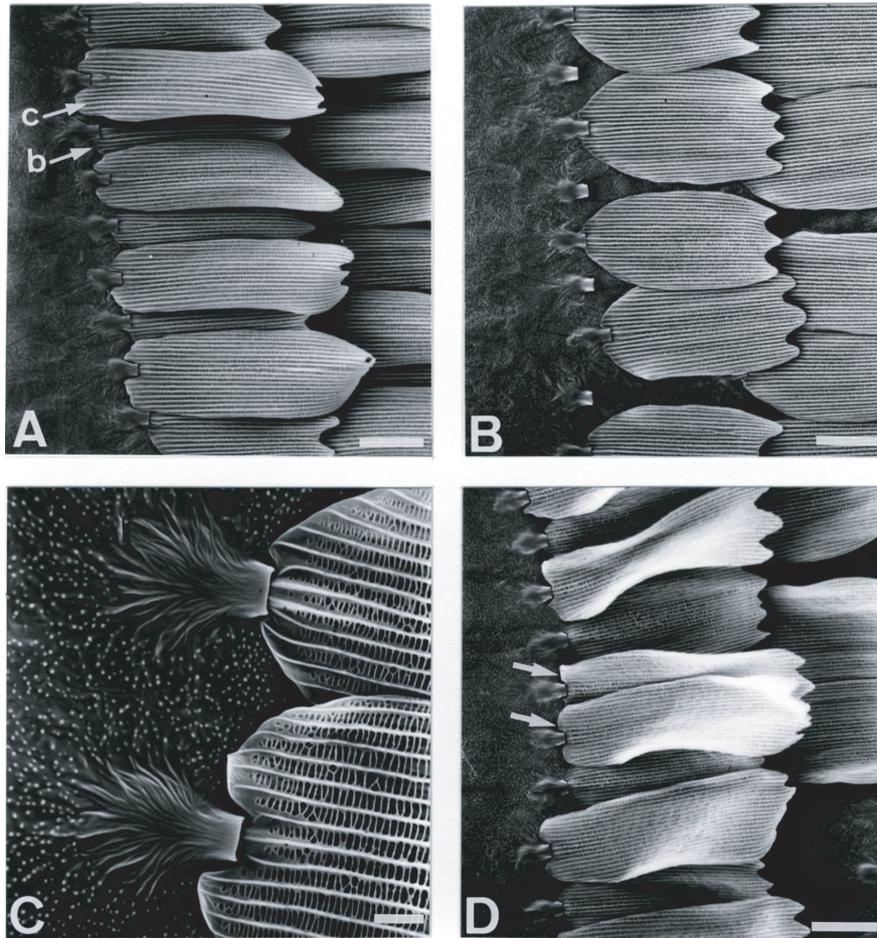


Fig. 3. Scanning electron micrograph of scales and sockets of the *Pieris* wing (female) (Yoshida and Aoki, 1989). Some scales are removed along the anteroposterior scale row. The exposed sockets, to which the scales are attached, are visible. (A) c: cover scales, b: basal scales. Cover and basal scales are alternately arranged. Bar: 30 μm . (B) Pairs of basal scales and sockets are separated by the sockets without scales. Bar: 30 μm . (C) Basal parts of cover (upper) and basal (lower) scales. Shape of the part near the socket of a cover scale differs from that of the basal one. Bar: 5 μm . (D) Two cover scales, pointed by arrows, are adjacent. Bar: 30 μm .

cover scales, since cover scales are located over basal scales and more detachable than basal ones as described above. If the exposed lower layer composed of basal scales present nearly the same functions as those of the upper layer, the functions of the wing surface are conserved, except for the elusion function.

Here I propose the third possible role of the layered structure of scales. In scale detaching out of the wing, most of cover scales slide over basal scales, that is, the lower surfaces of cover scales and the upper surfaces of basal scales are rubbed together. The upper and lower surfaces of a scale is different in morphology; the former has several longitudinal ridges and many hollow areas between them while the latter is fairly flat (Fig. 5). Thus, the effective area rubbed together in this case is much smaller than that in the case of the two flat surfaces rubbed together. Consequently, the friction is smaller in the former than in the latter; the latter case would occur if a monolayer of scales directly contacted the wing membrane surface. Furthermore, the direction of these longitudinal ridges is the same as that of the scale detaching (Fig. 5), which also contributes to lowering the friction. Taking the scale surface morphology described above into account, the layered structure of scales may be effective

in scale detaching.

To further investigate significance of the layered structure of scales, it would be worthwhile to study functions of cover and basal scales respectively

4. Development of the Layered Structure Composed of Cover and Basal Scales

As described above, morphology of the layered structure composed of two kinds of scales is mainly formed through combination of two types of arrangement: first, fairly precise alternation of cover and basal scales within anteroposterior scale rows, and second, partial overlapping of adjacent scales rows. Development of these two types of arrangement is respectively described below.

4.1 Alternation of two kinds of scales

The unadjacent distribution of pattern elements has been often explained in terms of lateral inhibition mechanism in a wide range of systems including mathematical (Page, 1959), physicochemical (Mackenzie, 1962), and biological ones (Doe and Goodman, 1985; Yoshida, 1989, 1990; Honda *et al.*, 1990; Tanemura *et al.*, 1991). In the models on biological systems, randomly differentiated cells inhibit the adjacent undifferentiated cells from being differentiated

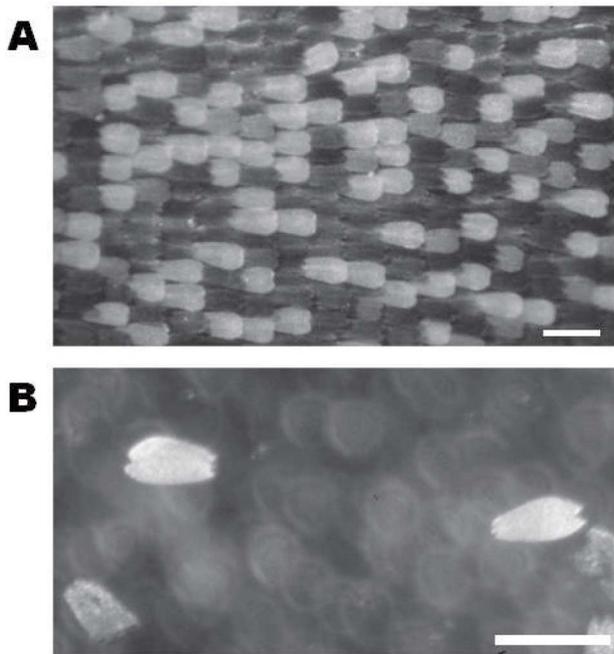


Fig. 4. Scales with blue color on the *Papilio* wing. (A) Brightest scales present blue color. Bar: 200 μm . (B) Two scales on black paper present blue color. Bar: 200 μm .

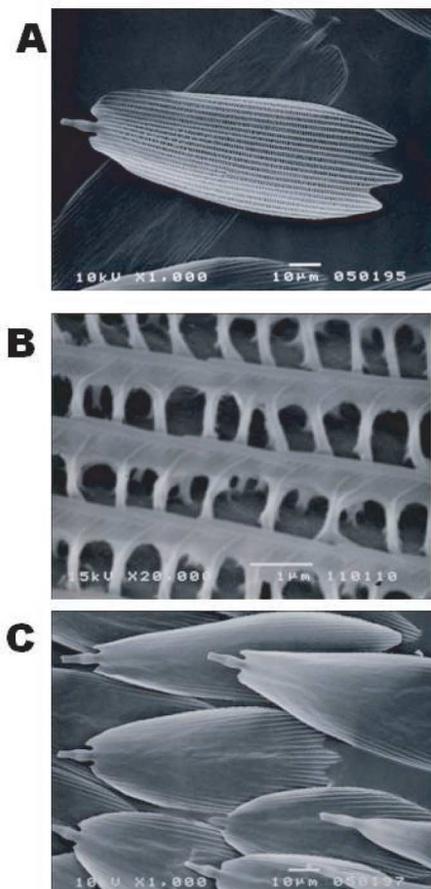


Fig. 5. Scanning electron micrograph of the scale surfaces of *Pieris* (female) (Yoshida, 2002). (A) Upper surface. Bar: 10 μm . (B) Magnified view of the upper surface. Bar: 1 μm . (C) Lower surface. Bar: 10 μm .

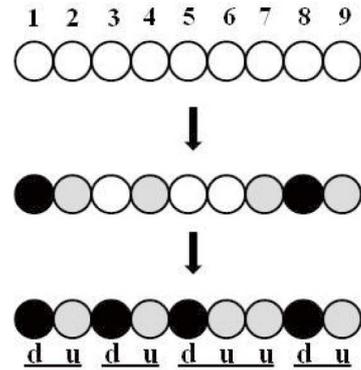


Fig. 6. One-dimensional model of random differentiation of cells under lateral inhibition. Nine cells are arranged within a row. White cells are sensitive both to differentiation signal and to inhibition one. Differentiation and inhibition proceed downward in the figure. Black cells are differentiated, while gray ones are inhibited from differentiation. After the differentiation completion, four alternation units (d-u) and one unalternation unit (d-u) are arranged within a row.

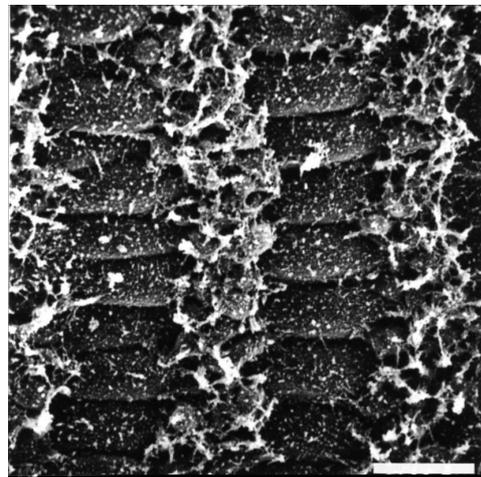


Fig. 7. Scanning electron micrograph of the rows of the scale precursor cells morphologically homogeneous (Yoshida and Aoki, 1989). Bar: 10 μm .

(=lateral inhibition), and consequently unadjacent distribution of differentiated cells is completed (Fig. 6). In the lepidopteran wing epidermis, a single cover or basal scale (cell) is differentiated from a single precursor cell at the pupal stage. Immediately before this scale differentiation, the scale precursor cells morphologically homogeneous are arranged in the anteroposterior direction of the wing (Fig. 7). Thus, the pattern that the two kinds of cells are not adjacent is formed from the likely homogeneous cell population of precursor cells arranged anteroposteriorly in the pupal wing epidermis. This system is closely similar to the one-dimensional model described by Tanemura *et al.* (1991), in which the one-dimensional pattern that differentiated cells are not adjacent while undifferentiated elements are occasionally adjacent, and the ratio of the differentiated cell number to the undifferentiated one is about 1:1.3; this ratio is about the same as that of

two kinds of scale precursor cells in the butterfly wing epidermis (Yoshida and Aoki, 1989). It can be viewed as the system being composed of two kinds of units, that is, d-u and d-u-u (d: differentiated, u: undifferentiated); the former is viewed as an alternation unit and the latter as an unalternation one. From the ratio of 1:1.3, it is estimated that the ratio of the number of d-u-u to the total number of d-u and d-u-u is about 30%. Within the scale rows in the lepidopteran wing, however, both c (cover) and b (basal) scales were rarely adjacent; c-b's, which are alternation units, are repeated in most regions of the scale rows while c-c-b's and c-b-b's, which are unalternation units, were rarely observed (Yoshida and Aoki, 1989). The ratio of the number of c-c-b and c-b-b to the total number of c-b, c-c-b, and c-b-b was about 4%, which is much less than the ratio, 30%, of the unalternation unit in the random differentiation system. It appears that this difference of these two ratios is too large to explain the fairly precise alternation of cover and basal scales within a row only by the mechanism of random differentiation under lateral inhibition. It is likely that some novel mechanism may be involved in development of the alternation of cover and basal scales.

4.2 Partial overlapping of adjacent sales rows

As described above, a single scale row does not completely cover the wing surface, since the basal parts of scales are fairly narrow (Fig. 3). In the intact wing, however, the "exposed" region of the wing surface is covered with the wide apical parts of the scales within the proximally adjacent scale row, and consequently the intact wing surface is completely covered with scales. A scale is wide in its apical part while narrow in its basal part whose narrowest tip is plunged into the socket. In all the scales of the wing, their apical directions correspond to the distal direction of the wing and their basal directions to the proximal one, and consequently all the "exposed" region of the wing surface is covered with the wide apical parts of (almost) all the scales. A scale is developed from a cellular protrusion which a scale forming cell extends, and all the scale forming cells extends their protrusions in the proximodistal direction of the wing epidermis (Süffert, 1937; Stossberg, 1937; Greenstein, 1972; Yoshida and Aoki, 1989). This coordinated cell polarity, called "planar cell polarity", is observed in a wide range of biological systems (Lawrence, 1966; Fanto and McNeil, 2004) and is indirectly involved in the complete covering of the whole wing surface with scales.

5. Conclusion

This article has addressed morphology, function, and development of the scale layer arranged on the wing surface. These three aspects of the scale layer have been poorly studied, although those of a single scale have been long and well studied. However, as this article has reviewed and discussed, some novel mechanisms are likely involved in those

aspects of the scale layer on the lepidopteran wing. Studies on them will probably give new insights into lepidopteran wings, and biological mechanics and developmental biology as well.

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