

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 compose 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