Mapping of the wing scale types of *Pieris brassicae* (Linnaeus, 1758) and *Pieris rapae* (Linnaeus, 1758) (Lepidoptera: Pieridae)

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Abstract: Butterfly wing scales exhibit a multitude of different shapes depending on their function their exact location on the wing and on the species. In this study, all scale types present on the wings of both sexes of *Pieris brassicae* (Linnaeus, 1758) and *Pieris rapae* (Linnaeus, 1758) (Lepidoptera: Pieridae) were sampled. Based on SEM pictures, scale types were discriminated from each other by using their shape and their proportions as parameters. These data served to create a map of the distribution pattern of different scale types on the wings. These maps were used to test whether wing uppersides and undersides are distinct with respect to the scale types occurring and the way they are arranged on the wing. Furthermore, we investigated whether scale shape depends on scale colour and on the sex of the butterfly and whether scale type distribution differs between the sexes and the species. The results indicate that scale type arrangement always follows a similar pattern, although scale shape differs at least slightly depending on wing surface, sex and species. Moreover, scale shape seems to be more influenced by its position on the wing than by its colour. Throughout, a high individual and intraspecific variability in scale shape was noticed.

Keywords: *Pieris brassicae, Pieris rapae,* scanning electron microscopy, butterfly wing scales, individual variability, intraspecific variability.

Versuch einer Kartierung der Flügelschuppen-Typen von *Pieris brassicae* (Linnaeus, 1758) und *Pieris rapae* (Linnaeus, 1758) (Lepidoptera: Pieridae)

Zusammenfassung: Flügelschuppen von Schmetterlingen sind je nach Art völlig unterschiedlich geformt; aber auch die Funktion der Schuppe sowie ihre genaue Lage auf dem Falterflügel bestimmt ihr Erscheinungsbild. In der vorliegenden Arbeit wurden alle unterscheidbaren Schuppentypen von *Pieris rapae* (Linnaeus, 1758) und *Pieris brassicae* (Linnaeus, 1758) (Lepidoptera: Pieridae) zusammengetragen; jeweils von einem weiblichen und einem männlichen Exemplar. Auf der Grundlage von REM-Photos wurden die einzelnen Schuppentypen anhand ihres Umrisses und ihrer Proportionen voneinander unterschieden und ihre Verteilungsmuster auf den Flügeln untersucht. Auch die Frage nach einem möglichen Zusammenhang von Form und Farbe der Schuppen wurde berücksichtigt, ebenso wie eventuelle Unterschiede im Beschuppungsmuster zwischen den Geschlechtern und/oder den beiden Arten. Die Ergebnisse deuten darauf hin, dass bei *Pieris brassicae* und *Pieris rapae* die An-ordnung der Schuppentypen einem generellen Muster folgt, unabhängig von Art und Geschlecht. Die Form der Schuppen variiert allerdings in zum Teil erheblichem Maße zwischen Flügelober- und -unterseite sowie zwischen den Geschlechtern und Arten. Ein deutlicher Zusammenhang zwischen Farbe und Form der Schuppe zeigte sich nicht. Insgesamt ist sowohl die individuelle als auch die intraspezifische Variabilität in der Schuppenform überraschend hoch.

Introduction

There exists already a large amount of literature on butterfly wing scales, for example concerning their evolutionary origin (Grodnitsky & Kozlov 1991, Galant et al. 1998), their ontogenesis (Ghiradella 1974, Ghiradella & Radigan 1976, Honda et al. 2000), the ways of colour production (Ghiradella et al. 1972, Huxley 1976, Nijhout 1985, Stavenga et al. 2004, 2006, Morehouse et al. 2007) and their morphology (Müller 1956, 1957, Mosbacher & Seyer 1983, Moss & Gibbs 1995, Anken 1995a, b, 1996, Janssen et al. 2001, Simonsen 2007, Yoshida & Emoto 2010). Yet, to our knowledge, a complete description of all the different scale types present on the wings of a given butterfly species is still lacking.

The aim of this work is therefore to map the types of cover scales (including vein scales) on all wing surfaces of *Pieris brassicae* (Linnaeus, 1758) and *Pieris rapae* (Linnaeus, 1758), (Lepidoptera: Pieridae). From a human point of view, *P. brassicae* and *P. rapae* wings exhibit a white background colour that is slightly yellowish on the wing underside. This colour is produced by pteridine pigments that are incorporated in the scale structure (Watt 1964, Watt & Bowden 1966). Well-defined black markings occur on wing uppersides and on forewing underside. Single black scales are distributed among the white ones at the wing base. The pigments that produce the black colour belong to the group of me lanins (Watt & Bowden 1966, Nijhout 1985). Due to this rather simple wing pattern, it should be possible to construct a complete overview of the scale types and that is why these two species have been chosen. The iden tification of scale types was done based on SEM pic tures. Specifically, the following questions were addres sed:

- How are the different scale types arranged on the wing?
- Do vein scales differ in their shape from scales collected from areas between veins?
- Are black and white scales alike in their shapes at places on the wing where they co-occur? Does scale shape co-vary with the colour of the scale or with its location on the wing?
- Do the scale types of wing upperside and underside differ?
- Are males and females distinct regarding the scale types found on their wings?
- Is there a difference between *P. brassicae* and *P. rapae* concerning the shape and distribution of their scale types?

Materials and methods

Specimens

One ♂ and one ♀ of *P. brassicae* and *P. rapae* were used for scale type sampling. Additionally, four further specimens of both sexes of *P. brassicae,* all with the same collection data, were surveyed in order to recognize possible intraspecific variation in scale shape. All butterflies originated from the same region in Lower Franconia, Germany.

Choice of the sampling locations on the wings

Scales were taken from the upperside and underside of the right forewing and hindwing. The sampling locations for the scale type mapping were chosen based on a preliminary check of the scale clothing of *P. brassicae* and *P. rapae* by means of a stereomicroscope (Leica Wild M8, 12- to 40-fold magnification) to highlight regions on the wings where scales differed in shape or size. The exact sampling positions in flat wing regions and on prominent veins are shown in Fig. 1. Three scales were taken from each location and sampling was mainly restricted to cover scales where they could clearly be discriminated from ground scales. Basically, the restriction to cover scales was just due to the simple reason of easier sampling.

Preparing the scales and taking SEM pictures

Scales were removed from the wing with the aid of an eyelash that had been fixed in paraffin wax at the top of a glass pipette, under a stereomicroscope at 40-fold magnification. Scales were then mounted on a SEM specimen holder covered with double-sided adhesive tape. The scales were subsequently coated with gold-platinum in a sputter (coater in intervals: 20 s) until a total sputtering time of 150 s was attained. An interruption of 30 s after each sputtering interval was used to prevent melting of the glue in the adhesive tape, to avoid sinking of the scales. Analysis of the scales was carried out on a scanning electron microscope (Zeiss DSM 962) at 230-fold magnification. The SEM was operated at an acceleration voltage of 15 kV; the distance between the front lens and the sample surface was 10 mm. SEM pictures of scales were taken using the program *Scandium.* Scale types were defined with respect to their shape and proportions (length to width ratio), which were judged by eye and not measured. Large differences in scale size were taken into account on a qualitative basis, too. Wing scale outlines were drawn after printed SEM pictures and were combined with an illustration of the respective butterfly wing where the distribution pattern of the sampled scale types was indicated (Figs. 2a–d).

Results

Pieris brassicae scales from the wing uppersides

On wing uppersides of both ♂♂ and ♀♀, there is one white main scale type dominating most of the wing area, except at the wing base, the costal and the distal margin. In the ♂, it is characterized by a longish clubbed shape (Fig. 2a: 1A, 1E) while in the ♀, it is pear-shaped and only about half as long as the ♂ scales (Fig. 2a: 1C, 1F). Black scales from the forewing apex and from the black postdiscal markings (only present in the ♀) are quite similar in shape to the white scales nearby, although the ♂ black scales are reduced in length by about a third (Fig. 2a: 1B, 1D). Scales with the shape of a long triangle co-occur in high densities with the main scale type of the ♂ (Fig. 3A). They are much more easily removable than other scales and at their top they bear a structure resembling a tuft of hair. These are scent scales (androconia), serving the dissemination of sexual pheromones (Halfter et al. 1990).

White cover scales from the wing base are more heterogeneous in shape and more compact than the main scale type (Fig. 2a: 2A, 2B, 2C, 2D).

Near the forewing costal margin, scales become narrower and in the ♂ they are remarkably shorter than the main scale type (Fig. 2a: 3A, 3B). On the hindwing, ♂ costal margin scales represent a very distinct scale type, lacking any clubbed appearance (Fig. 2a: 3C). In the ♀, scales remain pear-shaped in this area (Fig. 2a: 3E). Scales from the black apex on the hindwing have a roughly similar shape to the white costal margin scales nearby (Fig. 2a: 3D, 3F).

Towards the distal margin of forewing and hindwing, scales more or less keep the shape of the main respective scale type, but are much smaller (Fig. 2a: 4A, 4C, 4E, 4F). At the same place, black scales are shorter than white scales (Fig. 2a: 4B, 4D).

Black and white fringe scales, taken from the outermost distal margin, have the highest length to width ratio of all sampled scales and their shape rather looks flagellate (Fig. 2a: 5). They were found on the distal and inner margin of all wings, but for simplicity, they are here only demonstrated on the hindwing.

Another scale type occurs at the hindwing inner margin (below the anal vein). Particularly in the male, its shape differs significantly from the main scale type and is rather similar to the costal margin scales (Fig. 2a: 6A, 6B).

Vein scales share some general features: compared with scales from adjacent flat regions they are more slender and shorter with mostly straight lateral margins (Fig. 2a: 7A–D). Yet, there is a certain overall heterogeneity in vein scales and black vein scales are slightly smaller than white ones. Scales from the costal vein are extremely slender and were only found on the forewing (Fig. 2a: 8A, 8B).

Pieris brassicae scales from the wing undersides

On wing undersides of both sexes, scales largely resemble the pear-shaped main scale type on ♀ wing uppersides (Fig. 2b). Nevertheless, there are slight variations in

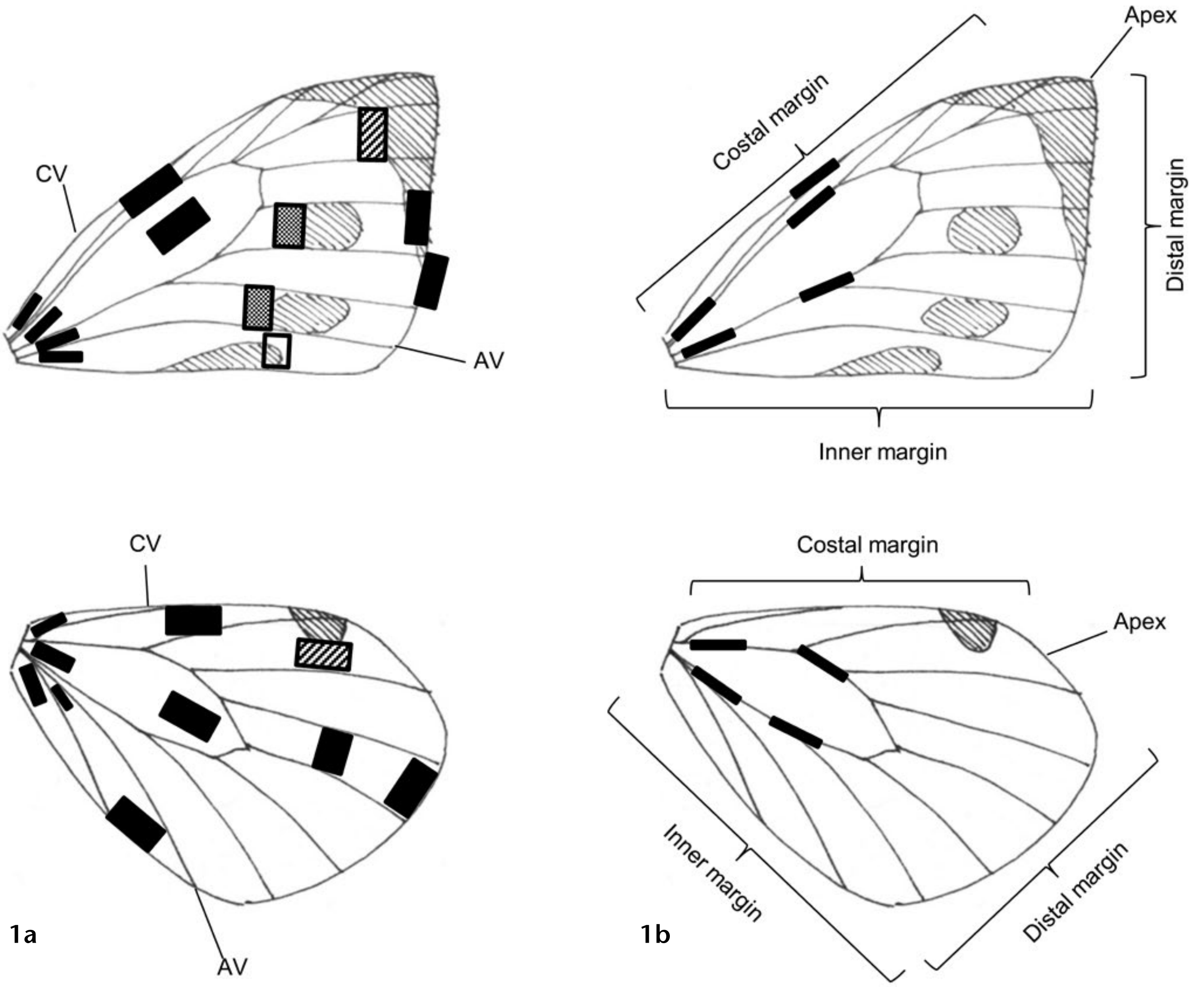


Fig. 1: Scale sampling locations and wing area nomenclature. **Fig. 1a:** Sampling locations between the veins on all four wing surfaces; striped and transparent rectangles: not sampled on wing undersides because the black apices and the black spot at the inner margin are absent; dotted and transparent rectangles: not sampled on forewing upperside of the *P. brassicae* ♂, because the respective black spots are absent. AV: Anal vein, CV: Costal vein. **Fig. 1b:** Sampling locations on the veins and indication of the wing margin names used in the text.

shape and size of this scale type depending on the wing area. In the lower half of the forewing along its horizontal axis, white scales are smaller and slightly more roundish (Fig. 2b: 1A, 1C) than in the upper half (Fig. 2b: 2A, 2C). Also at the wing base, white scales are smaller and in the ♀ broader (Fig. 2b: 3A, 3B).

On the hindwing underside, scale shape between these areas is more homogeneous in both sexes (Fig. 2b: 2E, 2F, 3C, 3D).

Shape differences between white and black scales in the areas 1 and 2 on the forewing are larger in the ♀ than in the ♂.

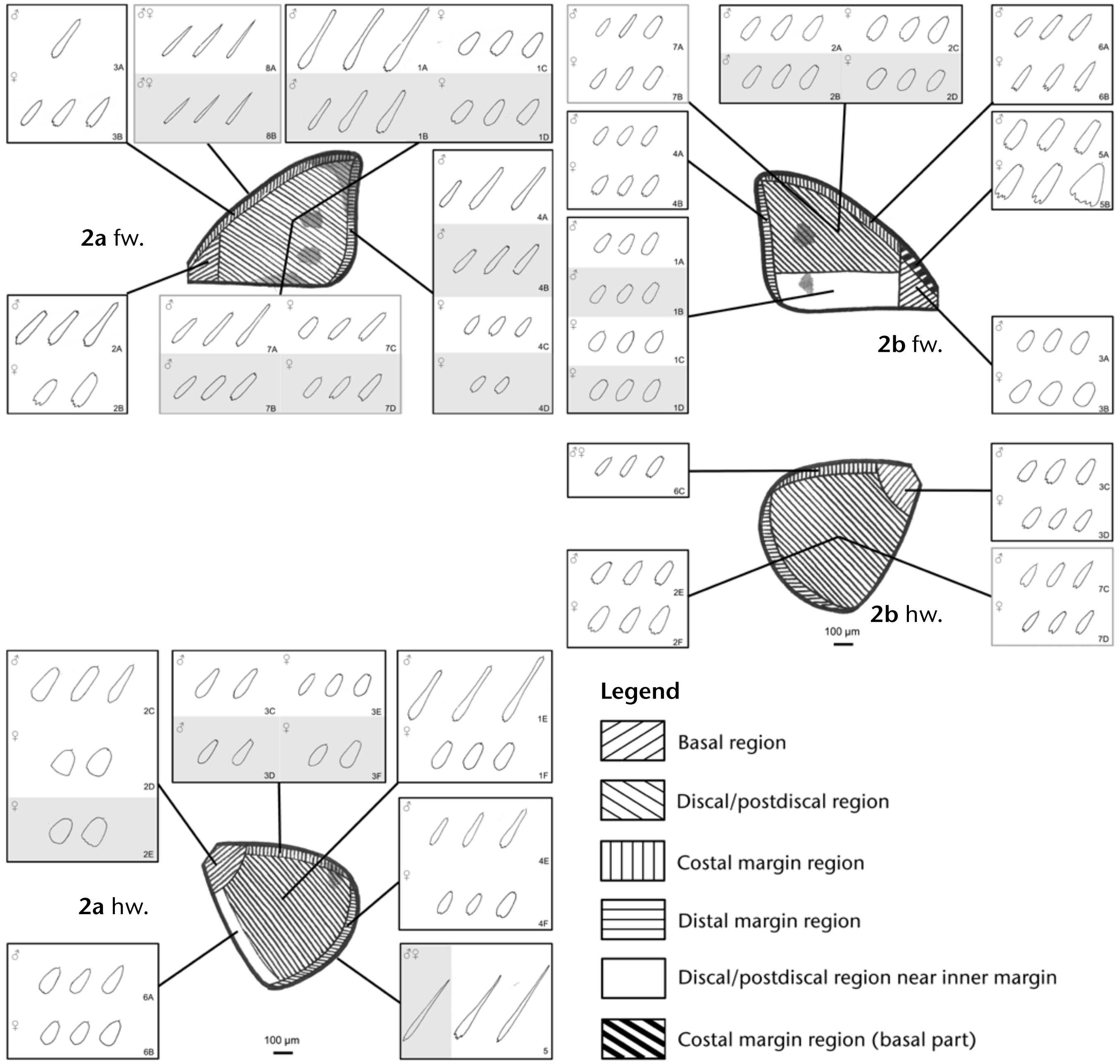
Towards the distal margin, scale size decreases (Fig. 2b: 4A, 4B). At the distal margin of the hindwing, it was mechanically impossible to remove scales using the method adopted.

A very conspicuous scale type stands out against the rather homogeneous mass of scales on ♂ and ♀ forewing undersides. It is located in the basal area directly below the costal vein, exhibits very pronounced processes at its apical margin (some nomenclature of scale morphology is shown in Fig. 4) and represents the largest scales mapped on this wing surface (Fig. 2b: 5A, 5B). Apart from that, scales near the costal margin are slenderer than the remaining scales (Fig. 2b: 6A–C).

Vein scales are partly narrower and smaller than scales from the respective flat wing areas (Fig. 2b: 7A–D). Variability in shape is high on the forewing whereas hindwing vein scales are all more or less fusiform with two processes. In nearly all areas sampled on wing uppersides and undersides, the design of the scales' apical margins proves to be very variable, ranging from rounded or scalloped to dentate with variable numbers of processes.

Pieris rapae scales from the wing uppersides

In each sex, there is one white scale type covering most of the wing area except from the basal region, the costal



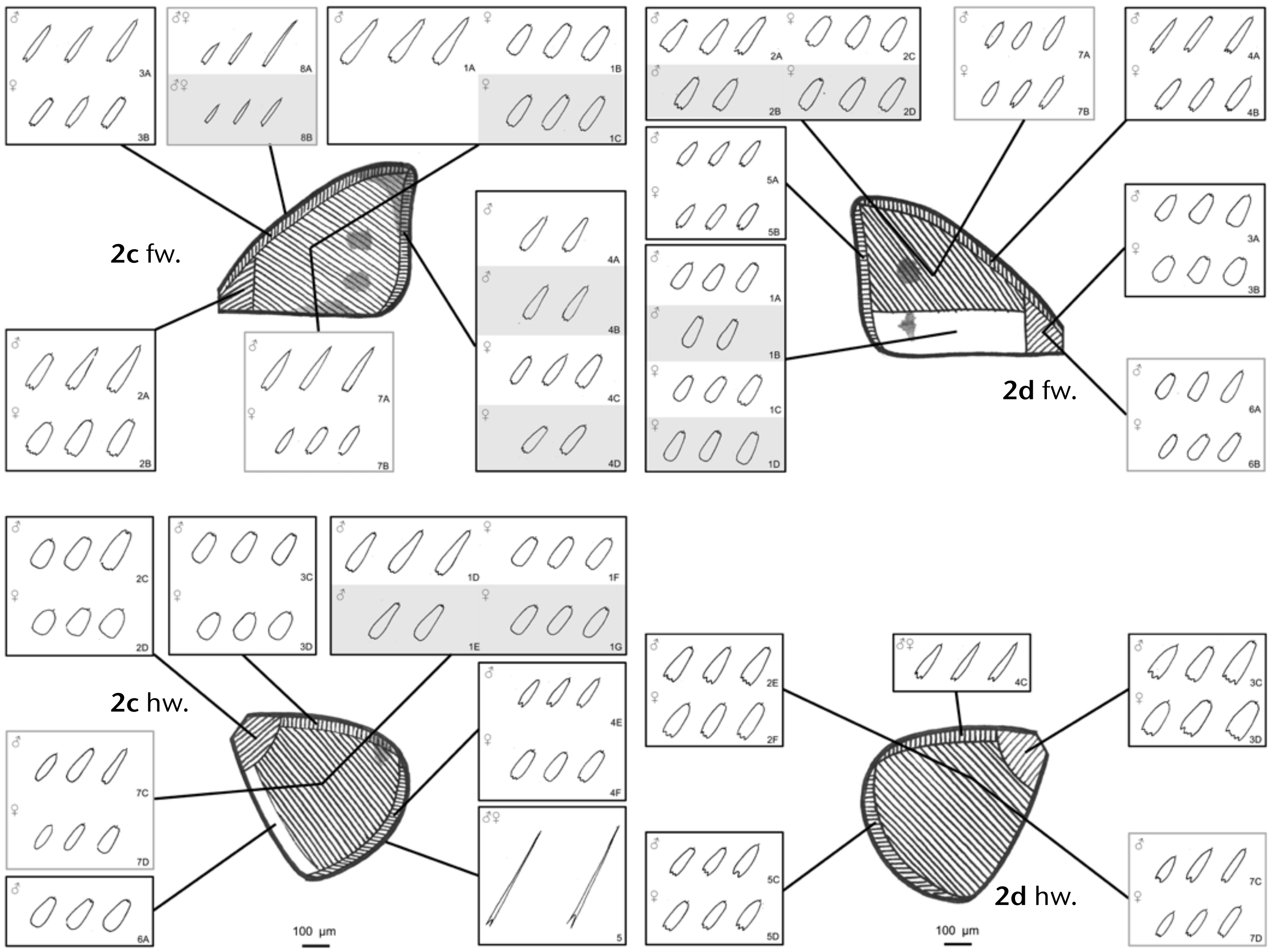
and distal margin and the ♂ hindwing inner margin. In the ♂, this main scale type can be best described as club-shaped although being just about half as long as the clubbed main scale type of *P. brassicae* (Fig. 2c: 1A, 1D). Apart from the fringe scales (Fig. 2c: 5), it represents the longest scale type mapped on ♂ wing uppersides. The respective scales of the ♀ are about one third shorter and exhibit a different shape (Fig. 2c: 1B, 1F).

Scales from the black markings (apex and postdiscal spots) and this white main scale type look similar in the ♀ (Fig. 2c: 1C, 1G). Black scales of the ♂ hindwing apex are about 10 % shorter than the white main scale type (Fig. 2c: 1E); on the forewing, only ground scales could be found at the black markings.

Forewing white basal scales do not differ in shape and size from the main scale type (Fig. 2c: 2A, 2B) whereas on the hindwing, they are more compact in each sex and also quite heterogeneous in shape (Fig. 2c: 2C, 2D).

In the direction of the costal margin, scales become slenderer on the forewing (Fig. 2c: 3A, 3B) whereas at the hindwing costal margin, ♂ scales are rather rectangular and those of the ♀ are roundish (Fig. 2c: 3C, 3D).

Towards the distal margin, scale size decreases (Fig. 2c: 4A, 4C, 4E, 4F). Black scales (originating from the marginal part of the black forewing apex) resemble the white distal margin scales in their shape and size (Fig. 2c: 4B, 4D). The different shapes of distal margin scales between forewing and hindwing can probably be attributed to the fact that on ♂ hindwings, scales were removed from the outermost distal margin whereas otherwise, they were sampled closer to the submarginal region.



Figs. 2a–d: Maps of the collected scale types. *P. brassicae* wing uppersides (**2a**) and undersides (**2b**). *P. rapae* wing uppersides (**2c**) and undersides (**2d**). Black scales are shaded in light grey, vein scales are enclosed in a grey instead of a black box. fw. = forewing, hw. = hindwing.

Fringe scales exhibit the highest length to width ratio of all scales mapped on ♂ and ♀ wings (Fig. 2c: 5).

Although variable in shape, vein scales are generally smaller and mostly slenderer than the scales from the adjacent flat areas, especially in the ♂ (Fig. 2c: 7A–D). Costal vein scales are the slenderest ones, occurring on the forewing (Fig. 2c: 8A, 8B) and black costal vein scales are at least one third shorter than white ones.

Scent scales are evenly distributed all over the ♂ wing uppersides except for the very basal region and the distal and costal margin areas. They are longish triangular in shape, bear several hairs on the top and their surface seems porous in some places (Figs. 3B, 3C).

Pieris rapae scales from the wing undersides

In both sexes scale shape differs clearly between the upper and the lower half of the forewing underside. White scales from the lower half are rather edged and mostly unsculptured (Fig. 2d: 1A, 1C) whereas those from the upper half are larger and roughly pear-shaped with dentate apical margins (Fig. 2d: 2A, 2C). This same difference in shape is also found in the black scales from the upper postdiscal spot (Fig. 2d: 2B, 2D) versus the lower postdiscal spot (Fig. 2d: 1B, 1D).

Forewing white basal scales are more compact than scales from the discal and postdiscal regions (Fig. 2d: 3A, 3B) whereas on the hindwing, such a difference is only notable in the female (Fig. 2d: compare 3C and 3D with 2E and 2F). Black basal scales have not been sampled since they were either very sparsely spread or absent.

Scales near the costal vein decrease in width as opposed to scales from non-marginal regions (Fig. 2d: 4A–C). Towards the distal margin, a strong reduction in scale size is observed, particularly on the forewing (Fig. 2d: 5A–D).

In general, scales from ♂ and ♀ are quite similar in shape on both wings, although those of the ♂ occasionally tend to be longer and have a slenderer bottom.

Vein scales are altogether narrower and partly shorter than scales from flat areas nearby (Fig. 2d: 6A, 6B, 7A–D). Vein scales at the forewing base (Fig. 2d: 6A, 6B)

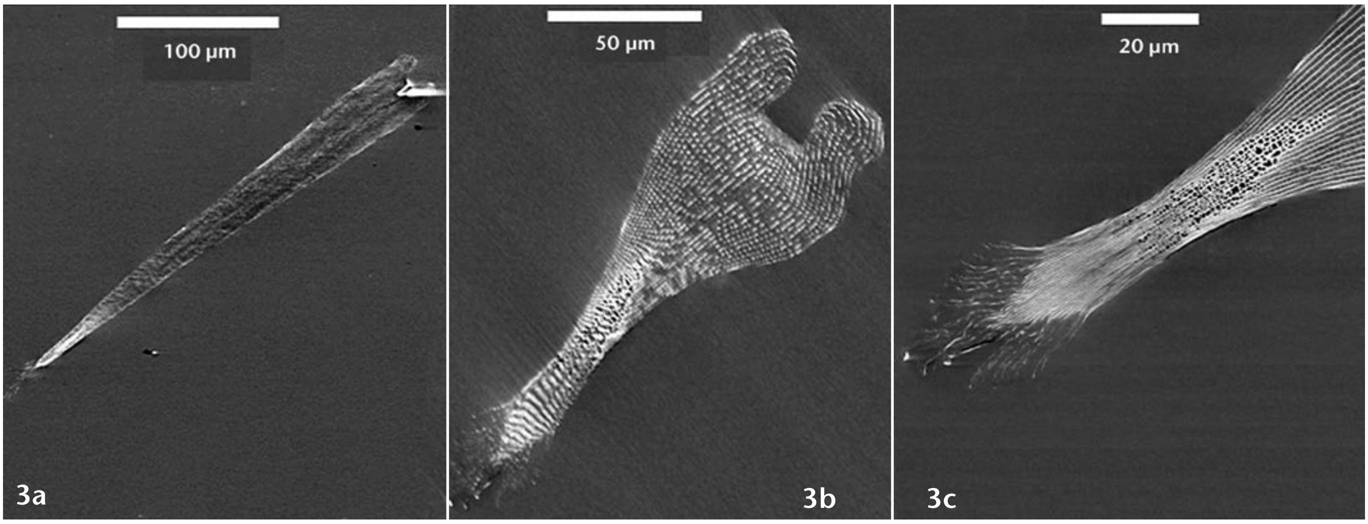


Fig. 3: Pierid scent scales. **3a:** Scent scale of *Pieris brassicae*. — **3b:** Scent scale of *Pieris rapae*. **3c:** Detail of a *P. rapae* scent scale; the hairs and the pores are clearly visible.

are more compact than vein scales in the discal region (Fig. 2d: 7A, 7B).

On all four wing surfaces examined, the scales' apical margins are very variable.

Discussion

The mapping uncovers a general pattern, independent of wing surface, sex and species: the larger part of the wing area is covered by one main scale type, whereas other distinct scale types occur, respectively, at the wing base, the costal margin, the distal margin and the ♂ hindwing upperside inner margin.

At the distal margin, scales strongly decrease in size. This trend of reduction in scale size at the distal margin does not even seem to be genus- or family-specific, since it has also been reported in Nymphalids (Kusaba & Otaki 2009, Kohnle & Wölfling 2012). Except for the hindwing upperside, scales always lose width near the costal margin. Scales at the wing base regularly exhibit a smaller length to width ratio as opposed to scales from other areas.

Vein scales are often smaller with a higher length to width ratio than scales from the flat neighboring areas. These characteristics of vein scales were already mentioned by Döring (1949). Costal vein scales look identical among the sexes and the species examined. The high preservation of their shape raises questions about some special purpose they might serve. When occurring together, these very slender scales perhaps create more surface roughness on the leading edge of the wing and thus a better uplift force (Nachtigall 1967) than would be achieved by means of broader scales.

The comparison of black and white scales from adjacent areas suggests that scale shape depends more on the position of the scale on the wing than on its colour. Cover scales from the black markings on the wing uppersides and forewing undersides very closely resemble the white cover scales from the adjacent areas in proportions and shape. The few exceptions found (Fig. 2a: compare 3E and 3F) are probably due to the low sample sizes that did not allow the demonstration of all scale type variations present at a certain place. On wing uppersides, black cover scales tend to be smaller than white ones (Figs. 2a: 1B, 3D, 4B, 4D, 5, 7B, 7D and Fig. 2c: 1E, 8B).

Although in both species, the distribution pattern of distinct scale types is essentially the same between the sexes; ♂ scale types on wing uppersides throughout exhibit a larger length to width ratio than ♀ ones (Figs. 2a and 2c). Furthermore, ♂ scales from wing uppersides are also much longer than on wing undersides, whereas in the ♀, the wing surfaces are not so distinct in scale shape. Considering this, one might suppose that the elongated scales are a sex specific trait fulfilling some special function. Among the long clubbed scales of the ♂, scent scales of similar length occur in both species and cover exactly the same distribution area. Perhaps, the long scales help to protect the scent scales from mechanical stress that might harm or remove them. Indeed, scent scales have proven to fall easily off the wing even if only little pressure is applied with the lash. This is a trait typical for scent scales of Pieridae (Halfter et al. 1990). In conformance with Halfter et al. (1990), they have furthermore only been observed on wing uppersides, a fact making protective long cover scales superfluous on wing undersides.

In both *Pieris* species, variation in scale shape turned out to be quite high within the individual. Although the proportions (e.g. the length to width ratio) are often consistent among scales from a certain location, finer details such as widening and tapering of the lateral margins vary from scale to scale. This is consistent with the results of Müller (1957) who measured and described distal margin scales in different *Colias* species. The most variable attribute, however, appears to be the design of the apical margin, a fact also mentioned by Allyn & Downey (1975), by Anken & Bremen (1996) in Papilio-

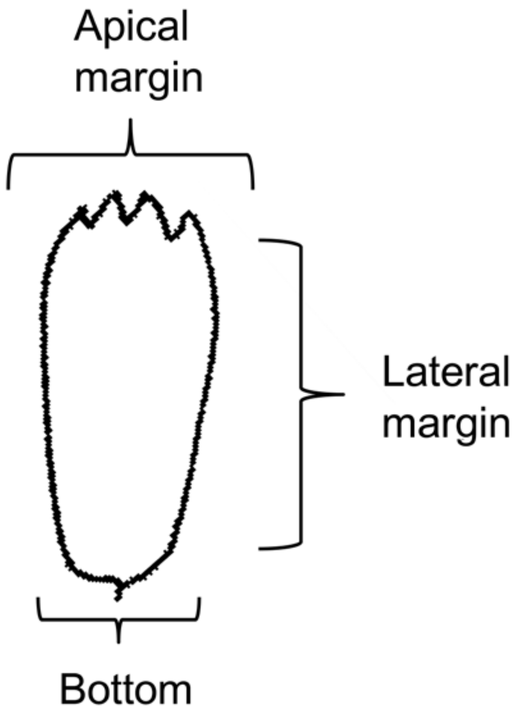


Fig. 4: Nomenclature of wing scale structure (after Allyn & Downey 1975). The stalk at the bottom is attached to the wing membrane.

nidae species and by Müller (1957). As Müller (1957) described for *Colias* species, also in *P. brassicae* a high intraspecific variation was observed when checking four additional ♂♂ and ♀♀ with the same collection data for consistency of scale apical margin design. Hence, the length to width ratio seems to be a more appropriate parameter for discriminating scale types. Yet, to allow for the variability of scale shape and to highlight instead the essential commonalities of scale types, sample size should be increased to about ten (Anken 1995a).

Since our merely descriptive pilot study has shown that there are differences in scale shape between wing surfaces and between sexes and that scale type distribution appears to follow a general pattern, it might be rewarding to follow up this topic with some larger quantitative analyses.

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