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Authors: Yoshida, Akihiro, and Emoto, Jun

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# Variations in the Arrangement of Sensory Bristles along Butterfly Wing Margins

Akihiro Yoshida<sup>1\*†</sup> and Jun Emoto<sup>2</sup>

<sup>1</sup>*JT Biohistory Research Hall, 1-1 Murasaki-cho, Takatsuki, Osaka 569-1125, Japan*

<sup>2</sup>*Biological Laboratory, Nanzan University, Yamazato-cho, Showa-ku, Nagoya 466-8673, Japan*

The surfaces of insect wings exhibit numerous sensilla, which have been suggested to have a behavioral function. Some evidence suggests that the sensory bristles along the wing margin of lepidopteran insects (butterflies and moths) are involved in the regulation of wing movement. We investigated the arrangement of sensory bristles along the wing margins of 62 species of papilionoid butterflies, using light-microscopic examination of mounts of whole wings after removing the scales surrounding the bristles. In the majority of the wings examined, bristles were located on the ventral wing surfaces and were continuously distributed along the wing margins, except in the vicinity of the wing bases. In some wings, bristles were also located on the dorsal wing surfaces, and were continuously or discontinuously distributed along the wing margins of different species. In a minority of the species studied, we observed bristle distribution in the vicinity of the wing base, discontinuous bristle distribution on both the dorsal and ventral wing surfaces, or an absence of bristles along the wing margins. This variation in the arrangement of bristles along the wing margins is discussed in relation to the reception and transmission of sensory information in the wings.

**Key words:** butterfly, wing, bristle, sensory organ, pattern variation

## INTRODUCTION

Insect wings typically exhibit a large number of sensilla on the wing veins, wing margins, and around the wing bases (Vogel, 1911; Zacwilichowski, 1933, 1934a, b; Altman et al., 1978; Palka et al., 1979). The morphology and physiology of wing sensilla have been well studied in many insects. However, the behavioral role of sensilla has been examined in relatively few cases. Hiraguchi et al. (2003) reported that hair-like sensilla around the hindwing tip constitute mechanosensilla, and are involved in the jumping escape response of the cricket *Gryllus bimaculatus*. Page and Matheson (2004) reported that widely scattered mechanosensilla on the forewing veins of the locust *Schistocerca gregaria* are involved in hindleg scratch behavior. The many sensilla found on insect wings, have traditionally been assumed to be involved in wing movement. For example, Gettrup (1966) reported that campaniform mechanosensilla near the wing base play an important role in the regulation of wing movement in the locust *Schistocerca gregaria*. Since wing-thorax articulation is distorted to generate the force necessary for wing movement, particular attention has been paid to proprioception around the articulation (Orona and Agee, 1987; Yack and Fullard, 1993; Frye, 2001). However, in a study of

the silkworm moth, *Bombyx mori*, Ai et al. (2010) reported that bristles (chaetic sensilla) distributed along the wing margin are wing beat receptors, and are likely to be necessary for maintaining the wing beat. These results indicate that sensilla located on the wing margins far from the articulation play an essential role in the regulation of the wing's own movement, in addition to the proprioceptive function of sensilla located around the articulation at the site of force generation. Ai et al. (2010) also demonstrated that the wing sensilla of the small white cabbage butterfly, *Pieris rapae*, generated neuronal responses to stimulation via vibratory airflow. These results suggest the possibility that the sensory bristles along the wing margins of a wide range of lepidopteran insects (butterflies and moths) may function as mechanosensilla, generating neuronal responses to vibratory stimuli. These mechanosensilla may thus play a significant role in the regulation of wing movement.

The distribution pattern of bristles along the wing margin is reported to be similar in *Bombyx* (Ai et al., 2010) and *Pieris* (Yoshida et al., 2001), in that the bristles are located exclusively on the ventral surface and are continuously distributed from the anterior to the lateral margin in the forewing, and from the anterior to the posterior margin in the hindwing, except in the vicinity of the wing bases. In the inchworm moth, *Cheimatobia brumata*, Vogel (1911) illustrated the same bristle arrangement as that of *Bombyx* and *Pieris*. On the other hand, Clever (1958) reported that the wax moth, *Galleria mellonella*, and the small wax moth, *Achroia grisella*, not only exhibit the same pattern of bristle arrangement as *Bombyx*, *Pieris*, and *Cheimatobia*, but also

\* Corresponding author. Phone: +81-75-392-6098;

Fax : +81-75-392-6098;

E-mail: yoshida.akihiro09@gmail.com

† Present address: 113-2 Arisugawa-cho, Kawashima, Nishikyo-ku, Kyoto 615-8191, Japan  
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possess sensory bristles on the dorsal wing surfaces. To further investigate variations in bristle arrangement, we examined the wings of 62 species of butterflies in the superfamily Papilionoidea. We found that the majority of wings exhibited the same bristle arrangements as previously reported. However, a minority of the wings exhibited bristle arrangements with several novel features. In the current report, we describe these arrangements and discuss them in relation to the reception and transmission of sensory information in the wings.

## MATERIALS AND METHODS

### Specimens

Among lepidopteran insects, species within the superfamilies Papilionoidea, Hesperioidea, and Hedyloidea are classified as butterflies (Wahlberg et al., 2005). We examined bristle arrangements along the forewing and hindwing margins of 62 species of Papilionoidea from 17 subfamilies: two from Papilionidae, three from Pieridae, four from Lycaenidae, and eight from Nymphalidae (Table 1).

Dried wings of papilionoid butterflies were examined using scanning electron microscopy (SEM) and light microscopy. In the light microscopic observation, the forewing and the hindwing, isolated from the right or left side of the body, were examined. The sex of the butterflies was not recorded, because we have not observed any differences between males and females in wing-bristle arrangements in several decades of research into lepidopteran species.

### SEM and light microscopy

Morphological studies with SEM and light microscopy were performed using procedures similar to those described by Yoshida et al. (2001), except that we did not employ Nomarski differential contrast optics in the light microscopy.

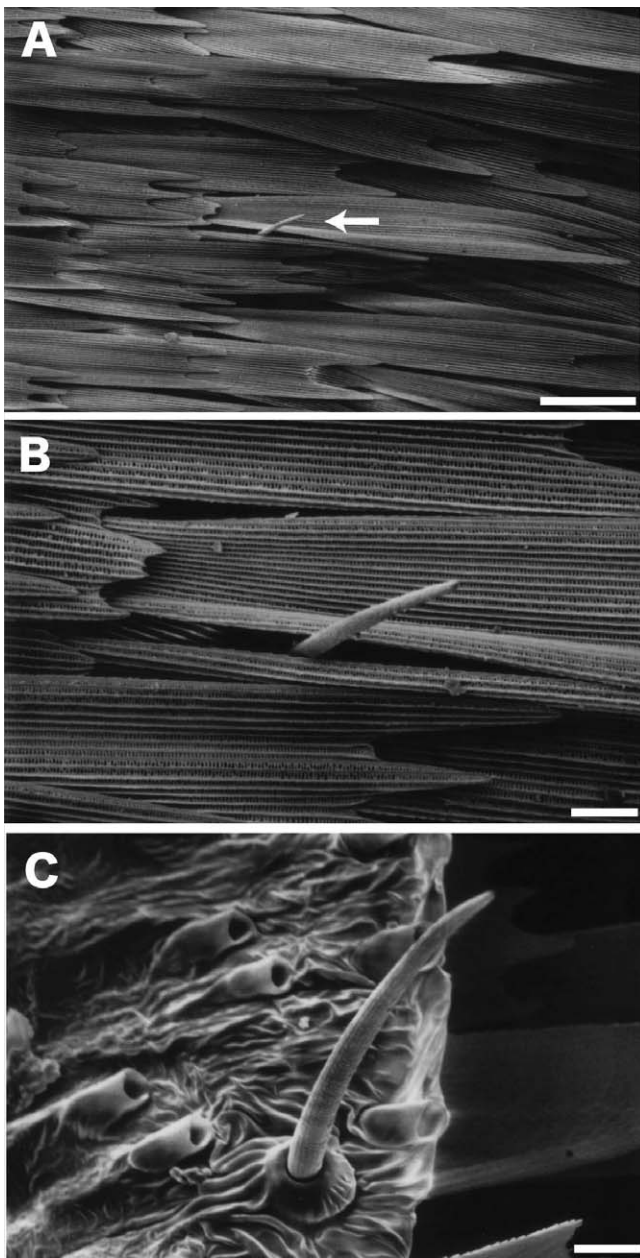
## RESULTS

### Morphology of the sensory bristle along the wing margin

Figure 1 shows the structure of a sensory bristle along the wing margin of *Lycaena phlaeas* (Lycaenidae; Lycaeninae)

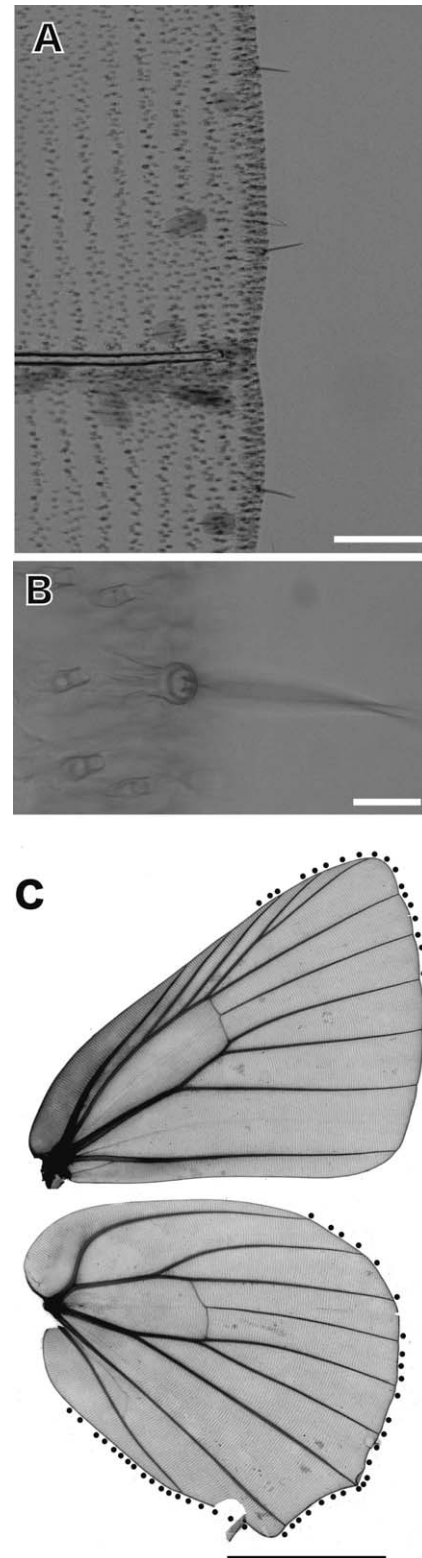
**Table 1.** Applied species, bristle arrangement feature, and number of applied individuals. <sup>a</sup>L: Lycaena, C: Curetis, E: Euploea, V: Vagrans, P: Pachliopta, J: Japonica, G: Graphium, N: Parnassius (No bristle).

	Family	Subfamily	Species	Arrangement feature <sup>a</sup>		No. of applied individuals
				Forewing	Hindwing	
1	Papilionidae	Parnassiinae	<i>Parnassius glacialis</i>	N	N	6
2		Parnassiinae	<i>Sericinus montela</i>	V, P	P, J	3
3		Papilioninae	<i>Lamproptera meges</i>	N	N	2
4		Papilioninae	<i>Graphium sarpedon</i>	G	G	2
5		Papilioninae	<i>Graphium nomius</i>	G	G	2
6		Papilioninae	<i>Papilio xuthus</i>	V, P	P	4
7		Papilioninae	<i>Papilio polytes</i>	L	P	1
8		Papilioninae	<i>Papilio hystaspes</i>	L	P	1
9		Papilioninae	<i>Byasa alcinous</i>	V, P	P	1
10		Papilioninae	<i>Atrophaneura semperi</i>	G	G	1
11		Papilioninae	<i>Pachliopta kotzebuea</i>	V, P	P	1
12	Pieridae	Dismorphiinae	<i>Leptidea amurensis</i>	L	L	1
13		Pierinae	<i>Appias lycinda</i>	L	L	1
14		Pierinae	<i>Pieris rapae</i>	L	L	2
15		Pierinae	<i>Pieris melete</i>	L	L	1
16		Pierinae	<i>Anthocharis scolymus</i>	L	L	1
17		Pierinae	<i>Hebomoia glaucippe</i>	L	V	1
18		Coliadinae	<i>Colias acuta</i>	L	L	1
19		Coliadinae	<i>Eurema hecabe</i>	L	L	1
20		Lycaenidae	Theclinae	<i>Rapala arata</i>	L	J
21	Theclinae		<i>Hypolycaena sipylus</i>	L	J	1
22	Theclinae		<i>Narathura japonica</i>	L	L	1
23	Theclinae		<i>Japonica saepestriata</i>	L	J	1
24	Theclinae		<i>Callophrys ferrea</i>	V	L	2
25	Polymmantinae		<i>Zizeeria maha</i>	L	L	1
26	Polymmantinae		<i>Caleta roxus</i>	L	J	2
27	Polymmantinae		<i>Jamides pura</i>	L	L	1
28	Lycaeninae		<i>Lycaena phlaeas</i>	L	L	5
29	Curetinae		<i>Curetis acuta</i>	Cf	Ch	4
30	Nymphalidae	Libytheinae	<i>Libythea celtis</i>	L	L	2
31		Heliconiinae	<i>Argyreus hyperbius</i>	L	L	1
32		Heliconiinae	<i>Brenthis daphne</i>	L	L	1
33		Heliconiinae	<i>Vagrans sinha</i>	V	V	1
34		Heliconiinae	<i>Cupha arias</i>	V	V	1
35		Heliconiinae	<i>Cirrochroa tyche</i>	V	V	1
36		Nymphalinae	<i>Symbrenthia lilaea</i>	V	V	1
37		Nymphalinae	<i>Araschnia burejana</i>	E	E	1
38		Nymphalinae	<i>Kaniska canace</i>	V	V	1
39		Nymphalinae	<i>Polygonia c-aureum</i>	P	P	3
40		Nymphalinae	<i>Precis almana</i>	V	V	1
41		Limenitidinae	<i>Neptis sappho</i>	E	E	1
42		Apaturinae	<i>Sasakia charonda</i>	E	E	1
43		Charaxinae	<i>Polyura nepenthes</i>	V	V	3
44		Charaxinae	<i>Morpho menelaus</i>	E	E	1
45		Satyrinae	<i>Lethe diana</i>	L	L	2
46		Satyrinae	<i>Lethe confusa</i>	E	E	1
47		Satyrinae	<i>Mycalesis francisca</i>	L	L	1
48		Satyrinae	<i>Zethera musa</i>	E	E	1
49		Satyrinae	<i>Zethera pimplea</i>	E	E	1
50		Satyrinae	<i>Ragadia mindorana</i>	E	E	3
51		Satyrinae	<i>Ypthima motschulskyi</i>	L	L	1
52	Satyrinae	<i>Ypthima argus</i>	L	L	1	
53	Satyrinae	<i>Minois dryas</i>	L	V	1	
54	Danainae	<i>Danaus chrysippus</i>	V	V	2	
55	Danainae	<i>Danaus melanippus</i>	E	E	1	
56	Danainae	<i>Danaus affinis</i>	E	E	1	
57	Danainae	<i>Parantica vitrina</i>	E	E	1	
58	Danainae	<i>Ideopsis juvena</i>	E	E	1	
59	Danainae	<i>Ideopsis similis</i>	E	E	1	
60	Danainae	<i>Salatura genutia</i>	E	E	1	
61	Danainae	<i>Tirumala hamata</i>	E	E	1	
62	Danainae	<i>Euploea mulciber</i>	E	E	2	



**Fig. 1.** Scanning electron micrograph images of a sensory bristle on the ventral wing surface of *Lycaena phlaeas*. **(A)** Oblique view of the apical region of the bristle (arrow) surrounded by scales. **(B)** Magnified view of (A). **(C)** Oblique view of the bristle after removing the surrounding scales. Scale bar: 50  $\mu\text{m}$  (A), 10  $\mu\text{m}$  (B, C).

observed using SEM. This oblique view revealed the following features: (1) the apical part of the bristle is exposed above the surrounding scales, (2) the bristle projects along the wing in a roughly distal direction, (3) the angle between the bristle and the wing surface is much larger than the angle of the surrounding scales, (4) the apical part of the bristle is tapered, and (5) the bristle socket is easily distinguishable from those of the surrounding scales, as the former was shaped like the basal half of a cone, while the latter is cylindrical. These morphological features were common to all wings examined.



**Fig. 2.** Light micrographs (A, B) and illustration of the bristle arrangement (C) of *Lycaena phlaeas*. **(A)** Three bristles along the wing margin. **(B)** Magnified view of the bristle, focused on the socket not on the shaft. **(C)** Bristle arrangement of the forewing (upper) and hindwing (lower). Black dots represent the locations of the bristles on the ventral wing surface (same as in Figs. 3–9). We observed 20 bristles located on the forewing and 43 on the hindwing. Scale bar: 200  $\mu\text{m}$  (A), 20  $\mu\text{m}$  (B), 5 mm (C).

The diameter of the basal part of the *Lycaena* bristle was estimated to be less than 10  $\mu\text{m}$ . The bristle length was difficult to estimate in the oblique view, but measurements made on light micrographs of a whole mount of the wing after removal of surrounding scales (Fig. 2A, B), indicated that it was approximately 80  $\mu\text{m}$ .

#### Bristle arrangement in *Lycaena phlaeas*

As shown in light micrographs of the *Lycaena* wing (Fig. 2A, B), the locations of the bristles along the wing margin were easily visualized. The morphology of the bristle shafts and sockets clearly distinguished them from the surrounding scales. Bristles on the dorsal and ventral surfaces could be identified by focusing the microscope down through the wing. The locations of all of the bristles along the wing margin of *Lycaena* were determined from whole mounts of the wings (Fig. 2C). In *Lycaena*, in both the forewing and hindwing, the bristles were exclusively located on the ventral surfaces of the wing margins, and were continuously distributed, except in the vicinity of the wing margins.

We examined the wings of the other 61 species using the same methods as for *Lycaena* and observed several variations in bristle arrangements (Table 1). Features similar to those of *Lycaena* were observed in the forewings of 27 species and the hindwings of 19 species, including *Lycaena*. Below, we describe seven other bristle arrangements exhib-

iting different features. No bristles were present on the posterior margins in any forewings examined.

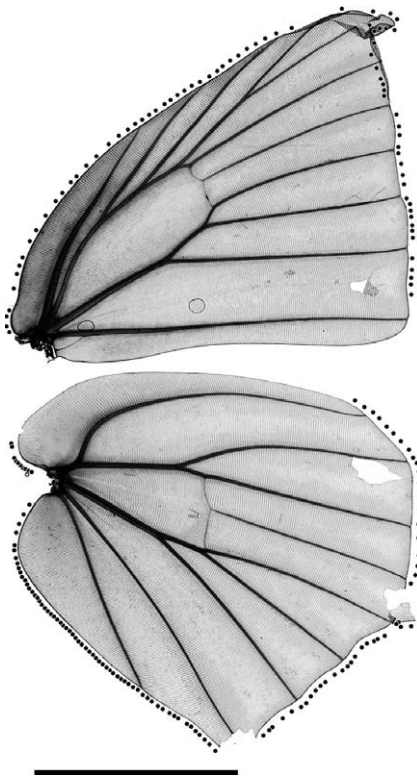
#### Bristle arrangement in *Curetis acuta*

The wings of *Curetis acuta* (Lycaenidae; Curetinae) are illustrated in Fig. 3. The bristles were located exclusively on the ventral wing surface, as in *Lycaena*. In the forewing, however, the distribution of bristles along the anterior margin extended to the neighborhood of the articulation between the wing and the body; the terminal bristle was located within 50  $\mu\text{m}$  from the wing base. This close proximity was substantially more prominent than in the forewings of the other species examined (Table 1). In the hindwing, the bristle distribution also extended to immediately near the articulation both along the anterior margin and along the posterior margin. The terminal bristle along the anterior margin was located within 500  $\mu\text{m}$  from the wing base, and that along the posterior margin was within 1 mm of it. This close proximity was also substantially more prominent than in the hindwings of the other species examined (Table 1).

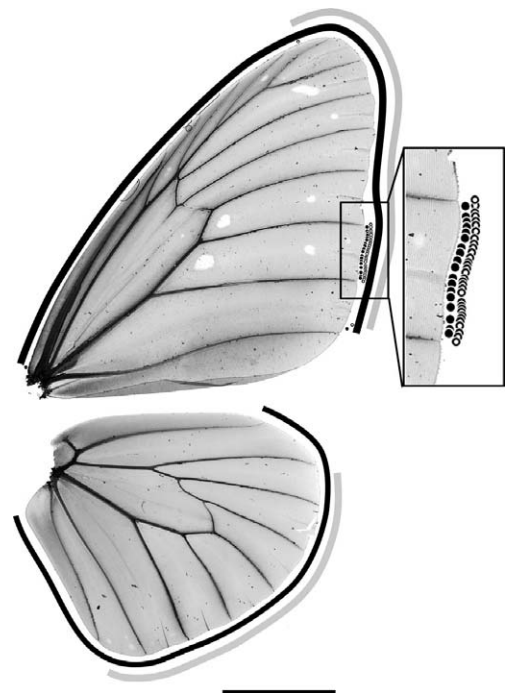
In the anterior margin of the hindwing, the bristles were localized immediately near the articulation. This feature was observed only in the *Curetis* hindwing.

#### Bristle arrangement in *Euploea mulciber*

The wings of *Euploea mulciber* (Nymphalidae; Danainae) are illustrated in Fig. 4. The bristles were continuously dis-



**Fig. 3.** Bristle arrangement of the forewing (upper) and the hindwing (lower) of *Curetis acuta*. White dots represent the locations of the bristles on the dorsal surface (as in Figs. 4–6 and 8). We observed 76 bristles in the forewing and 118 in the hindwing. In this specimen, only one bristle was observed on the dorsal surface of the hindwing. In the other specimens, however, all the bristles were on the ventral surfaces. Scale bar: 1 cm.



**Fig. 4.** Bristle arrangement of the forewing (upper) and hindwing (lower) of *Euploea mulciber*. The black line represents the bristle distribution region on the ventral wing surface and the gray line that on the dorsal surface. A magnified view of the area within the square is shown at the right, in which the locations of the individual bristles are represented by dots. We observed 189 bristles on the ventral surface and 87 on the dorsal surface of the forewing, and 169 on the ventral surface and 92 on the dorsal surface of the hindwing. Scale bar: 1 cm.

tributed not only on the ventral wing surface, as in *Lycaena*, but also on the dorsal surface. This arrangement was observed in the forewings and hindwings of 16 species, including *Euploea multiciber* (Table 1).

Along the anterior margin of the *Euploea* forewing, the terminal bristle on the ventral surface was located 1–2 mm away from the articulation. This distance in the *Euploea* forewing was much shorter than in other forewings exhibiting this type of bristle arrangement, but much longer than that of the *Curetis* forewing.

#### Bristle arrangement in *Vagrans sinha*

The wings of *Vagrans sinha* (Nymphalidae; Argynninae) are illustrated in Fig. 5. As in *Euploea*, the bristles were distributed on both the ventral and dorsal wing surfaces. In this case, however, those on the dorsal surface were localized around the distal terminals of the wing veins. Those on the ventral surface were continuously distributed along the wing margin, as in *Euploea*. This feature of arrangement was observed in both the forewings and the hindwings of eight species, including *Vagrans sinha*, in only the forewings of three other species, and in only the hindwings of two other species (Table 1).

#### Bristle arrangement in *Papilio xuthus*

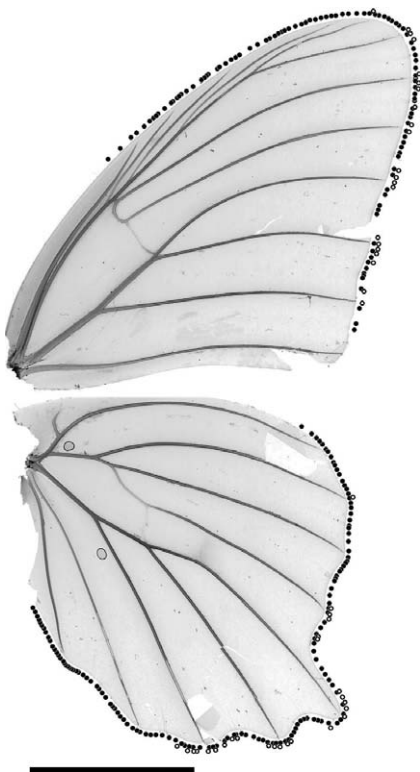
The wings of *Papilio xuthus* (Papilionidae; Papilioninae) are illustrated in Fig. 6. The bristles were distributed on both

the ventral and dorsal wing surfaces as in *Euploea* and *Vagrans*. However, in contrast to *Vagrans*, some were localized around the distal terminals of the wing veins on both surfaces. In the forewing, the bristles along the lateral margin were localized around the distal terminals of the wing veins, while those along the anterior margin were continuously distributed as in *Euploea* and *Vagrans*. In the hindwing, all of the bristles were localized around the distal terminals of the wing veins. These features of arrangement were observed in both the forewings and hindwings of four species (including *Papilio xuthus*), and in only the hindwings of two species (Table 1).

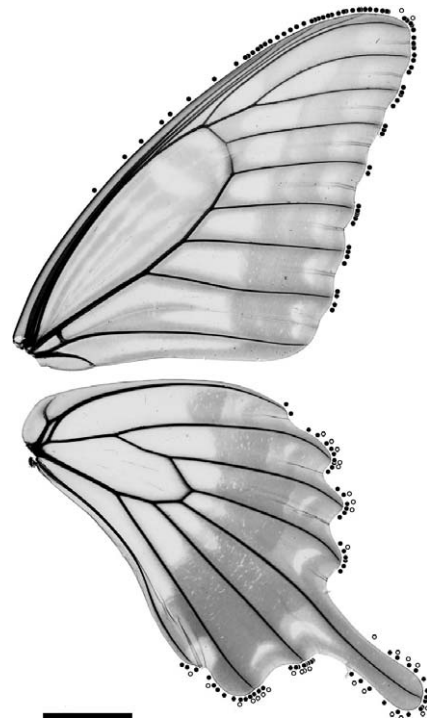
#### Bristle arrangement in *Japonica saepestriata*

The wings of *Japonica saepestriata* (Lycaenidae; Theclinae) are illustrated in Fig. 7. The bristles were exclusively located on the ventral wing surface, as in *Lycaena*. The bristles in the forewing were continuously distributed, as in *Lycaena*, while those in the hindwing were distributed along the posterior side of the long tail protruding from the lateral margin, but were absent along its anterior side. This feature of arrangement in the *Japonica* hindwing was observed in only the hindwing tails of five species (including *Japonica saepestriata*; Table 1).

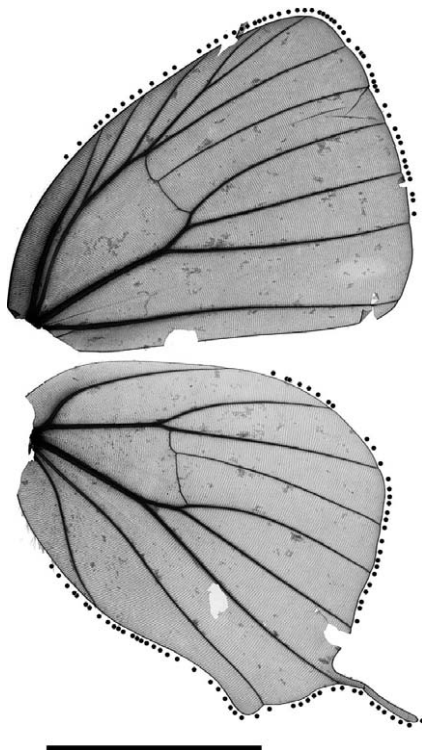
*Sericinus montela*, one of these five species, exhibited a similar arrangement to *Japonica saepestriata* in the long tail of the hindwing, and a similar arrangement to *Pachiliopta* in other parts of the hindwing margin. The other four species, including *Japonica saepestriata*, however, exhibited a similar arrangement to *Lycaena* in the hindwing



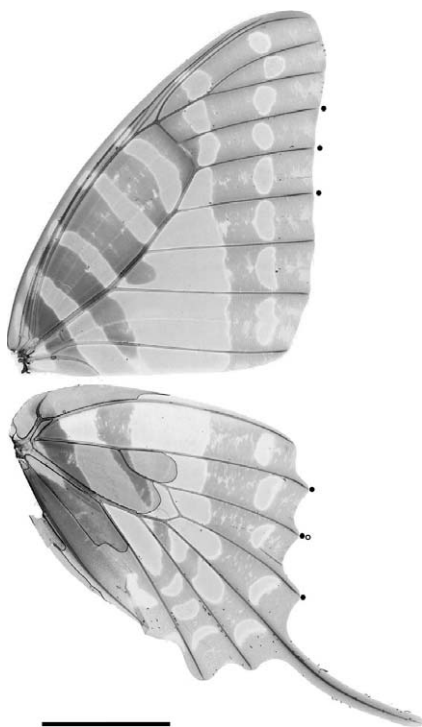
**Fig. 5.** Bristle arrangement of the forewing (upper) and hindwing (lower) of *Vagrans sinha*. Since a small piece of the lateral wing margin was lost, there is a possibility that a few of the bristles were lost. We observed 100 bristles on the ventral surface and 21 on the dorsal surface of the forewing, and 138 on the ventral surface and 26 on the dorsal surface of the hindwing. Scale bar: 1 cm.



**Fig. 6.** Bristle arrangement of the forewing (upper) the hindwing (lower) of *Papilio xuthus*. We observed 73 bristles on the ventral surface and 2 on the dorsal surface of the forewing, and 60 on the ventral surface and 30 on the dorsal surface of the hindwing. Scale bar: 1 cm.



**Fig. 7.** Bristle arrangement of the forewing (upper) the hindwing (lower) of *Japonica saepestriata*. Since a small piece of the lateral wing margin was lost, it is possible that a few bristles were lost. We observed 73 bristles in the forewing and 57 bristles in the hindwing. All the bristles are on the ventral surfaces. Scale bar: 1 cm.



**Fig. 8.** Bristle arrangement of the forewing (upper) the hindwing (lower) of *Graphium nomius*. We observed three bristles on the ventral surface of the forewing, and three on the ventral surface and one on the dorsal surface of the hindwing. Scale bar: 1 cm.



**Fig. 9.** Bristle arrangement of the forewing (upper) the hindwing (lower) of *Parnassius glacialis*. The wings exhibited no bristles along their margins. Scale bar: 1 cm.

margin, except in the long tail.

#### **Bristle arrangement in *Graphium nomius***

The wings of *Graphium nomius* (Papilionidae; Papilioninae) are illustrated in Fig. 8. In this specimen, each bristle was located at a wing vein terminal. This feature of arrangement was observed in the forewings and the hindwings of three species (including *Graphium nomius*; Table 1).

#### **Bristle arrangement in *Parnassius glacialis***

The wings of *Parnassius glacialis* (Papilionidae; Parnassiinae) are illustrated in Fig. 9. The six individuals examined completely lacked bristles along the margins of both forewings and hindwings. The two *Lamproptera meges* (Papilionidae; Papilioninae) individuals examined also completely lacked bristles in both the forewings and hindwings.

### **DISCUSSION**

In this report, we describe nine bristle arrangements observed in the Papilionoidea. Table 2 summarizes the morphological features of all the arrangements observed.

The bristle arrangements of *Lycaena* and *Euploea* have been described previously (Vogel, 1911; Clever, 1958; Yoshida et al., 2001; Ai et al., 2010). However, the current reports of bristle arrangements of *Curetis*, *Vagrans*, *Papilio*, *Japonica*, *Graphium*, and *Parnassius* are new to Lepidoptera research. In specimens from the Pieridae and Lycaenidae families, most of the wings in the current study exhibited a similar arrangement to *Lycaena*. Arrangements similar to those in *Graphium* and *Parnassius* were observed only in Papilionidae. The *Papilio* arrangement was observed in five species of the Papilionoidea family, and a single species in the other three families. In Nymphalidae, the *Euploea*

**Table 2.** Morphological features of all the arrangements illustrated. <sup>a</sup> L: *Lycaena*, Cf: *Curetis* forewing, Ch: *Curetis* hindwing, E: *Euploea*, V: *Vagrans*, P: *Papilio*, J: *Japonica*, G: *Graphium*, N: *Parnassius* (No bristle). The dash means absence of bristles in the area in question, except for the last column. In the last column, Yes or No is indicated for wings with protrusions having bristles, and the dashes are filled in the other wings.

Arrangement illustrated <sup>a</sup>	Wing surface of bristle distribution	Arrangement continuity		Immediately near the wing base	Exclusively at the wing terminals	Absence along the anterior margin of the wing protrusion
		Ventral	Dorsal			
L	Ventral	Yes	–	–	No	–
Cf	Ventral	Yes	–	Yes	No	–
Ch	Ventral	No	–	Yes	No	–
E	Both	Yes	Yes	–	No	–
V	Both	Yes	No	–	No	–
P	Both	No	No	–	No	No
J	Ventral	No	–	–	No	Yes
G	Ventral, Both	No	No	–	Yes	–
N	–	–	–	–	–	–

and the *Vagrans* arrangements were predominant, differing from the other three families. In all of the Nymphalidae species examined, the forewing and the hindwing of each species exhibited the same arrangement. These differences suggest that bristle arrangement along the wing margins could provide useful characteristics for the identification of families of lepidopteran insects.

In all of the lepidopteran bristle arrangements reported previously, and in the present results, bristles were absent from the whole of the posterior margin of the forewing, and from the majority of the anterior margin of the hindwing. Most lepidopterans connect their forewings and hindwings during flight and, consequently, these two regions abut one another. Thus, these regions do not constitute the effective margins of the connected wings during flight (Brodsky, 1994; Yoshida et al., 2001). In the anterior margin of the hindwing, however, only the small region immediately adjacent to the articulation is exposed to airflow during flight (See Fig. 4A in Yoshida et al., 2001); the *Curetis* hindwing has the sensory bristles in this region. These morphologies suggest that the sensory bristles along the wing margin of lepidopterans may be arranged for the efficient detection of airflow, possibly indicating that they play a role in generating neuronal responses concerned with the regulation of wing movement.

In the arrangements observed in *Euploea*, *Vagrans*, and *Papilio*, bristles were distributed on both the ventral and dorsal wing surfaces. Ai et al. (2010) reported that in *Bombyx*, which exhibits the *Lycaena* arrangement, the sensory neuron of the bristle generates action potentials when the bristle shaft is displaced, such that the angle between the oblique shaft and the wing surface is increased. They hypothesized that displacement of the bristles on the ventral wing surface is caused by changes in air pressure induced by wing elevation. Assuming the neurons associated with bristles on the dorsal surface generate action potentials in the same manner as those of *Bombyx* bristles on the ventral surface, we hypothesize that the dorsal bristle neurons generate action potentials during wing depression. Thus, it is possible that sensory inputs from the wing margins occur during both wing elevation and wing depression.

In the arrangements found in *Vagrans*, *Papilio*, and *Graphium*, the bristles are localized around the wing vein

terminals. *Graphium* represents an extreme case, in which a single bristle is located at the vein terminal. The nerve network within the wing is connected to the thoracic nerve ganglion. As the network consists of nerves running through the wing margins and the wing veins (Vogel, 1911; Nardi, 1983; Ai et al., 2010), it may be inferred that action potentials generated at the bristle neurons are transmitted via the nerves along the wing margin, then along the wing veins, and, finally, to the thoracic nerve ganglion of the central nervous system. Thus, it is likely that the bristles localized

around the wing vein terminals in *Vagrans*, *Papilio*, and *Graphium* transmit more synchronized sensory information to the central nervous system compared with evenly-distributed bristles. Moreover, this more synchronized sensory input may contribute to species-specific wing movements.

The functional significance of the following features remains unclear: (1) the bristle distribution immediately adjacent to the wing base in *Curetis*; (2) the absence of bristles along the anterior side of the protrusion on the lateral wing margin in *Japonica*; and (3) the absence of bristles along the whole wing margin in *Parnassius*. Consideration of the features common to all arrangements suggests that each characteristic bristle arrangement may contribute to the regulation of wing movements specific to each species. These variations in bristle arrangement indicate that bristle arrangements may play an important role in determining species-specific mechanisms of wing movement regulation in lepidopteran insects.

It has been reported previously that the wings of some lepidopteran species possess another type of hair-like sensilla (referred to as ‘sensory scales’; squamiform sensilla) located along their margins (Vogel, 1911; Clever, 1958; Yoshida and Emoto, 2010). We have also observed these in a large number of other species, including *Parnassius glacialis* and *Lamproptera meges*, which lack sensory bristles (Emoto and Yoshida, unpublished data). Taken together with previous findings, our results indicate that, in addition to the sensory systems associated with the wing-thorax articulation and the hair-like and campaniform sensilla on the wing veins, lepidopteran insects also possess elaborate sensory systems composed of hair-like sensilla along the wing margins.

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## REFERENCES

Ai H, Yoshida A, Yokohari F (2010) Vibration receptive sensilla on the wing margins of the silkworm moth *Bombyx mori*. *J Insect*



- Physiol 56: 236–246
- Altman JS, Anselment E, Kutsch W (1978) Postembryonic development of an insect sensory system: ingrowth of axons from hindwing sense organs in *Locusta migratoria*. Proc Roy Soc Lond B 202: 497–516
- Brodsky AK (1994) The evolution of insect flight. Oxford University Press, New York
- Clever U (1958) Untersuchungen zur Zelldifferenzierung und Musterbildung der Sinnesorgane und des Nervensystems im Wachsmottenflügel. Z Morph Ökol Tiere 47: 201–248
- Frey MA (2001) Effects of stretch receptor ablation on the optomotor control of lift in the hawkmoth *Manduca sexta*. J Exp Biol 204: 3683–3691
- Gettrup E (1966) Sensory regulation of wing twisting in locusts. J Exp Biol 44: 1–16
- Hiraguchi T, Yamaguchi T, Takahata M (2003) Mechanoreceptors involved in the hindwing-evoked escape behaviour in cricket, *Gryllus bimaculatus*. J Exp Biol 206: 523–534
- Nardi J (1983) Neuronal pathfinding in developing wings of the moth *Manduca sexta*. Dev Biol 95: 163–174
- Orona E, Agee HR (1987) Thoracic mechanoreceptors in the wing bases of *Heliothis zea* (Lepidoptera: Noctuidae) and their central projections. J Insect Physiol 33: 713–721
- Page KL, Matheson T (2004) Wing hair sensilla underlying aimed hindleg scratching of the locust. J Exp Biol 207: 2691–2703
- Palka J, Lawrence PA, Hart HS (1979) Neural projection patterns from homeotic tissue of *Drosophila* studied in *bithorax* mutants and mosaics. Dev Biol 69: 549–575
- Vogel R (1911) Über die Innervierung der Schmetterlingsflügel und über den Bau die Verbreitung der Sinnesorgane auf denselben. Z Wiss Zool 98: 68–134
- Wahlberg N, Braby MF, Brower AVZ, de Jong R, Lee M-M, Nylin S, et al. (2005) Synergistic effects of combining morphological and molecular data in resolving the phylogeny of butterflies and skippers. Proc Roy Soc B 272: 1577–1586
- Yack JE, Fullard JH (1993) Proprioceptive activity of the wing-hinge stretch receptor in *Manduca sexta* and other atympanate moths: a study of the noctuid moth ear B cell homologue. J Comp Physiol A 173: 301–307
- Yoshida A, Emoto J (2010) Sensory scales along the wing margin of *Pieris rapae* (Lepidoptera: Pieridae). Ann Ent Soc Am 103: 988–992
- Yoshida A, Noda A, Emoto J (2001) Bristle distribution along the wing margin of the small white cabbage butterfly (Lepidoptera: Pieridae). Ann Ent Soc Am 94: 467–470
- Zacwilichowski J (1933) Über die Innervierung und die Sinnesorgane der Flügel von Schanabelfliegen (*Panorpa*). Bull Int Acad Pol Sci Ser B 2: 109–124
- Zacwilichowski J (1934a) Über die Innervierung und die Sinnesorgane der Flügel von Schabe *Phyllodromia germanica* L. Bull Int Acad Pol Sci Ser B. 2: 89–103
- Zacwilichowski J (1934b) Über die Innervierung und die Sinnesorgane der Flügel von Feldheuschrecke *Stauroderus biguttulus* (L.). Bull Int Acad Pol Sci Ser B 2: 187–196

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