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A Small Proportion of Agouti Hairs on Back, Contributing to Wild-Colored Coat Appearances in the Japanese House Mice

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ABSTRACT

The proportions of the agouti and non-agouti hairs on the backs of skin specimens of wild-colored and black-colored coats from the wild-caught Japanese house mice and laboratory mice were analyzed. Hairs (> 50 hairs) were picked up from each position (3 mm^2) on the center and right and left sides of the back, and the morphology and the pigmentation of the hairs were observed. In the wild-colored coat, the hairs were divided into two types: awl and auchene hairs for the agouti ones, and three types: guard, awl, and auchene hairs for the non-agouti ones. In addition, all non-agouti hairs, all of the hairs were classified into two types: those with entirely dense eumelanin and those with partially dense eumelanin and sparse eumelanin. In both coat types, awl hairs were the most common regardless of whether they were agouti or non-agouti. The difference in appearance between the wild- and black-colored coats was caused only by the presence of the agouti awl and auchene hairs in lower proportions (< 15.3 ± 8.4 at the center and < 40.2 ± 13.5% at the sides). Moreover, the proportion of agouti hairs differed significantly between the center and the right/left sides, being higher on the right/left sides than in the center. This indicated the presence of an obscure dark zone along the median line at the back of the wild-colored coat.

INTRODUCTION

In general, the wild-colored (agouti) coat of the house mouse, *Mus musculus*, is entirely grayish-brown in color (Galbraith, 1964; Silvers, 1979; Lyon *et al*., 1996; Griffiths *et al*., 2000; Ohdachi *et al*., 2015). The Japanese house mice also carry wild-colored coats, but their bellies are lighter than their backs. This trait is well known to be expressed by the A^w allele at the agouti locus (Hamajima, 1969; Lyon *et al*., 1996). However, the Japanese house mouse coat color and brightness vary due to individual variation (Suzuki and Iwasa, 2013; Myoshu and Iwasa, 2018). In particular, the belly color varies considerably, ranging from snow white to dark gray (Suzuki and Iwasa, 2013; Myoshu and Iwasa, 2018). Conversely, the back color of the Japanese house mice appears to be consistently grayish-brown (Suzuki and Iwasa, 2013; Myoshu and Iwasa, 2018). These findings suggest the presence of a novel allele similar to the *a* allele, which leads to the specific coat coloration in the Japanese house mice (Iwasa *et al*., 2018).

The agouti phenotypes, which are determined by the dominant agouti alleles, such as *A* and A^w, consist of the bands of the phaeomelanin and eumelanin pigments along a hair shaft (e.g., Hoekstra, 2006). In contrast, the recessive allele, such as *a*, expresses no bands and only the eumelanin pigments in a hair. Thus, agouti hairs with the aforementioned bands visually produce a wild-colored coat appearance. However, the coat hairs of mice contain over-hairs with various amounts of pigment and under-hairs with little pigment (Dry, 1926; Galbraith, 1964; Grüneberg, 1969; Kondo, 1994, 2013). Therefore, to date, it is unclear which hairs influence and contribute to the appearance of a wild-colored coat when considering the composition of the hairs.

In this study, we analyzed the composition of hairs from the wild-colored coats of mice, comparing them with those from the black-colored coats of mice. We evaluated which hairs and how they cause the wild-colored appearance.

MATERIALS AND METHODS

We used 16 flat skin specimens of *M. musculus* (Fig. 1). To eliminate variations in coat color due to age, such as

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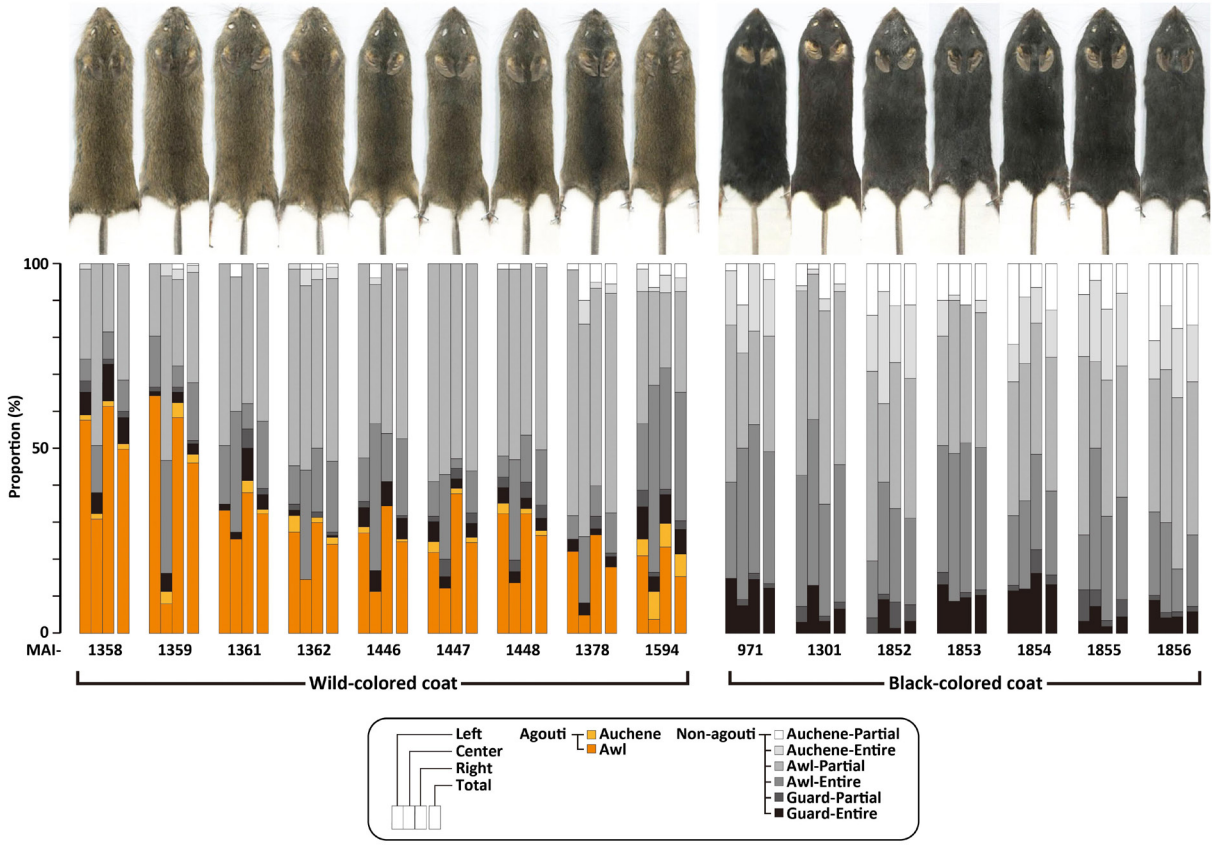

Fig. 1. Coat color appearances of flat skin specimens and frequencies of the eight types of agouti and non-agouti hairs examined in this study. Each frequency of each hair type is described in Table I.

a blackish colored coat in a juveniles, we only used individuals with a postnatal age of over 90 days old with fully developed adult coat coloration (Suzuki and Iwasa, 2013). These individuals were born in our laboratory. To confirm the coat color phenotypes, we examined the genetics of mouse coat colors, particularly those related to dominant alleles at the agouti locus that express the wild-colored coat (Lyon *et al*., 1996). We used offspring from a pregnant wild-caught mouse, as well as F1 and F2 offspring from cross-breeding experiments involving a wild-caught mouse and a laboratory mouse C57BL/6 for wild-colored mice (n = 9) and black-colored mice (n = 7) (Table I), based on the genetic scheme in mice (Lyon *et al*., 1996; Suzuki and Iwasa, 2013).

According to previous studies (Silvers, 1979; Kondo, 1994), hairs are considered to consist of over-hairs and under-hairs, with only the former being related to coat coloration. Thus, we used over-hairs for the current analysis. Over-hairs were sampled from three 3 mm^2 positions (center, left and right) on the back of a flat skin at a horizontal line as the base of the forefeet (Fig. 1). The over-hairs (Table I) sampled from these three positions were placed on a slide glass and were spread out as much as possible under a binocular microscope to avoid overlap. Then, Canada balsam was gently dropped onto the slide and a cover glass was placed on top. The hair samples were observed under a light microscope using a x2 objective lens.

The over-hairs were classified into three types: guard (monotrich) hairs (> 6 mm), awl hairs (< 6 mm and without constriction) and auchene hairs (< 6 mm and with constrictions), based on the morphological features according to previous studies (Dry, 1926; Sundberg and Hogan, 1994) (Fig. 2), without zig zag type hairs that have not been obtained. In addition, these hairs were also classified into three types: agouti hair (containing phaeomelanin and eumelanin), entire type of non-agouti hair (containing only dense eumelanin) and partial type of non-agouti hair (containing dense eumelanin and sparse eumelanin), based on the phaeomelanin and eumelanin distributions and densities (Fig. 2).

Table I. Proportions (%) of the hair types in each specimen of *Mus musculus* examined in this study.

Coat color	Origin	Specimen No.	Post-natal days	Position*	Agouti hair			Non-agouti hair				Auchene	
					Guard	Awl	Auchene	Guard		Awl			
					—	—	—	Entire	Partial	Entire	Partial	Entire	Partial
Wild	Offspring of a wild caught pregnant mouse	MAI-1358	95	Left (*n*=66)	0	57.6	1.5	6.1	3.0	6.1	24.2	1.5	0
				Center (*n*=71)	0	31.0	1.4	5.6	0	0.0	0.0	0	0
				Right (*n*=70)	0	61.4	1.4	10.0	1	7.1	18.6	0	0
					0	49.8	1.4	7.2	1.4	8.7	30.9	0.5	0
		MAI-1359	95	Left (*n*=81)	0	64.2	0	1.2	1.2	13.6	19.8	0	0
				Center (*n*=62)	0	8.1	3.2	4.8	0	30.6	50.0	3.2	0
				Right (*n*=72)	0	58.3	4.2	2.8	1.4	5.6	23.6	2.8	1.4
					0	46.0	2.3	2.8	0.9	15.8	29.8	1.9	0.5
		MAI-1361	95	Left (*n*=63)	0	33.3	0	1.6	0	15.9	49.2	0	0
				Center (*n*=55)	0	25.5	0	1.8	0	32.7	36.4	0	3.6
				Right (*n*=58)	0	37.9	3.4	8.6	5.2	6.9	37.9	0	0
					0	32.4	1.1	4.0	1.7	18.2	41.5	0	1.1
		MAI-1362	95	Left (*n*=66)	0	27.3	4.5	1.5	1.5	10.6	53.0	1.5	0
				Center (*n*=68)	0	14.7	0	0	0	29.4	50.0	4.4	1.5
				Right (*n*=70)	0	30.0	1.4	0	1.4	17.1	45.7	2.9	1.4
					0	24.0	2.0	0.5	1.0	19.1	49.5	2.9	1.0
	Offspring of a pair of a wild-caught mouse × C57BL/6N	MAI-1378	94	Left (*n*=63)	0	22.2	0	3.2	0	6.3	66.7	0	1.6
				Center (*n*=61)	0	4.9	0	3.3	0	18.0	57.4	6.6	9.8
				Right (*n*=60)	0	26.7	0	1.7	3.3	8.3	53.3	1.7	5.0
					0	17.9	0	2.7	1.1	10.9	59.2	2.7	5.4
		MAI-1446	166	Left (*n*=59)	0	27.1	1.7	5.1	1.7	11.9	52.5	0	0
				Center (*n*=53)	0	11.3	0	5.7	0	39.6	37.7	1.9	3.8
				Right (*n*=61)	0	34.4	0	6.6	0	13.1	45.9	0	0
					0	24.9	0.6	5.8	0.6	20.8	45.7	0.6	1.2
		MAI-1447	90	Left (*n*=73)	0	21.9	2.7	5.5	1.4	9.6	58.9	0	0
				Center (*n*=65)	0	12.3	0	3.1	4.6	23.1	56.9	0	0
				Right (*n*=74)	0	37.8	1.4	2.7	2.7	2.7	52.7	0	0
					0	24.5	1.4	3.8	2.8	11.3	56.1	0	0
		MAI-1448	90	Left (*n*=71)	0	32.4	2.8	4.2	2.8	5.6	50.7	0	1.4
				Center (*n*=66)	0	13.6	0	3.0	3.0	27.3	51.5	0	1.5
				Right (*n*=71)	0	32.4	1.4	2.8	4.2	12.7	46.5	0	0
					0	26.4	1.4	3.4	3.4	14.9	49.5	0	1.0
		MAI-1594	96	Left (*n*=67)	0	20.9	4.5	9.0	4.5	17.9	35.8	6.0	1.5
				Center (*n*=79)	0	3.8	7.6	3.8	1.3	50.6	25.3	1.3	6.3
				Right (*n*=64)	0	23.4	6.3	7.8	1.6	32.8	20.3	4.7	3.1
					0	15.2	6.2	6.7	2.4	34.8	27.1	3.8	3.8
Balck	C57BL/6N	MAI-971	274	Left (*n*=84)	0	0	0	14.8	0	25.9	42.6	14.8	1.9
				Center (*n*=70)	0	0	0	7.4	1.9	40.7	25.9	13.0	11.1
				Right (*n*=94)	0	0	0	14.5	1.8	40.0	25.5	18.2	0
					0	0	0	12.3	1.2	35.6	31.3	15.3	4.3
		MAI-1301	97	Left (*n*=69)	0	0	0	2.9	4.4	35.3	50.0	1.5	5.9
				Center (*n*=73)	0	0	0	13.0	0	44.9	39.1	1.4	1.4

Table continues on next page.....

Coat color	Origin	Specimen No.	Post-natal days	Position*	Agouti hair			Non-agouti hair				Auchene	
					Guard	Awl	Auchene	Guard		Awl			
					—	—	—	Entire	Partial	Entire	Partial	Entire	Partial
				Right (*n*=66)	0	0	0	3.2	1.6	30.2	52.4	3.2	9.5
					0	0	0	6.5	2.0	37.0	47.0	2.0	5.5
	Offspring of a pair of [a wild-caught mouse × C57BL/6N] x [a wild-caught mouse × C57BL/6N]	MAI-1852	101	Left (*n*=54)	0	0	0	0	4.2	15.3	51.4	15.3	13.9
				Center (*n*=54)	0	0	0	9.1	1.5	30.3	21.2	30.3	7.6
				Right (*n*=55)	0	0	0	1.4	7.0	25.4	39.4	15.5	11.3
					0	0	0	3.3	4.3	23.4	37.8	20.1	11.0
		MAI-1853	101	Left (*n*=68)	0	0	0	13.1	3.3	34.4	29.5	9.8	9.8
				Center (*n*=69)	0	0	0	8.6	0	40.0	41.4	1.4	8.6
				Right (*n*=63)	0	0	0	9.7	1.4	40.3	37.5	0	11.1
					0	0	0	10.3	1.5	38.4	36.5	3.4	9.9
		MAI-1854	101	Left (*n*=72)	0	0	0	11.6	1.4	18.8	36.2	10.1	21.7
				Center (*n*=66)	0	0	0	11.9	0	23.9	37.3	17.9	9.0
				Right (*n*=71)	0	0	0	16.1	6.5	25.8	35.5	9.7	6.5
					0	0	0	13.1	2.5	22.7	36.4	12.6	12.6
		MAI-1855	101	Left (*n*=61)	0	0	0	3.3	8.3	15.0	48.3	16.7	8.3
				Center (*n*=70)	0	0	0	7.4	4.4	38.2	23.5	22.1	4.4
				Right (*n*=72)	0	0	0	1.8	1.8	28.1	36.8	19.3	12.3
					0	0	0	4.3	4.9	27.6	35.7	19.5	8.1
		MAI-1856	101	Left (*n*=69)	0	0	0	9.0	1.5	22.4	35.8	10.4	20.9
				Center (*n*=67)	0	0	0	4.3	1.4	24.3	41.4	17.1	11.4
				Right (*n*=62)	0	0	0	4.3	1.4	11.6	46.4	18.8	17.4
					0	0	0	5.8	1.5	19.4	41.3	15.5	16.5

*n, numer of hairs observed.

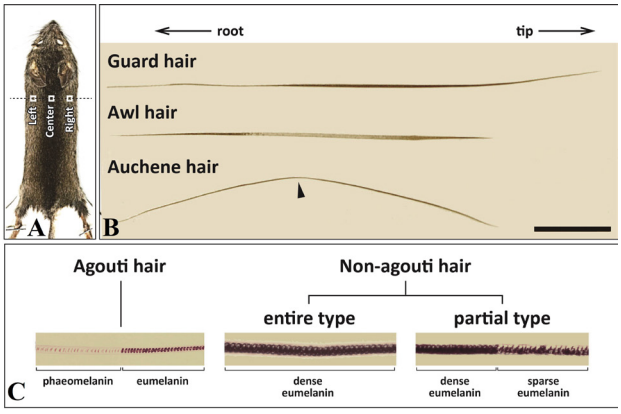

Fig. 2. Sampling positions, center, left and right, of hairs on a dorsal surface of a flat skin (a). The present hair classification to three types, guard, awl and auchene hairs, according to previous studies (Dry, 1926; Grüneberg, 1969) based on its length and morphological features. The present hair classification to three types, agouti, non-agouti entire type and non-agouti partial type hairs, based on eumelanin and phaeomelanin densities. A dotted line (a) indicates a horizontal line as the base of fore feet. An arrowhead indicates a constriction. See text in detail.

RESULTS

First, we compared the wild-colored coats between the offspring from a wild-caught mouse and the offspring from a wild-caught mouse x C57BL/6N for all of the frequencies of all of the hair types by a one-way ANOVA in each hair type (Table I and Fig. 1). In the partial type hairs of the auchene hairs of the non-agouti hairs at the left position, the significant difference in frequency of occurrence between the two offspring was detected (p = 0.034, Table II). However, all residual hair types were not significantly different between the two offspring ($p > 0.05$, Table II). Thus, we recognized that both offspring carried the same wild-colored coats In the wild-colored coat specimens, the guard hairs showed only the non-agouti hairs and the awl hairs were the most frequent among the agouti hairs (29.0 ± 11.8%) and the non-agouti hairs included both the entire type (17.2 ± 7.7%) and the partial type (43.3 ± 11.7%) (Tables I, III). On the other hand, no agouti hairs were observed in the black-colored coat specimens and the awl hairs were also the most frequent among the non-agouti hairs, including both the entire type

Table II. Each *p* value for each hair type by *t*-test in the wild-colored coats between offspring from a wild-caught mouse and offspring from a wild-caught mouse x C57BL/6N.

Position	Agouti hair			Non-agouti hair					
	Guard	Awl	Auchene	Guard		Awl		Auchene	
	—	—	—	Entire	Partial	Entire	Partial	Entire	Partial
Center	—	0.962	0.426	0.302	0.062	0.258	0.532	0.493	0.099
Left	—	0.979	0.265	0.053	0.278	0.651	0.063	0.383	0.034*
Right	—	0.967	0.705	0.655	0.497	0.235	0.103	0.542	0.239

*Significantly differed at $p = 0.05$.

Table III. Frequencies (mean ± *S.D.*, %) of the hair types in the present specimens of *Mus musculus*.

Coat color	Position	Agouti hair				Non-agouti hair						
		Guard	Awl	Auchene	Total	Guard		Awl		Auchene		Total
		—	—	—		Entire	Partial	Entire	Partial	Entire	Partial	
Wild	Center	0	13.9±9.0	1.4±2.6	15.3±8.4	3.5±1.8	1.0±1.7	29.3±11.3	46.1±10.7	1.9±2.4	3.0±3.4	84.7±8.4
(*n* = 9)	Left	0	34.1±2.6	2.0±1.4	36.1±15.2	4.1±2.6	1.8±1.4	10.8±4.4	45.7±15.7	1.0±2.0	0.5±0.7	63.9±15.2
	Right	0	38.1±13.3	2.2±2.1	40.2±13.5	4.8±3.5	2.4±1.6	11.8±9.0	38.3±13.9	1.3±1.8	1.2±1.8	59.8±13.5
	Total	0	29.0±11.8	1.8±1.8		4.1±2.1	1.7±1.0	17.2±7.7	43.3±11.7	1.4±1.5	1.5±1.8	
Black	Center	0	0	0	—	8.8±3.0	1.3±1.6	34.6±8.4	32.9±8.9	14.8±10.6	7.6±3.6	100
(*n* = 7)	Left	0	0	0	—	7.6±6.3	3.6±2.9	24.1±9.2	43.0±8.7	5.6±12.1	6.9±9.7	100
	Right	0	0	0	—	7.3±6.2	3.1±2.5	28.8±9.8	39.1±8.5	12.1±7.9	9.7±5.4	100
	Total	0	0	0		8.0±3.9	2.6±1.5	29.2±7.7	38.0±5.0	12.6±7.3	9.7±4.2	

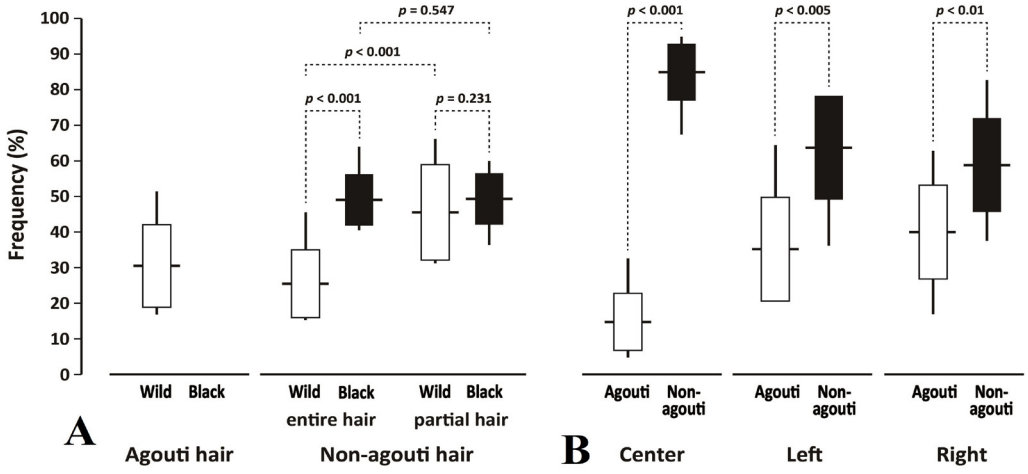

Fig. 3. Frequencies of agouti and non-agouti hairs in the wild-colored and black-colored coats (a) and those at center, left and right positions for the agouti and non-agouti hairs (b).

(29.2 ± 7.7%) and the partial type (38.0 ± 5.0%) (Tables I, III). For the agouti and non-agouti hairs, their composition was compared between the wild- and black-colored coats by a one-way ANOVA. According to this, the entire type hairs of the non-agouti hairs were significantly more frequent in the black-colored coat than in the wild-colored coat ($p < 0.001$, Fig. 3A). However, the frequencies of the non-agouti partial type hairs did not differ between the wild- and black-colored coats ($p = 0.231$, Fig. 3A). In addition, the frequencies of the partial type hairs were

significantly higher than those of the entire type hairs in the wild-colored coats ($p < 0.001$, Fig. 3A) but those of the entire type and partial type hairs appeared equally in the black-colored coats ($p = 0.547$, Fig. 3A).

The frequencies of agouti and non-agouti hairs at three positions were compared (Table III and Fig. 3B). At the center position of the dorsum, non-agouti hairs (84.7 ± 8.4%) were obviously more frequent than agouti hairs (15.3 ± 8.4%). At the left and right positions, however, the non-agouti hairs (63.9 ± 15.2% at the left position and 59.8 ± 13.5% at the right position) were also more frequent than the agouti hairs (36.1 ± 15.2% at the left position and 40.2 ± 13.5% at the right position), but the frequency differences were smaller than at the center position.

DISCUSSION

In the wild-colored coats, non-agouti hairs were apparently more frequent than agouti hairs, and black-colored coats consisted of only non-agouti hairs (Tables I, III and Figs. 1, 3). For example, a previous study (Ryder, 1973) found that wild sheep (*Ovis aries*) have black-, brown- and white-colored non-agouti hairs, as well as agouti hairs with grayish bands. Therefore, the lower dominance of the agouti hairs amongst all hairs, and the high frequency of non-agouti hairs is considered to be an appropriate phenomenon in the wild-colored mouse coats (Dry, 1926; Grüneberg, 1969; Galbraith, 1964; Tables I, III).

In addition, the entire type hairs of the non-agouti hairs were also more frequent than the partial type hairs in the wild-colored coats (Table III and Fig. 3A). In addition, the entire type and partial type hairs were equally abundant in the black-colored coats. Furthermore, there was no statistically significant difference in the frequencies of partial type hairs between the wild- and black-colored coats (Fig. 3a). Considering the composition of the hairs, it is suggested that the presence of the agouti hairs and the low frequency of entire type hairs in non-agouti hairs are strongly related to wild-coloration. On the other hand, the absence of the agouti hairs and the high frequency of the entire type hairs cause the black-colored appearance, regardless of differences in eumelanin density. Therefore, the appearance of mouse coats does not appear to be influenced by differences in eumelanin density associated with partial type hairs (Dry, 1926; Galbraith, 1964; Grüneberg, 1969).

According to the results of each sampling position on wild-colored coats, non-agouti hairs were much more frequent than agouti hairs in the center position (Fig. 3B). On the other hand, non-agouti hairs were slightly more prevalent than agouti hairs in the left and right positions (Fig. 3B). These results imply the presence of an obscure dark zone along the median line on the back (Fig. 1). This phenomenon has been observed in older individuals of other mouse and vole species (Ohdachi *et al*., 2015; Iwasa, 2018), and seems to be a common feature in the house mice as well.

In the agouti hairs of the wild-colored coats, awl and auchene hairs were recognized, but the guard hairs were not observed (Tables I, III). This finding is consistent with previous research (Grüneberg, 1969) showing that the frequency of agouti hairs was apparently higher in the awl hairs than in the guard hairs. In addition, auchene hairs partially resembled awl hairs in terms of their characteristics, except for the constrictions (Fig. 2). Thus, it is assumed that the awl hairs and the auchene hairs are basically identical based on pigment distributions (Dry, 1926; Grüneberg, 1969) and that the awl hairs are mostly important in providing the wild-colored appearance. In fact, the visual difference between wild- and black-colored coat appearances is caused by the lower frequencies of agouti awl and auchene hairs, ranging from 15.3 ± 8.4 to 40.2 ± 13.5% (Table III and Fig. 1).

DECLARATIONS

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IRB approval

This study was conducted in accordance with the animal experiment guideline of Nihon University, Kameino, Fujisawa, Kanagawa, Japan.

Generative AI and AI-assisted technology statement

The authors declare that no generative AI and AI assisted technology was used in the creation of this manuscript.

Statement of conflicts of interest

The authors have declared no conflict of interest.

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