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OBSERVATIONS ON DIFFERENT TYPES OF HAIR WHORLS IN MAMMALS, AND THE INHERITANCE OF HAIR WHORLS IN SWINE

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The production of hair is one of the characteristics which differentiate mammals from the other classes of vertebrates. It is not surprising that a character so distinctive and of such morphlogic significance should attract the attention of systemists and experimental investigators.

Much attention has been given to the origin and homology of hair, and several theories have been advanced to account for its origin but no one of them has received unqualified acceptance. A study of the literature suggests that the most acceptable view appears to be that hair is a structure for which there is no known antecedent in the lower forms. Considerable speculative attention has been given to the question of whether hair was originally protective or sensory. It appears that the hair on living mammals may serve both of these functions. The protective function is obvious and at least the specialized tactile hairs serve in the role of sense perception.

Hair is essentially a specialized epidermal outgrowth, usually containing more pigment than the surrounding unmodified epithelium. Apparently it begins with a thickening of the ectoderm, followed by a modification of the subjacent mesenchyme growing obliquely downward, and forward to a depth proportional to the size of the hair which is to be produced. Since the hair follicle as a rule grows obliquely forward under the epidermis, the hair commonly points backward or downward. However, there are areas in which the backward slope of the hair is reversed giving rise to various types of hair whorls.

The question of whorls has received attention for more than two centuries. Landauer¹ has recently made extensive studies of the literature on hair-direction and he points out that Osiander in 1816 was apparently the first investigator to give attention to the problem of hair-direction. Osiander observed that in the case of human embryos the hair-direction on the forehead followed the course of the *Arteria frontalis*, and he suggested that the hair direction was due to electric causes, particularly the origin of the vortices. Since the time of Osiander numerous investigators have studied hair-direction. (Space will not permit a review of the question here, the reader will find an extensive review by Landaur*.) Some observers have maintained that hair-direction is merely an expression of the direction of the movement of the animal and of specific tension exerted on the skin by the portion of the muscles used by the moving animal.

Kidd² has offered three rules on the direction of hair as follows:

1. Primitive arrangement of hair on the body is from the tip of the snout to the end of the tail, and on the legs from the proximal to the distal ends.

2. Morphological changes in the conformation of the body may cause deviations from the original arrangement of the hairs.

3. All of the other changes, such as reversed areas, whorls, featherings, crests, and tufts must be explained as consequences of the influence of physical forces, acting on the surface of the animal.

Landauer[•] points out that Voight's experiments led him to the conclusion that the direction of hair is determined during development of the hair germs as a result of a fixed connection of the distal part of the primordium with the connective tissue, while the inner end is in loose connection with it. Thus the hair should follow the more rapidly growing surface of the skin and so grow in a sloping direction. Furthermore, stretching of the skin does not take place in the same degree on all points of the surface of the body, since in some places a rapid growth of the skin is followed by a rapid extension, and in other places (auxiliary and inguinal regions) a slow growth causes a slow extension of the skin.

Jones³ attributes the disturbed or reversed areas in the hair stream to the toilet habits of animals. He regards the reversals and whorls as purely Lamarckian traits.

OBSERVATIONS

Observations have been made on the different types of hair whorls that occur among the different classes of farm animals at the Oklahoma Agricultural Experiment Station in connection with a study of the mode of inheritance of hair whorls in swine. Some of the common types observed on horses, cattle, sheep and swine are shown in Figure 1. Considerable variation in the type and extent of hair whorls was observed for all species inspected. The observations on horses included 52 head, and single whorls were observed on the face about midway between the eyes in 89 per cent of the stock observed and double whorls on 11 per cent of the cases. A varying degree of disturbance in the hair stream was found to occur in the rear flank of horses, and the hair on each individual showed some disturbance in its direction at this point. Whorls were also observed on the ventral side of the neck, and at the base of the mane, but these

*Literature cited at the end of article.



Figure 1. (A) Whorls on the anterior side of arm pit in horses.

- (B) and (C) Whorls (tufts) on the ventral side of the neck in horses.
- (D) Type of hair parting common in the face of sheep. (E) Whorl at the base of the mane in horses.
- (F) Whorl in the hind flank in horses.
- (G. J. K.) Types of whorls observed in Swine.
- (H) No parting of hair in the face observed on some sheep. (L) Single whorl in the face of cattle.
- (M) Whorl in the face of horses. (I) Whorl over the withers in Cattle. (N) Plain face in cattle.
- (O) Two whorls in the face of cattle.

appear to occur infrequently. Each of these were found on only 3 per cent of the horses inspected. Whorls at the anterior side of the arm pit were found on all of the horses that were observed. A total of 1,042 cattle were inspected and single whorls were found in the face of 90 per cent, two whorls on 1 per cent, and whorls were absent on 9 per cent of the cases, while one animal had three whorls in the face.

A single whorl was observed on the back of 93 per cent, two whorls on 6 per cent, and one animal had three, while 1 per cent did not show evidence of a whorl on the back. Numerous observations were made on sheep for whorls in the face but it proved to be difficult to classify these. In some cases there was no evident tendency for the hairs to whorl (H. Fig. 1), while in others there was a definite parting of the hairs (D. Fig. 1).

Data available are inadequate to offer a suggestion regarding the inheritance of these types, but the view that they are entirely due to mechanical causes is questioned. It is difficult to harmonize the fact that some animals within the same species have a single whorl in the face, some two, and others none, on a mechanical basis.

WHORLS IN SWINE

Experimental results secured at the Oklahoma Station clearly show that the whorls which occur over the loin, and rump are hereditary. Although the type and extent of the whorls vary (G. J. K. Fig. 1) it is not at all difficult to identify the disturbance when present.

From numerous matings involving different genotypes 438 individuals have been produced in this study. Matings have been repeated to produce a sufficiently large number of animals to give reasonable verification of the genotypes. The data support the hypothesis that the swirl is due to the interaction of two dominant complementary genes which may be present in either a homozygous or heterozygous combination to produce the swirl. This hypothesis has been previously offered by Craft 4, and confirmed by Nordby 5. Nordby observed swirls on the neck of his experimental stock, but they have appeared only on the rump, over the loin and in the face of the stock at the Oklahoma Station. Nordby points out that parents with a swirl on the neck tend to produce offspring with swirls in the same zone and that parents showing a swirl in this region.

Matings		Observed		Ratio Expected	Numbers Expected	
		Swirls	Non-Swi	rls	Swiris	Non-Swirls
S.s.S.s.	X S,s,S,s,	79	60	9:7	78.2	60.8
8,8,8,8,8, 8,8,8,8,	X 8,8,8,8, X 8,8,8,8,	12	4	3:1	12.	4.
S.a.S.s.	S, 8, 8, 8, 8, X 8, 8, 8, 8, 8, 8, 8, 8, 8, 8, 8, 8, 8,	86	29	3:1	86.25	28.75
8,8,8,8,8 8,8,8,8,	X S,8,S,8,	3	4	1:1	3.5	8.5
8,8,8 <u>,</u> 8,	X 8,5,8,5,	17	56	1:3	18.25	54.75
8,8,8,8	8,8,8,8,8, X 8,8,8,8,	31	32	1:1	81.5	81.5
8,8,8,8,	X 8,8,8,8,	4	24	1:3	7.	21.
		232	206			

TABLE SHOWING THE GENOTYPES TESTED, AND THE NUMBERS PRODUCED BY THE DIFFERENT MATINGS At present the factors which may determine the location, and the types of swirl hair in swine are not accounted for by these data. It does appear reasonable, however, to assume with Nordby that since the hair disturbances vary in size, shape, and direction, it is probable that genetic factors also influence, or determine these variations. Pictet and Ferrero (6) suggest that a dominant gene causes rosettes to spread over the body of the guinea pig, and that the recessive allelomorph limits the rosettes to the lumbar region. Furthermore, that another dominant gene causes the rosettes to develop on the head. It is possible that a similar genetic situation may exist for the location of the swirls in swine, but data available do not give a satisfactory fit to such a hypothesis.

Since whorls in swine are almost universally called swirls, the letter S is employed here as a symbol to denote the genes involved.

According to the hypothesis the following genotypes should occur among the individuals showing a swirl; (a) $S_1S_1S_2S_2$, (b) $S_1S_1S_2S_3$, (c) $S_1S_1S_2S_2$, (d) $S_1S_1S_2S_2$; the genotypes of individuals lacking a swirl should be as follows: (a) $S_1S_1S_2S_2$, (b) $S_1S_1S_2S_2$, (c) $S_1S_1S_2S_2$, (d) $S_1S_1S_2S_2$, (e) $S_1S_1S_2S_2$.

The different genotypes mated are shown in the table. Seven different boars have been used, and with one exception the number of litters produced from the service of each is sufficient to give a reasonable test of the genotype of the boar. The sows have all produced two or more litters, with the exception of four cases. Where two or more litters have been produced by a sow the number of pigs produced is considered sufficient to give a reasonable indication of the genotype of the sow.

Three different swirled sows mated to a non-swirl boar assumed to be homozygous for the genes for a smooth hair-coat produced 73 pigs, 17 of the pigs had a swirl and 56 were smooth. This closely approximates a ratio of one swirl to three non-swirl. If the three sows were hybrid for both pairs of genes a ratio of 1:3 should be expected. The same boar was mated with three additional swirled sows and 63 pigs were produced, 31 swirled and 32 non-swirled. If these sows were homozygous for one pair of the suspected genes and heterozygous for the other pair a 1:1 ratio of swirled to non-swirled should be expected. Another mating was observed that gave approximately a 1:1 ratio but only seven pigs were produced. It involved a swirled boar that had proved to be probably heterozygous for both pairs of the hypothecated genes. The numbers are too small to warrant the genotypic classification of the sow but since such a mating is possible it is shown in the table.

The number of pigs produced from matings where both parents were suspected of being heterozygous for both pairs of genes totals 139 pigs. These matings involve three boars and seven sows. While the numbers are not sufficiently large to give positive proof of the genotypes of the parents, the approximation to a 9:7 ratio of swirled to non-swirled pigs was strikingly close in each case. If the parents were heterozygous for the two pairs of genes and swirls are due to the presence of both dominant genes a 9:7 ratio should be expected.

SUMMARY

1. The results of observations on the occurrence of different types of hair whorls among the common farm animals are presented.

2. Fifty-two horses and 1,042 cattle were observed for hair whorls. Single whorls occurred in the face of 89 per cent of the horses and 90 per cent of the cattle. Two whorls were observed in the face of 11 per cent of the horses and 1 per cent of the cattle. Whorls were absent from the face of 9 per cent of the cattle observed.

3. Whorls in the face, hind flank and the anterior side of the arm pit appeared on all the horses observed, but on the ventral side of the

neck and at the base of the mane whorls appeared in only 3 per cent of the cases observed.

4. A single whorl was found on the back of 93 per cent of the cattle. and two whorls were observed on 6 per cent, one animal had three, and 1 per cent of the cattle did not show evidence of a whorl over the back. The data are considered inadequate to suggest a mode of inheritance for the hair disturbances observed among horses and cattle but the view that they are entirely due to mechanical causes is questioned. Sheep show partings and whorls in the face but these proved to be difficult to classify in the stock observed.

5. Experimental data are presented which are interpreted to show that swirls over the loin and rump in swine are due to the interaction of two complementary dominant genes.

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