THE PHYSIOLOGY OF HORN GROWTH: A STUDY OF THE MORPHOGENESIS, THE INTERACTION OF TISSUES, AND THE EVOLUTIONARY PROCESSES OF A MENDELIAN RECESSIVE CHARACTER BY MEANS OF TRANSPLANTATION OF TISSUES [1]

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FIVE PLATES (THIRTY-SIX FIGURES)

Starting from the point of view of particulate inheritance, this study was made on a single-gene determined character in the hope that a clearer understanding of the developmental processes of the character, with the aid of further knowledge on the interaction between allelomorphic pairs and the differentiation of parts as influenced by the interaction of tissues during the varied stages of ontogeny, might be a step toward the dissolution of the vast unknown lying between particulate heredity and the organism as a whole.

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site and that the horn spike is built up by other processes than those commonly ascribed to normal bone formation. The membrane which extends over the horn spike and is continuous with the frontal periosteum, is produced from connective or dermal tissues and may act only as a protective sheath, or take the place of periosteum.

The localization of the various parts of the spike in the apparently indifferent tissues of the spike anlage, makes it possible to cut out the portions forming different parts of the horn spike and provides a means of observing in a new light the formation of this limiting membrane.

In animal no. LIII (fig. 31) the three free transplants growing separately near the center of the head far from their original location were found to be enveloped by a limiting membrane. A limiting membrane was also found in the original locus between the small spike that grew there and the sheath above it. The membranes surrounding the free transplants were concerned with bone formation alone and not with keratin sheath formation. Thus the protective membrane, which is considered as the continuation of the frontal periosteum, can be regenerated from any portion of the horn spike anlage even in that part taken from the dermis.

The genetic factors responsible for the production of all the apparently separate manifestations in the expression of a character that has been shown by Spillman ('05), Lloyd-Jones ('16), Gowen ('18), Lush ('26) and others, to be due to a single factor difference, have been dealt with in a preliminary way in the introduction.

The experimental work reported upholds the view that the os cornu is active in stimulating the manifestation of fusion and boss formation, and is possibly active in directing the keratinization of the sheath.

As it was previously thought that scurs do not contain a bony core, there was then a reason to entertain interest in a duplicate or multiple action of genes, each controlling a part of the character—one of which (the gene determining the bony core) was dominated by the allelomorph in those animals carrying scurs.

Evidence from the natural occurrence of horns as all or none structures, as well as from the experimental results here reported, points toward a genetic interpretation in which separate but closely linked genes are required for the differentiation of each part of the horn and in which all tissues lie dormant until stimulated by the os cornu through the medium of an interaction of tissues.

The presence of 'knobs' on the heads of polled goats cannot be considered as due to a separation of the gene for boss formation from the gene for spike formation. In goats, the genes for knobs is allelomorphic to the presence of horns.

If it were possible to find a breed of 'polled' goats which lacks even these bony protuberances, and if it were found that a genetic factor difference exists between them and the other two types, the problem would be entirely different. In an examination of the heads of polled goats of the Toggenburg, Saanan and mixed breeds in various parts of Wisconsin and Illinois, none were found that lacked these excrescences.

In animals of the family Bovidae, both os cornu and horny sheath are present. The horn sheath is shed and renewed in the prong horn antelope. In the deer the os cornu is shed and the epidermis, which is not keratinized, is shed also, both being renewed annually. The giraffe's horn might be considered as an os cornu covered by normal skin, i.e., lacking the gene for sheath formation. But the epidermis is changed to a certain extent by the growth of tufts of long coarse hair.

Horns of the rhinoceros are considered by almost all writers as a structure composed entirely of hair, containing no bony core. In reality the composite hair is similar to the bony sheath of domestic cattle, and a bony excrescence is present, but in a very diminished form.

An examination of the skulls of rhinoceros in the Field Museum of Chicago, the Exhibition Hall of Heads and Horns in the New York Zoölogical Park, the Museum of Natural History, Washington, D. C., and various other collections containing skulls of extinct and living rhinoceros show that the bony protuberance (os cornu?) is a prominent growth in some cases, although it usually appears as a rough deposit of bone on the nasal bones. The protuberances are often similar to the rough bony excrescences noticed on the skulls of scurred cattle. Whether they are parallel structures or represent the os cornu complete and fused is not known. But a broad statement that the rhinoceros horn lacks the part analogous to the horns of cattle may not be correct.

Accumulating these varied contradictory ideas into a composite picture, there stands out but one fact—the close correlation of parts in the production of the complete horn. There is no genetic evidence that the determining factors separate from each other. In addition, evidence has here been given to show that the os cornu anlage influences the tissues below it to change their course of development, and while the experimental work did not show that the epidermis was also actively stimulated to keratinize by the os cornu anlage, yet the possibility exists for such an action prior to birth of the animal. The os cornu, then, is considered the dominating characteristic and the part controlled by the gene *p* for horns.

As a suggestion derived from the results of the experiments reported on the relation of connective and dermal tissues in causing the formation of an osseous spike, could it not be possible that the genetic factors controlling the shape of skeletal structure act through this same method?

There are various excrescences present on a skull such as the frontal eminence, the parietal crest, and the facial tuberosity. Even the broad flat areas of table bone vary in their width, length, and surface conformation. Some skulls have a concave (deeply dished) area between the eyes; others are high and bulbous in the same region. The frontal eminence may be sharp and prominent, or broad and receding. All bones of the skeleton are subject to variations in size and shape which can be considered as inherited, since they are common or specific to strains and families. Is it not possible that the connective tissue, which is the original precursor of

the periosteum, continues to lead, by directive action, the manner and rapidity of bone deposited by the osteoblasts in the periosteal layers below it?

There is an indication of such an effect in the transplantation of a pedicled flap of poll periosteum.

Summary

The os cornu forming tissues of calves and kids would not stimulate normal, non-sheath-forming skin to keratinize. The rapidly proliferating epidermis occurring in cicatricial tissue artificially produced over ossifying os cornu would not keratinize. Failure to obtain any reaction between the two tissues was attributed to the age and specialization already attained even at the birth of the animal. They were 'set' in the direction of their differentiation and could not be redirected.

There appears to be a possibility that the os cornu may stimulate the epidermis during early embryonic life of the animal, especially in view of the fact that it takes an active part in fusing through frontal periosteum as it makes attachment to the skull and forms the basilar supporting structure of the horn.

Keratin tissue migrating over connective scar tissue from keratin forming cells failed to stimulate bone growth beneath it.

The view was favored that perhaps the os cornu is the leading character controlled by the genetic factor *p* for horns.

The suggestion is made that the shape and form of all skeletal parts may be influenced by the connective tissues above the periosteum, and that the genetic factors responsible for size and shape of bone work through this medium.

CONCLUSIONS

From the transplantation of horn-forming tissues of calves and kids, the following results have been observed:

1. The horn core is the product of an ossification originating in tissues above the frontal periosteum. The horn core anlage lies in the connective and dermal tissues.