Zoology. — *"On the phylogeny of the hair of mammals"*. By Prof. P. N. VAN KAMPEN. (Communicated by Prof. WEBER).

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In his work on "Die in Deutschland lebenden Arten der Saurier" (1872) and later on [1]), in a paper in which he rejects MAURER's well-known theory on the derivation of the hairs of mammals from epidermal sense-organs, LEYDIG draws the attention to the resemblance between the structure of the hairs and the so-called thigh or femoral organs of the lizards, which he considers to be a transition form between ordinary epidermal proliferations and hairs.

Less attention has been paid to this remark than it would have deserved. For the structure of the afore-mentioned organs, whose function is not known (they probably participate in the act of copulation) closely resembles in fact the structure of a hair in a simplified form [2]): they are cylindrical rods, composed of horny epidermal cells, and sunken into a follicle of the skin. They differ from hairs principally by the absence of a cutis papilla and by the fact that they do not show a differentiation in medulla, cortex and cuticle. It is true that according to MAURER [3]) they are composed of two kinds of cells, but the arrangement of these cells is quite different from the one of the elements of the hair.

As not one of the hypotheses which try to derive hairs from epidermal organs of lower Vertebrates and among which the afore-mentioned one of MAURER, based on a large body of facts, is best known, has been generally aknowledged (indeed, BOTEZAT [4]) in his review on these theories comes to the conclusion that none of them can be maintained and that the hairs in the mammals independently have taken their origin in the skin) it is desirable to examine, whether the idea uttered by LEYDIG might contain perhaps a germ of truth. Against a direct derivation of hairs from femoral organs it may be advanced that these organs among the recent reptiles

[1]) Biol. Centralbl., XIII, 1893.

[2]) LEYDIG compares them, in my opinion wrongly, to a bundle composed of hairs glued together.

[3]) Die Epidermis und ihre Abkömmlinge. Leipzig, 1895, p. 212 ff.

[4]) Anat. Anzeiger, XLVII, 1914/15.

only occur with the Lacertilians and with these far from generally, often only with the male and, besides, always in a very limited number. Elsewhere among Reptiles, organs in some degree comparable with femoral organs are only found with crocodiles, where, according to VOELTZKOW's description [1]), they lie between the scales of the back.

But, though it would be difficult to assume the direct origin of the hairs from femoral organs, the question might still be raised, whether there might not be a connection between them, in so far that they have a common origin. If this were the case, their origin might probably be traced most easily with the last-mentioned, more simply constructed organs, which in this way might throw a light on the origin of the hair.

The morphological significance of the thighorgans has been elucidated by the research of SCHÄFER [2]). This author not only confirms what has already been recorded by earlier investigators, viz. that with Lacerta the femoral organs of the male are most strongly developed in the breeding time, but he emphatically points out that in that period no keratinisation of the cells takes place. But of more importance is what he found with Sceloporus acanthinus: with this Iguanide no horny cells are formed in the organs, but instead of them a secretion, which is composed "aus einer völlig zerfallenen, dem Secret von Talgdrüsen ähnlich sehenden Masse". SCHÄFER comes to the conclusion that the thighorgans are glandulae celluliparae, related to those sebaceous glands, which are not connected with hairs. Keratinisation occurs only, when the secretion is slow. In connection with this conclusion the statement of MAURER [3]) is of importance, that with Lacerta the contents of part of the cells of the thighorgans is of a fatty nature.

These facts point to a close connection of the femoral organs with "holocrinous" cutaneous glands, and the conclusion that they can be derived from such glands is obvious. The difference between them is not great: if the fatty secretion in a sebaceous gland were replaced by keratinisation of the cells, then a horny rod would be formed, which would show great resemblance to the thighorgans. Now the eleidin, which appears with mammals in the process of keratinisation, according to MAURER has a fatty character [4]), while on the

[1]) Abhandl. Senckenberg. Naturf. Ges., XXVI, H. 1, 1899.

[2]) Archiv f. Naturgesch., LXVIII, Bd. I, 1902.

[3]) l. c., p. 220.

[4]) GOETTE (Arch. f. mikr. Anat., IV, 1868) also describes the occurrence of fat-globules in the young epithelial hair-germ of the sheep.

other side it is known, that the cells of the sebaceous glands of the Mammalia contain eleidin-granules and can even partly undergo keratinisation[1]). One must indeed imagine the sebaceous cells to originate from ordinary epithelium-cells, which had already the capacity of keratinisation and it is not surprising that this capacity reappears now and then.

So the femoral organs of Lacerta have arisen from cutaneous glands; they have preserved the structure of those glands, chemically however they are modified, in connection with the strong keratinisation, which is characteristic of the skin of reptiles in general.

If the femoral organs can be derived from cutaneous glands, one can imagine the same thing in the case of the hairs of mammals. Only in this case the differentiation has become greater and the structure of the organ is more complicated, in consequence of the more important function the hair has in the life of mammals. The hair papilla is to be considered of secondary origin and to have arisen in connection with the richer nutrition, which had become necessary for the stronger growth.

But there is still another phenomenon that can be easily explained by this hypothesis. The origin of the hair as a solid epidermic thickening quite agrees with that of cutaneous glands, but also with that of the femoral organs, according to the descriptions of MAURER and SCHÄFER. As to the thighorgans, the first author already directs the attention to this similarity with cutaneous glands of the amphibians, but attaches much importance to the difference between them, which lies in the fact that the smooth muscular fibres of the glands of the amphibians are absent in the femoral organs. In this point I cannot agree with him: these muscular fibres, which in the cutaneous glands are necessary for the extrusion of the secretion, are from their very nature superfluous in the entirely horny thighorgans, and so it is perfectly clear, that they have disappeared. And the same is true for the hairs, where they are absent as well. Another point, to which MAURER attaches much importance, is the peculiar arrangement of the matrix-cells, which appears in the very first origin of the hair and of the dermal sense organ in the same manner. It seems to me however that this arrangement may be explained by the pressure of the surrounding cells upon the growing germ and so in different cases may appear in similar circumstances.

Since the researches of DE MEIJERE[2]) an attempt to explain the origin of the hair must take into consideration their arrangement on the skin.

[1]) Cf. SCHÄFER, Text-Book of Microscopic Anatomy, 1912, p. 476.
[2]) Morph. Jahrb., XXI, 1894.

In those places where in mammals scales occur, the hairs are inserted generally in groups behind them. In this point they therefore differ from the thighorgans, which are placed in the middle of scales. It is true, that not too much value ought to be attached to this fact, but yet I want to point out in the first place that the afore-mentioned dermal organs of the crocodiles, described by VOELTZKOW, are arranged between the scales, and further, that the similarity in location of hairs and femoral organs becomes greater, if the considerations of PINKUS [1]) in connection with the "hairdiscs" described by him, are right. If, as he thinks, a "Haarbezirk", that is the whole complex of scale rudiment, hair group and hairdisc, answers to the scale of reptiles, then the hairs are placed in the middle of the region of the scale, just the same as is the case with the thighorgans. PINKUS, who derives the hairdiscs from tactile spots of reptiles, cannot find an explanation for the origin of the hairs: "Das Säugetierhaar hat kein Homologen in dem Gebiet der Reptilienschuppe; sein Platz ist leer." By the hypothesis, developed before, this objection against PINKUS' theory is done away with.

MAURER has directed the attention to another arrangement of the hairs; still before the hairgroups are formed, in mammalian embryos the placing of hairs in longitudinal rows may be stated. From this fact MAURER deduces an argument for his before mentioned theory, because epidermal sense organs generally show a similar arrangement. This argument however becomes worthless by the observation

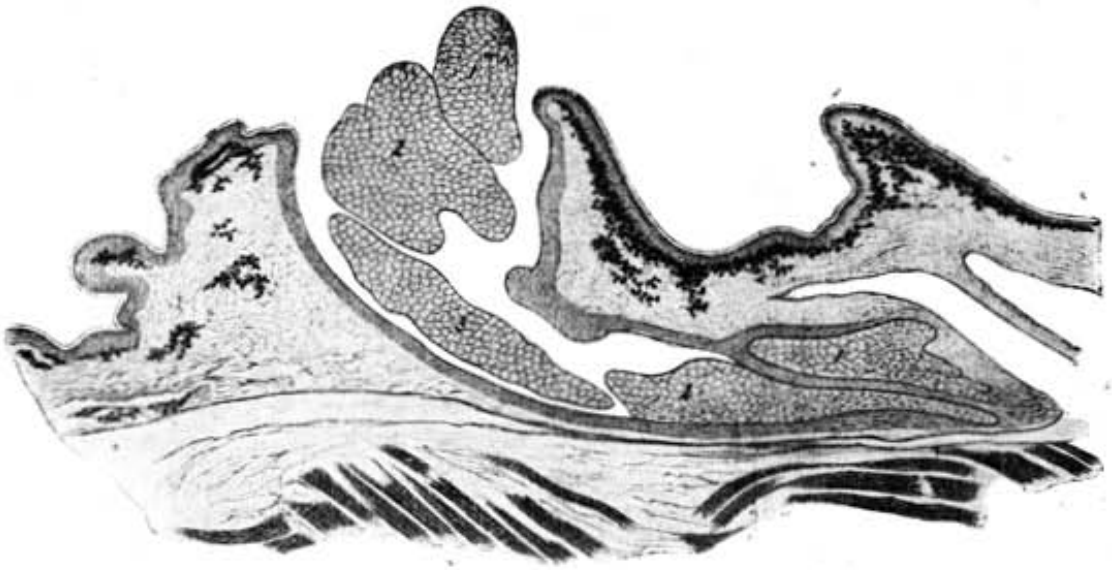

Fig. 1 Lacerta agilis. Bundle of three femoral organs (1—3).

[1]) Arch. f. mikrosk. Anat., LXV, 1905.

of MAURER himself[1]), that also the first germs of the dermal glands of Triton and Anura occur in rows.

The dermal glands of Promammalia have thus developed in the Mammalia in diverging direction: the hairs, as well as the dermal glands of the mammals have arisen from them. The complex of hair and sebaceous glands is to be derived either from a compound gland, the follicles of which have taken a different direction of development, or what seems more probable to me, from the union of a number of glands into one follicle, in the same way as hairs may be united into a bundle. This last derivation may be strengthened by the fact that a number of femoral organs too, sometimes form a bundle with a common follicle. I found this in Lacerta agilis (see fig. p. 143).

[1]) l. c., p. 159.