Zoology. — *"Rhythmical Skin-growth and Skin-design in Amphibians and Reptiles"*. By Prof. C. PH. SLUITER.

(Communicated at the meeting of March 27, 1920).

VALENTIN HAECKER[1]) in a few very important communications and later on in a synthetic exposition has tried to give due value to a factor, until now little or not at all appreciated, in the explanation of the origin of the skin-design. Previous investigators, among whom I refer to HARRISON, ALLEN, TORNIER, GROSSER, ZENNECK and especially to v. RIJNBERK, chiefly tried to find a connection between the transversal stripes of the vertebrata and the segmental arrangement of other organs. ZENNECK, among others, found a connection between the appearance of pigment in the skin and the situation of blood-vessels in embryos of Tropidonotus natrix. The well-known researches of v. RIJNBERK, partly made in collaboration with WINKLER, to which in some respects the work of others (SHERRINGTON, BOLK, LANGELAAN, etc.) is connected, try to find the most important factor for the origin of the skin-design in the segmental innervation of the skin.

Thus the — in my opinion — ill-chosen term of "dermatome" has found its way into the scientific terminology. This term gives the impression as if the skin itself had a metameric structure, while the expressions of "overlapping of the dermatomes", "summation and interferential zones of the dermatomes" all reinforce this erroneous view.

Though some of the investigators have made it plausible, that in a number of cases the innervation and the design of the skin are correlated, yet one cannot derive from it a general guiding principle in explaining the design of the skin, and I think that we find in HAECKER's principle a wider base on which one might build with profit. This principle is described by HAECKER as follows: the skin-design of the vertebrata (and I prefer to add: also of the invertebrata) is dependent on the fact that the growth and the differentiation of the skin are clearly rhythmical. This rhythm is sometimes in correlation

[1]) V. HAECKER. Entwickelungsgeschichtliche Eigenschafts- oder Rassenanalyse Z.f. ind. Abstammungs- und Vererbungslehre. Vol. 14, p. 260, 1915.

Idem. Zur Eigenschaftsanalyse der Wirbeltierzeichnung. Biolog. Centralblatt Vol. 36, p. 448, 1916.

Idem. Entwickelungsgeschichtliche Eigenschaftsanalyse. Jena 1918.

with the metamerism of the body, but generally independent of it and in a high degree autonomic.

It is evident that it is easiest to trace the phenomena of this rhythmical growth in young animals and especially in quickly growing larvae or embryos. Thus HAECKER found this rhythmical growth for the first time confirmed in the larvae of Axolotl, as here the size of the cells, of which the epidermis is constructed and the fact that it has only two layers of cells, was very favourable for the research.

The large number of embryos and larvae of reptiles and of amphibians of which the Zoological Laboratory at Amsterdam disposes, led me to investigate the rhythmical growth in the skin of these young animals with a view to afford a further confirmation of HAECKER's supposition, that this rhytmical growth is the nearest cause of the skin-design.

As to the larvae of the amphibians, I examined the skin of the of *Megalobatrachus maximus*-larvae of the famous hatch of the Aquarium of the Society "Natura Artis Magistra". These larvae show very early a skin pigmentation, but I never found a metameric design, as HAECKER did in Axolotl. The pigmentation of the Megalobatrachus-larvae might rather be called diffuse, but not absolutely, as it is obvious on closer examination that the pigment, especially on the ventral side, is arranged more or less regularly in small groups.

The idea struck me directly, whether this were a case of a type of skin-growth which was indicated by HAECKER as the "chess-board-type", — theoretically possible, but not yet observed — and which was accepted by him as the possible original type of the skin-growth of the vertebrata.

I found on microscopical examination of the skin of the larvae of *Megalobatrachus maximus*, but especially in a young stage of 30 m.m. length, where the pigment formation was only in its first development, that the epidermic-cells were arranged very regularly indeed, into square fields in which, evidently the growth had proceeded centrifugally (Fig. 1). The cells lying in the middle of every field were separated more sharply by more strongly developed marginal zones than the younger ones lying against the edge. The very first pigment granules appear in the middle of these square fields. This agrees with the observations, made by GUSTAV TORNIER [1]), who found that no pigment appears in cells that are still in the dividing stage, but as a rule in those parts of the skin which are growing rapidly. These spots, arranged regularly on the ventral side of the larvae

[1]) G TORNIER. Experimentelles über Erythrose. Sitz.ber. Ges. Naturf. Freunde. Berlin 1907.

have their origin in these accumulations of pigment. On the dorsal side, this design passes gradually into a more or less diffuse pigmentation.

The pigmentation however is not regularly diffuse on the dorsal

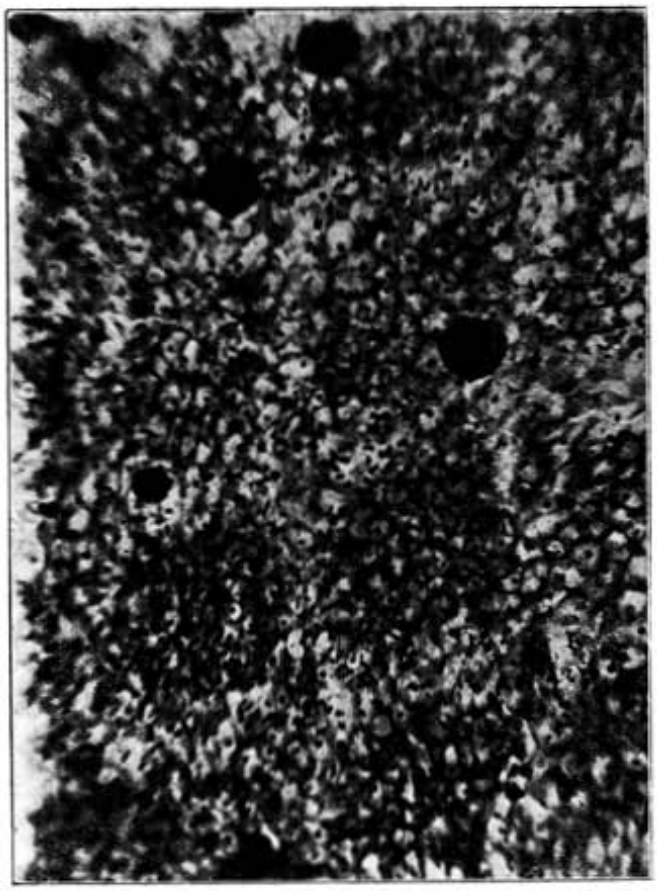

Fig. 1.

side, and especially not on the flanks of the bodies of the larvae. It is evident that the "cellstreams", described by HAECKER for the first time, are of importance for the pigmentation. The "cell-streams" were very obvious and strongly developed in the skin of the Megalobatrachus larvae, in a similar way as HAECKER found them in Axolotl. These cellstreams are series of cells, which, radiating from special centra, divide more quickly and shove in between other groups of cells. Thus they form regions of more intensely growing skin. (Fig. 2). This also seems to coincide with the distribution of pigment. I generally noticed that cellstreams radiated obliquely backwards from the well-known lateral sense organs. The pigment appears first close to the lateral sense-organs on the flanks of the

body, and spreads from there along the cellstreams over the flanks of the body. However in the case of Megalobatrachus there is no obvious pattern at all, which is probably connected with the fact that

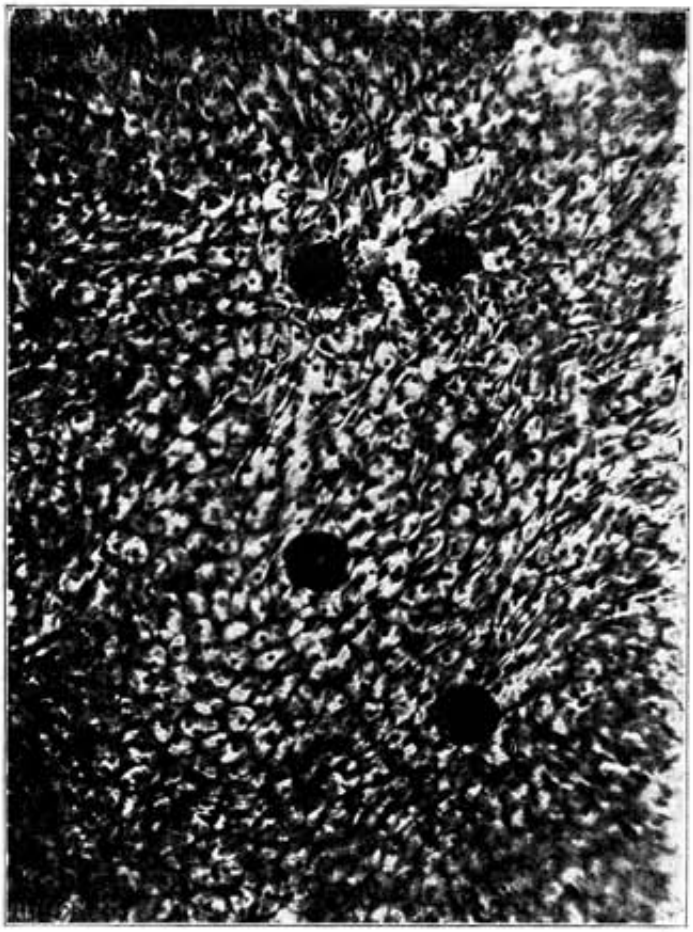

Fig. 2.

the lateral sense-organs are distributed over the skin in a strikingly irregular way. While in younger larvae the shades of colour in the pigmentation of the skin, owing to the cellstreams are obvious, they give place to a very regularly spread darker colour of skin in older larvae.

Once having found in Megalobatrachus, that the skin-growth, and in connection with this, the first appearance of the autochtone pigment, not only occurs in a similar way, as HAECKER found in Axolotl larvae, but that the "chess-board type" was evident in a specially young stage of development, which HAECKER supposed, but had not seen, — I tried to enlarge my investigation on the skin-growth in examining the embryos of different reptiles. The cytological exami-

nation, however, is much more difficult with these, as first of all the skin of the embryos of reptiles is not constructed of two layers of epidermic-cells only, but especially because these cells are much smaller, so that the directions of the cell grouping and the stages of division are much less visible than in the amphibian-skin with its large cells. Yet I succeeded at last in preparing large pieces of the skin of young embryos and in examining them entirely. Though my research on this subject is only in its first stage, I could state already that similar rhythmical growths appear in the skin of reptile-embryos, which coincide with the pigmentation. The development of the bodyform and with this the growth of the covering skin is much more complicated than in the generally simple cylindrical or barrel-shaped larvae of the amphibians. Many remarkable and important problems arise of this complication. It is evident that by preference those embryos are examined, that show peculiarities in their coat-patterns.

Thus I examined in the first place the embryos of Draco volans, of which a large number of very different ages were collected by Dr. L. DE BUSSY, at Medan, and presented to the Zoological Museum at Amsterdam. These embryos show a very clear and characteristic design, of which only a very indistinct image is left in the grown-up animals. First of all it may be stated that the design in question is quite independent of the metameric architecture of the rest of the body. This strikes us most in the design on the membrane between the prominent 5 or 6 ribs. In young embryos we see the appearance of 4 or 5 dark broad stripes which run obliquely across the ribs and thus cross the bloodvessels and nerves, which lie alongside the ribs (Fig. 3). We have probably to deal with a case of rhythmical, wavelike growth of the skin. Already at the first appearance these stripes appear as continuous pigment-zones in the intercostal membrane. A quicker growth and a coïnciding pigment formation take place there. The whole pattern on this membrane seems to me a typical illustration of the fact that this design is nothing but a consequence of the rhythmical skin-growth. Also on the rest of the body of young embryos of Draco volans, one finds a distinct connection between the first appearing design and the places of strongly developed growth. Large ribbed scales appear very early along the flanks of the body and they remain when the animal is adult. These scales, whose place does

Fig. 3.

not correspond to the metamerism of the rest of the body, at the same time indicate the place, where, for the first time pigmentation appears in the skin. We find the first trace of pigmentation in the beginning of the high ridge on the scales. Here of course is the place of most intense growth. From that point, the pigment spreads over the rest of the scale, to proceed from there gradually over the surrounding scales. Here also, I was able to observe cell-streams in many young embryos, where the large ribbed scales were only slightly to be distinguished. The design on the medial line of the back has likewise no connection whatever with the metamerism of the body. It forms crescent-shaped spots, with the opening turned backwards; they are placed at more or less regular distances and point also to a rhythmical skin-growth, though up to the present moment, I was not able to find any cell-streams.

At last I wish to point out some peculiarities which occur at the manifold transversal striping in the embryos of reptiles. It is well-known that EIMER accepted the longitudinal striped design as the original one and not only in the case of reptiles, but he made a general rule of this principle. Whether this theory is probable or not, may be left aside here; but in any case the fact remains difficult to explain, that in a great number of embryos of lizards, serpents and crocodiles very distinct cross-stripes appear first, even with forms, showing longitudinal stripes in the adult.

A number of embryos of *Lygosoma olivaceum*, collected partly by Dr. L. DE BUSSY, partly by myself, were at my disposal. The whole of the trunk and the tail shows sharply marked, broad, dark, nearly black stripes, which alternate with comparatively narrow, white stripes, without pigment in the skin. In the first place, not the slightest coincidence is to be found between the extension of this stripe design and the metamerism of the rest of the body. The left and the right side are not symmetrical, so that it often happens that a dark stripe meets a white one on the medial line of the back (Fig. 5). However it is well-known that this cannot form an argument against the metameric origin of the design, as the metameric spinal nerves and the bloodvessels to the left and the right are not always symmetrical. But also the number of the stripes is different on the two sides of the body and the following peculiarity of this difference is of great importance.

As is more than well-known, the embryos of all the reptiles lie more or less like a spiral in the egg and now one generally finds that the dark stripes become broader and split into two at their broadest point towards the convex side of the body, because at that

point a white stripe appears. In this way a few more stripes occur on the convex side of the embryo, than on the concave side (Fig. 6).

Fig. 5.

Fig. 6.

I saw the same phenomenon take place wherever the transversal striated parts of an embryo lay in a sharp curve. This was very obvious in the tail of the embryos of *Gecko verticillatus*, the well-known Tokkè of the Dutch Indian Archipelago. The embryo's tail is curled like a spiral, turned a little dorsally. And here too we find that considerably more cross-stripes appear at the ventral convex side than at the concave dorsal side. (Fig. 7). The same phenomena appear on the tail and the trunk of crocodile embryos, as is generally known.

Fig. 7.

The question is raised now: what is the origin of this phenomenon? I think that we must look for the explanation in the rhytmical skin-growth. At the convex side the growth is certainly more energetic than at the concave side, where the body is compressed and the skin is not so tightly stretched and has even a few folds. For the present it may be left an open question whether the reason is an insufficient nourishment at the concave side, caused by pressure on the blood-vessels and probably on the nerves, as GUST. TORNIER [1]) supposes has taken place in an analogous case of snake embryos, deformed pathologically.

[1]) G. TORNIER, l.c. p. 1210.

Though the proof has not been given at present that this is a case of more or less quick rhythm in the division of the skin-cells — as is the case with amphibians — we cannot help thinking that we must look for the principal cause of the stripe design of the skin in rhythmical skin-growth. This may sometimes coincide with the rest of the metamerism of the body, but as a rule it is quite independent of it.

The future will teach us whether the conclusion to which TORNIER arrives is not too optimistic. He thinks that it will be possible to infer partly the conduct of every lizard or snake directly from the skin-design. In the first place it is necessary to trace, whether in the case of reptiles too, the stronger pigmented places of the skin of the embryos actually coincide with the places in the epidermis, where an intenser growth, and consequently a quicker division of cells occurs. I found that with Draco volans this investigation is much more difficult, but not impossible and I hope to be able to give further data in a following communication.