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ON THE TOPOGRAPHY OF HERBST'S AND GRANDRY'S CORPUSCLES IN THE ADULT AND EMBRYONIC DUCK-BILL

BY

ANNA KROGIS.

8 text figures and 1 plate (4 figures).

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CONTENTS:

I. INTRODUCTION.

The subject chosen for the present paper is so far of interest as there hardly exist any researches as to the exact topography of the sensory corpuscles in the skin of birds. On the topography of Herbst's and Grandry's corpuscles I have seen only a short note in FR. HESSE's (1878) paper "Über die Tastkugeln des Entenschnabels," in which the author states the following (in translation): "In the upper bill the number of sensory spheres (Grandry's corpuscles) diminishes in the following succession: dentary, mucous membrane, margin, dorsal portion of cere." "Their number is equal to that of Herbst's corpuscules in the bill." "In the margin of the cere the approximal number of sensory spheres lying under 1 qmm of the skin surface might be at least 10." I underwent the task of making a thorough examination of the duck-bill by special measuring methods and particularly the interrelations of Grandry's and Herbst's corpuscles.

Investigations on the physiological function of both types of corpuscles are also wanting. Nearly all authors consider both of them as being tactile organs. Only two attempts can be mentioned to distinguish both kinds of corpuscles according to their physiological significance. JUSTUS CARRIÈRE (1882) brings in question whether Grandry's and Herbst's corpuscles are in effect tactile and not gustatory organs. Should both types be conceived as tactile organs, the ones might serve as receptors of coarser, the others of more delicate stimuli. CLARA MAX (1925) describes the sense-corpuscles in the snipe-bill and advances the supposition that Herbst's corpuscles might be considered as pressure-registring organs. These hypotheses are to the present time devoid of any physiological proofs. In the present paper, however, an anatomo-topographic base is brought forward for the opinion that both kinds of sense-corpuscles must be different in their function.

In connection with the three main questions to be dealt with, viz. 1) the topography of Herbst's corpuscles, 2) the topography of Grandry's corpuscles and 3) the numerical correlation of these corpuscles, the present paper is divided into three sections preceded by a description of the material used as well as the technique. In conclusion a short description of the topography of the sense-corpuscles in embryos is added.

In this place I wish to express my sincerest gratitude to my honoured tutor Prof. Dr. N. G. LEBEDINSKY, to whom I am indebted for the choice of the subject and constant advices during the work.

II. MATERIAL AND TECHNIQUE.

As material for the investigation of adult birds served the following four species, respectively races of ducks (together 5 individuals):

1. *Anas platyrhyncha platyrhyncha domestica* L.
2. *Anas platyrhyncha platyrhyncha* L.
3. *Anas (Querquedula) crecca crecca* L.
4. *Anas querquedula* L. (*A. circia* Bp.).
5. *Nyroca fuligula* L. (*Fuligula cristata* Ray).

The birds were received 24 hours at the utmost after having been shot. The cere was prepared and fixed in ZENKER's fluid. My task being to study the topography of the sense-corpuscles and not their histological structure and innervation, the comparatively long space of time between the moment of death of the birds and the fixation is of no great importance. The embryonic material was taken from the domestic duck and fixed daily beginning with the 18th day of incubation up to the time of eclosion—the 28th day. As in adult birds the cere only was taken for embedding. A number of objects

was embedded in a mixture of 52° + 56° + 58° C. paraffin in equal proportions and another portion in celloidin-paraffin, in which latter case 56° + 58° C. was used. It proved that it was easier to get complete series of sections from the material embedded in the latter way. For embedding were chosen quite distinct portions of the cere. To begin with this latter was divided by a sagittal longitudinal cut into two halves (fig. 1). From each half were cut four transverse strips. The first from close to the tip, the last from the basal portion of the bill, and the remaining two from spaces situated at equal distances from each other and the said tip- and basal strips. From the tip-strip, indicated by No. 1, in adult birds only a margin block could be obtained, the remaining portion being occupied by the hard bill-nail. From embryological specimens I was able to obtain from the same portion three blocks, which I shall indicate beginning with the bill-margin, i.e. in latero-medial direction, as 1 a, 1 b and 1 c. The following strip is marked No. 2 and the respective blocks, counting from the margin, as 2 a, 2 b and 2 c. The third strip is marked No. 3 and its respective blocks spoken of as 3 a, 3 b and 3 c. Ultimately the blocks of the last strip are indicated by 4 a, 4 b and 4 c. From each of these blocks there was taken a series of 25 sections, counting from the upper surface of the block. For conciseness the blocks are indicated in the following by their respective numbers and letters, the word "block" being omitted. The thickness of the sections was 10 μ. For staining the material from adult birds anilin-blue, orange and acid fuchsin after MALLORY were used, the embryonic material was stained with HEIDENHAIN's Hæmatoxylin and eosin.

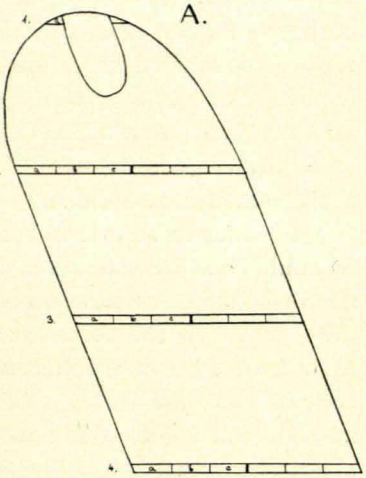

Fig. 1. Scheme of the cere. *A* tip, *B* base of the bill. 1, 2, 3, and 4 zones of the sections; *a*, *b*, *c* corresponding blocks.

The separate sections were sketched by the aid of EDDINGER's drawing apparatus reproducing the outlines of the section and of Herbst's and Grandry's corpuscles. The corpuscles were then counted separately in each series. In order to make it possible to compare their number, 1 qmm of the field, correspondingly magnified, was chosen as a unit. Each series being composed of 25 sections, and the thickness of each section being 10 μ (which makes a total of 250 μ = ¼ mm), it was necessary in order to obtain a space of 1 qmm, to take 4 mm in the longitudinal direction of the section. As the drawing was executed at a magnification of 56 × it was necessary to register the sensory corpuscles in each section on a space long 4 mm × 56. This space

was measured from the outer margin of the block a, from the inner margin of block c, and the middle of block b.

The following counting method proved to be the most precise and easiest. Every Herbst's corpuscle in the first section of each block was marked with a certain number and those reappearing in the next section were marked with the same number, whereas fresh corpuscles received new numbers in the usual succession. Together with the vanishing in a section of a certain corpuscle its corresponding number also disappeared. In this way the counting was conducted up to the 25th section of each block. In total about 1,500 drawings of sections were prepaired and used for counting Herbst's and Grandry's corpuscles. For calculation of the immersion of the corpuscles the same drawings were used. The actual distances were obtained by dividing the obtained measurements by the magnification-index—56.

In order to be able to compare the numbers found in embryos with those in adult birds, it was necessary, with regard to their bill being shorter and narrower than in that adult stage, to reduce correspondingly the unity of the area on which the corpuscles were counted. As the result of the counting a table of figures was received for each species. The number of Herbst's corpuscles in the series *a* of *Anas platyrhyncha domestica* L. was adopted as a basis and putting it equal to 100 the numbers of Herbst's and Grandry's corpuscles of all the other species were calculated accordingly. These percentage numbers were used for drawing the diagrams.

III. THE TOPOGRAPHY OF HERBST'S CORPUSCLES.

1. *Number of Herbst's corpuscles.*

Anas platyrhyncha platyrhyncha domestica L. The maximal number of Herbst's corpuscles on 1 qmm is 67, or in percentage 100 %, the minimal number 12 (18 %), the mean number 29 (43 %). (See tab. 1.)

Anas platyrhyncha platyrhyncha L. Maximal number of corpuscles on 1 qmm 106 (158 %), minimal number 13 (19 %), mean number 34 (51 %). (See tab. 2.)

Anas crecca crecca L. Maximal number of corpuscles on 1 qmm 66 (99 %), minimal number 9 (13 %), mean number 21 (31 %). (See tab. 3.)

Anas querquedula L. Maximal number of corpuscles on 1 qmm 93 (139 %), minimal number 11 (16 %), mean number 29 (43 %). (See tab. 4.)

Nyroca fuligula L. Maximal number of corpuscles on 1 qmm 41 (61 %), minimal number 7 (10 %), mean number 22 (33 %). (See tab. 5.)

The mean maximal number of Herbst's corpuscles on 1 qmm in all species examined taken together is 75 (112 %), the mean minimal 10 (15 %), the general mean number 27 (40 %).

Table 1. *Anas platyrhyncha platyrhyncha domestica* L.

Antereo-posterior No.	Latero-median sign	Herbst's corpuscles	%	Grandry's corpuscles	%
1	a	67	100	36	54
	a	51	76	32	48
2	b	27	40	16	24
	c	28	42	21	31
	a	28	42	20	30
3	b	18	27	26	38
	c	23	34	24	36
	a	14	21	14	21
4	b	17	25	16	24
	c	12	18	35	52

Table 2. *Anas platyrhyncha platyrhyncha* L.

Antereo-posterior No.	Latero-median sign	Herbst's corpuscles	%	Grandry's corpuscles	%
1	a	89	133	61	91
	a	106	158	92	137
2	b	24	36	18	27
	c	20	30	23	34
	a	28	42	32	48
3	b	20	30	33	49
	c	13	19	43	64
	a	14	21	36	54
4	b	13	19	66	99
	c	13	19	52	93

2. Distance of Herbst's corpuscles from the surface of the cere.

At closer examination of the sections it is easily recognized that Herbst's corpuscles are not in all regions of the cere situated at equal distances from its surface. In *Anas platyrhyncha platyrhyncha domestica* L. they are found near the margin of the cere, in block 1 a at a depth of 300 μ to 1,000 μ, or speaking more exactly, in the undermost layer of the marginal edge up to 1,000 μ, in the upper main layer up to 300 μ. In the blocks 2 a and 3 a the corresponding depths were 200 μ and 800 μ, in 4 a 300 μ and 500 μ. In the middle portion of the cere of the same duck Herbst's corpuscles are found in the blocks 2 b and 2 c at a depth of 200 μ to 300 μ, in blocks 3 b, 3 c, 4 b and 4 c, however, at only 100 μ to 300 μ.

Herbst's corpuscles are consequently in the front portion of the cere inserted deeper than at the base. Moreover inwards of the margin and towards the middle of the cere there remains only the upper main layer of corpuscles and therefore their immersion diminishes at that spot. In the wild duck, *Anas platyrhyncha platyrhyncha* L., there is found a different distri-

Table 3. *Anas crecca crecca* L.

Antereo-posterior No.	Latero-median sign	Herbst's corpuscles	%	Grandry's corpuscles	%
1	a	66	99	57	85
	a	40	60	26	38
2	b	18	27	11	16
	c	12	18	9	13
	a	17	25	21	31
3	b	11	16	36	54
	c	12	18	37	55
	a	9	13	55	82
4	b	11	16	70	104
	c	10	15	49	73

Table 4. *Anas querquedula* L.

Antereo-posterior No.	Latero-median sign	Herbst's corpuscles	%	Grandry's corpuscles	%
1	a	93	139	61	91
	a	30	45	43	64
2	b	18	27	32	48
	c	20	30	37	55
	a	20	30	52	78
3	b	25	37	44	66
	c	26	38	43	64
	a	11	16	56	84
4	b	18	27	81	121
	c	25	37	50	75

Table 5. *Nyroca fuligula* L.

Antereo-posterior No.	Latero-median sign	Herbst's corpuscles	%	Grandry's corpuscles	%
1	a	41	61	13	19
	a	37	55	21	31
2	b	17	25	24	36
	c	17	25	41	61
	a	25	37	11	16
3	b	21	31	29	43
	c	19	28	45	67
	a	7	10	19	28
4	b	18	27	24	36
	c	14	21	32	48

bution of Herbst's corpuscles. In block 1 a they are found 200 μ to 600 μ, in 2 a 200 μ to 800 μ, in 3 a 200 μ to 600 μ, and in 4 a 100 μ to 400 μ deep. Thus along the margin the spot of the deepest immersion of the corpuscles

is not located at the very tip of the bill but at a certain distance from it and generally they are situated less deeply than in the domestic duck. In all blocks taken from the middle portion the corpuscles are met with at a depth of 100 μ to 200 μ. In the wild duck also the corpuscles lye at the margin of the cere in several layers, in the remaining portions, however, in a single layer.

In *Anas crecca crecca* L. Herbst's corpuscles are situated in block 1 a at a depth of 100 μ to 600 μ, in 2 a at 100 μ to 400 μ, in 3 a at 100 μ to 200 μ, and in 4 a at 100 μ to 300 μ. In the blocks taken from the middle of the bill the immersion of the corpuscles is usually at 100 μ. In general the immersion of Herbst's corpuscles diminishes, as in the domestic duck, typically in the direction from the tip of the bill towards its base and from the margin towards the middle. Here also the deepest lying corpuscles are found in the marginal portion.

In *Anas querquedula* L. the corresponding immersion of Herbst's corpuscles is as follows. In block 1 a 100 μ to 500 μ, in 2 a 100 μ to 300 μ, in 3 a 100 μ to 300 μ, and in 4 a 100 μ to 400 μ. In the middle of the bill the depth of immersion of the corpuscles varies between 100 μ and 200 μ. Here also the mean depth of immersion diminishes towards the base and the middle of the bill.

Finally in *Nyroca fuligula* L. the corpuscles are found in block 1 a at a depth of 100 μ to 600 μ, in 2 a, 3 a, and 4 a at 100 μ to 400 μ. In the middle blocks 2 b, 3 b, and 4 b the immersion varies between 100 μ and 300 μ, and in 2 c, 3 c, and 4 c they are at the average at 100 μ to 200 μ, similar as in the previously named species.

From all said above it results that the diminuation of the depth of immersion of Herbst's corpuscles towards the base and the middle of the beak occurs as a rule in all species (with the exception of the wild duck).

3. *The horizontal distribution of Herbst's corpuscles.*

The maximal number of Herbst's corpuscles is found in *Anas platyrhyncha platyrhyncha domestica* L. in the anterior portion of the bill in block 1 a, the minimal number in 4 c. A comparison of the marginal blocks 1 a, 2 a, 3 a, and 4 a shows that the number of corpuscles constantly diminishes in the direction towards the base of the bill. The same is seen when comparing the blocks 2 b, 3 b, and 4 b, as well as 2 c, 3 c, and 4 c. Investigating the numerical variability of the occurrence of Herbst's corpuscles in the latero-median direction we see that their number diminishes very conspicuously towards the middle. It also is very remarkable that the number of corpuscles is diminished in 3 b, and on the contrary increases in 3 c. In the last strip, in 4 a, 4 b, and 4 c their number at first increases, and then, at the middle of the bill diminishes again. (See fig. 2.)

In *Anas platyrhyncha platyrhyncha* L. the maximal number of Herbst's corpuscles is found in block 2 a, their minimal number in 4 c. If we compare the number of corpuscles in 1 a, 2 a, 3 a, and 4 a, we see that it at first increases in 2 a in the direction towards the base of the bill, and then gradually decreases. An inspection of blocks 2 b, 3 b, and 4 b as well as 2 c, 3 c, and 4 c reveals that the number of corpuscles decreases in both cases towards the base of the bill. In latero-median direction the changes are alike

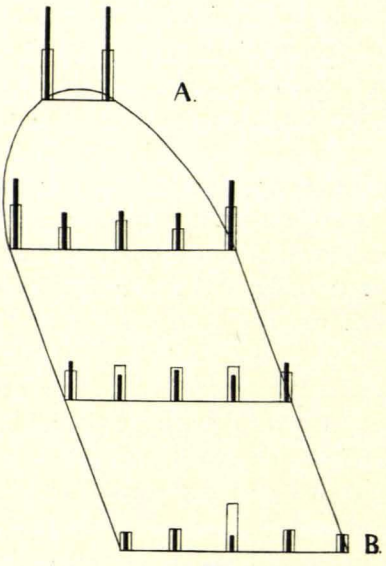

Fig. 2.

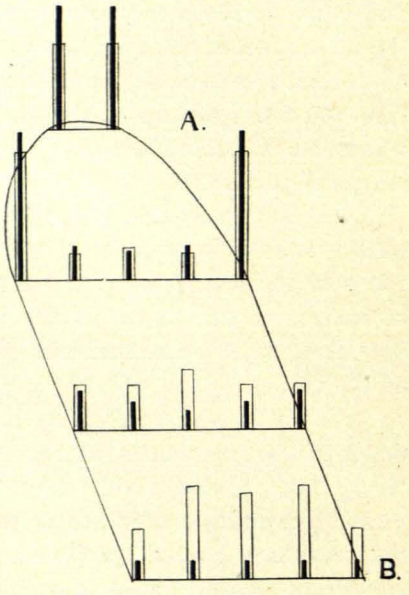

Fig. 3.

Fig. 2. *Anas platyrhyncha platyrhyncha domestica* L. Diagram of the topography of the corpuscles in the cere. *A* tip, *B* base of the bill. The horizontal lines, on which the rods are placed, show the directions of the sections through the bill (see text). The relative number of Herbst's corpuscles is marked by solid black rods, that of Grandry's by black framed rods. 1 mm of the diagram corresponds with the number of the corpuscles—8.
Fig. 3. *Anas platyrhyncha platyrhyncha* L. Lettering as on fig. 1.

in all portions of the bill: the number of Herbst's corpuscles decreases in all strips towards the middle of the beak. (See fig. 3.)

Anas crecca crecca L. The corpuscles attain their maximal number in block 1 a, their minimal in 4 a. From the comparison of their numbers in the blocks 1 a, 2 a, 3 a, and 4 a it clearly results that their number decidedly diminishes towards the base of the bill. The same can be seen in the blocks 2 b, 3 b, and 4 b, as well as 2 c, 3 c, and 4 c. In the latero-median direction of both median portions of the bill the number of Herbst's corpuscles diminishes towards the middle, in the proximal portion, however, it is somewhat increasing. (See fig. 4.)

Anas querquedula L. The maximal number of Herbst's corpuscles is found in block 1 a, the minimal in 4 a, their number diminishing gradually

towards the base of the bill. Comparing the blocks 2 b, 3 b, and 4 b we see that the number of corpuscles is increased in block 3 b, whereas it is equal in 4 b and 2 b. On the other hand their number is larger in the blocks 3 c and 4 c than in 2 c. In the latero-median direction the grouping of the corpuscles is the following. The number of corpuscles is smaller in block 2 b than in 2 a, in 2 c, however, it is somewhat larger than in 2 b. In the third

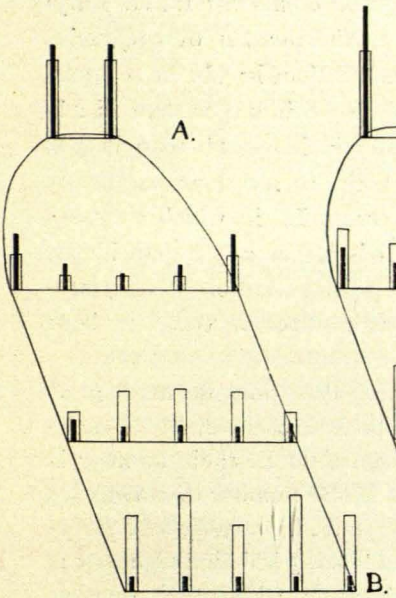

Fig. 4.

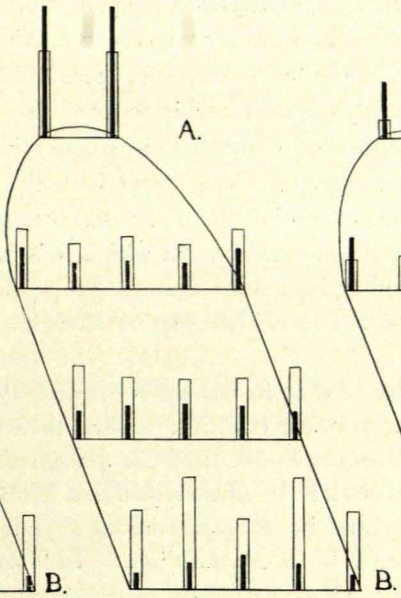

Fig. 5.

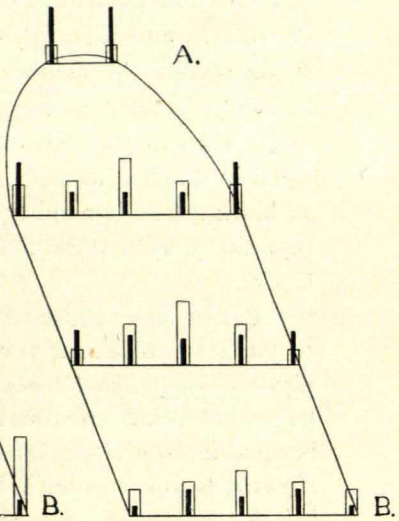

Fig. 6.

Fig. 4. *Anas crecca crecca* L. — Fig. 5. *Anas querquedula* L. — Fig. 6. *Nyroca fuligula* L. Lettering as on fig. 1.

portion of the bill, in block 3 a the corpuscles are scarcer than in 3 b and 3 c, where their number is practically equal. In the fourth portion their number increases gradually towards the middle of the bill. (See fig. 5.)

Nyroca fuligula L. The maximal number of Herbst's corpuscles is attained in block 1 a, their minimal number in 4 a. Comparing all marginal blocks with each other we see that the number of corpuscles diminishes gradually towards the base of the bill. On the other hand their number is larger in 3 b than in 2 b, in 4 b, however, it is almost equal to that in the latter. In the median row the number of corpuscles is larger than in 2 a, in 4 c, however, smaller than in 2 c. In the latero-median direction the grouping is the following. In the anterior (2) and the middle portion of the bill the number of corpuscles decreases towards the median plane of the bill. In the fourth portion their number is larger in the blocks 4 b and 4 c than in 4 a, at the same time it is smaller in 4 c than in 4 b. (See fig. 6.)

From a comparison of all species, resp. races, under investigation it results that the frequency of Herbst's corpuscles attains its maximal number in block 1 a. The only exception we see in *A. platyrhyncha platyrhyncha* L., in which species the maximal number is met with in 2 a. In the remaining species the number of corpuscles in block 2 a is smaller than in 1 a. In block 3 a their number is in all birds examined smaller than in 2 a, and again in 4 a smaller than in 3 a. In *A. platyrhyncha platyrhyncha domestica* L., *A. platyrhyncha platyrhyncha* L. and *A. crecca crecca* L. the number of corpuscles in the middle portion of the bill is larger in block 2 b than in 3 b. In *A. querquedula* L. and *Nyroca fuligula* L. their number in 3 b is larger than in 2 b. In all species the number of corpuscles is smaller in block 4 b than in 3 b, and only in *A. crecca crecca* L. it is equal in both. In 2 c their number is larger than in 3 c with exception of *A. crecca crecca* L., in which they are equal in number, and *A. querquedula,* in which it is larger in 3 c than in 2 c. In block 4 c their number is smaller than in 3 c, with exception of *A. platyrhyncha platyrhyncha* L., in which species their number is equal in both blocks.

It can be established that in the latero-median direction the number of corpuscles in block 2 a is larger than in 2 b in all birds examined. In *A. platyrhyncha platyrhyncha domestica* L. and *A. querquedula* L. their number is larger in block 2 c than in 2 b. In *Nyroca fuligula* L. the number of corpuscles is equal in both blocks, and in *A. crecca crecca* L. and *A. platyrhyncha platyrhyncha* L. it is smaller in block 2 c than in 2 b. In block 3 b their frequency is inferior to that in 3 a, with exception of *A. querquedula,* where their number in block 3 b is larger than in 3 a. In *A. crecca crecca* L. and *Nyroca fuligula* L. the number of Herbst's corpuscles in block 3 c is smaller than in 3 b, and in the remaining species it is larger in 3 c than in 3 b. In block 4 b their number is larger than in 4 a, with exception of *A. crecca crecca* L. In *A. platyrhyncha platyrhyncha domestica* L., *A. crecca crecca* L. and *Nyroca fuligula* L. their number in block 4 c is smaller than in 4 b. In *A. platyrhyncha platyrhyncha* L. their number is equal in the blocks 4 b and 4 c, and in *A. querquedula* L. it is smaller in block 4 b than in 4 c.

IV. TOPOGRAPHY OF GRANDRY'S CORPUSCLES.

1. *Number of Grandry's corpuscles.*

In *Anas platyrhyncha platyrhyncha domestica* L. the maximal number of Grandry's corpuscles is 36, or 54 %, the minimal number 14 (21 %), the mean number 24 (36 %). (See tab. 1.)

In *Anas platyrhyncha platyrhyncha* L. their maximal number is 92 (137 %), the minimal number 18 (27 %), and the mean number 47 (70 %). (See tab. 2.)

In *Anas crecca crecca* L. the maximal number of corpuscles is 70 (104 %), the minimal number 9 (13 %), the mean number 37 (55 %). (See tab. 3.)

In *Anas querquedula* L. their maximal number is 82 (121 %), the minimal number 32 (48 %), the mean number 50 (75 %). (See tab. 4.)

In *Nyroca fuligula* L. the number of Grandry's corpuscles is 45 (67 %), the minimal number 11 (16 %), the mean number 26 (39 %). (See tab. 5.)

The mean maximal number of Grandry's corpuscles on 1 qmm is 65 (97 %), the mean minimal number 17 (25 %), and the general mean number 37 (55 %) in all above named species of ducks.

2. *Distance of Grandry's corpuscles from the surface of the cere.*

The immersion of Grandry's corpuscles is fairly equal in the different portions of the cere.

Anas platyrhyncha platyrhyncha domestica L. The distance of Grandry's corpuscles from the surface of the cere varies in block 1 a within the limits of 100 μ and 300 μ. In all other blocks the immersion is somewhat less, between 100 μ and 200 μ. From this it can be seen that in the domestic duck the distance of the corpuscles from the surface of the cere is almost invariable in the whole bill.

Anas platyrhyncha platyrhyncha L. In the blocks 1 a and 2 a the corpuscles lye at a depth of 100 μ to 300 μ, in all others at 100 μ to 200 μ. We have here therefore the same distribution as in the domestic duck.

Anas crecca crecca L. The corpuscles are found in block 1 a at 100 μ to 300 μ, in all other blocks their immersion averages at 100 μ.

Anas querquedula L. In the blocks 1 a, 2 a, 3 a, and 4 a the corpuscles are at 100 μ to 200 μ, in the other blocks at about 100 μ.

Exactly the same distribution of the corpuscles is met with also in *Nyroca fuligula* L.

A comparison of all species investigated reveals that in all cases the mean distance of Grandry's corpuscles from the surface of the cere is at 100 μ to 200 μ. Only in the domestic and the wild duck (and less pronounced also in *Anas crecca crecca* L.) at the margin of the bill-tip there are found deeper lying corpuscles, the immersion of which, however, never exceeds 300 μ.

3. *The horizontal distribution of Grandry's corpuscles.*

Anas platyrhyncha platyrhyncha domestica L. The maximal number of Grandry's corpuscles is found in block 1 a, the minimal in 4 a. In the blocks

1 a, 2 a, 3 a, and 4 a the number of corpuscles decreases in the direction of the base of the bill, whereas it is much larger in 3 b than in 2 b and 4 b, being equal in these latter. In 2 c, 3 c, and 4 c the number of corpuscles increases gradually towards the base of the bill. In the latero-median direction the grouping is as follows. In the anterior portion of the bill the number of corpuscles increases in the succession 2 a, 2 c, 2 b, in the middle portion 3 b, 3 c, 3 a. In the hind portion I have found that their number increases towards the middle of the bill. (See fig. 2.)

Anas platyrhyncha platyrhyncha L. The maximal number of corpuscles is attained in block 2 a, the minimal in 2 b. Comparing the blocks 1 a, 2 a, 3 a, and 4 a, we see that their number is larger in 2 a than in 1 a, in 3 a smaller than in 2 a, in 4 a, however, it is larger than in 3 a. An investigation of the blocks 2 b, 3 b, and 4 b, and also 2 c, 3 c, and 4 c has shown that the number of corpuscles increases towards the base of the bill. In latero-median direction the following can be stated. The number of Grandry's corpuscles in block 2 b is strikingly smaller than in 2 a, in 2 c, on the contrary, somewhat larger than in 2 b. In the middle portion of the beak their number decidedly increases towards the middle of the bill. In the hindmost portion, lastly, their number is markedly larger in block 4 b than in 4 a, whereas in block 4 c it has hardly perceptidly diminished. (See fig. 3.)

Anas crecca crecca L. The maximal number of Grandry's corpuscles is found in block 4 b, the minimal in 2 c. The number of corpuscles in 2 a and 3 a is considerably smaller than in 1 a, whereas in 4 a it attains nearly the same level as in 1 a. If we compare the blocks 2 b, 3 b, and 4 b, as well as 2 c, 3 c, and 4 c, we see that the corpuscles increase considerably in number in the direction towards the base of the bill. In latero-median direction I have been able to establish the following grouping. In the row 2 a, 2 b, and 2 c the number of corpuscles decreases towards the middle of the beak, on the other hand increasing gradually latero-medially in the blocks 3 a, 3 b, and 3 c. The number of Grandry's corpuscles appears in block 4 b considerably larger than in 4 a, in 4 c, on the contrary, smaller than in 4 a and 4 b. (See fig. 4.)

Anas querquedula L. The maximal number of the corpuscles is located in block 4 b, the minimal in 2 b. In the blocks 2 a, 3 a, and 4 a it is smaller than in 1 a. In 2 a the number of corpuscles is smallest, and in 4 a larger than in 3 a. In the blocks 2 b, 3 b, and 4 b, as well as in 2 c, 3 c, and 4 c their number increases latero-medially decidedly in the direction of the base of the bill. In 2 b and 2 c they are less frequent than in 2 a, being more numerous in 2 c than in 2 b. In 3 a, 3 b, and 3 c the number of corpuscles decreases gradually towards the middle of the bill. In the hind portion their number is larger in block 4 b than in 4 a, in 4 c, however, smaller than in 4 a (See fig. 5.)

Nyroca fuligula L. The number of corpuscles attains its maximum in block 3 c, its minimum in 3 a, and is practically equal in 2 a and 4 a, being in these latter considerably larger than in 1 a, but in 3 a their number is smaller than in 1 a. The block 3 b contains more corpuscles than 2 b, whereas 4 b attains the same number as 2 b. Comparing the blocks 2 c, 3 c, and 4 c one sees that the number of corpuscles is larger in 3 c than in 2 c, but smaller in 4 c than in 2 c. In the latero-median direction the number of Grandry's corpuscles increases in the entire bill gradually towards the middle of the beak. (See fig. 6.)

From the comparison of all species of ducks investigated there results that the points, where the maximal and minimal numbers of Grandry's corpuscles are situated, are much subject to change. In *A. platyrhyncha platyrhyncha domestica* L. the maximal number of Grandry's corpuscles is found in block 1 a, in *A. platyrhyncha platyrhyncha* L. in 2 a, in *A. crecca crecca* L. and *A. querquedula* L. in 4 b, and in *Nyroca fuligula* L. in 3 c. The minimal number of these corpuscles is found in *A. platyrhyncha platyrhyncha domestica* L. in block 4 a, in *A. platyrhyncha platyrhyncha* L. and *A. querquedula* L. in 2 b, in *A. crecca crecca* L. in 2 c, and in *Nyroca fuligula* L. in 3 a. Comparing the number of Grandry's corpuscles in the blocks 1 a, 2 a, 3 a, and 4 a one sees that it diminishes in *A. platyrhyncha platyrhyncha domestica* L. towards the base of the bill. It is remarkable that in *A. platyrhyncha platyrhyncha* L. the number of corpuscles attains its maximum in 2 a, at the tip of the bill, however, it is smaller. In block 3 a their number is considerably reduced, in 4 a, on the contrary, increased. A similar arrangement is met with in *Nyroca fuligula* L. The number of corpuscles first increases (in 2 a), then diminishes and increases again at the base of the bill. In *A. crecca crecca* L. the number of corpuscles diminishes gradually, only in 4 a it is considerably increased and almost attains the number in block 1 a. In *A. querquedula* L. the number of corpuscles first diminishes in the antereo-posterior direction, and then increases considerably.

As to the variability of the number of corpuscles in the middle portion of the bill it is manifest that in block 2 b they are always scarcer than in 3 b. In *A. platyrhyncha platyrhyncha domestica* L. and *Nyroca fuligula* L. their frequency is equal in 2 b and 4 b. In *A. platyrhyncha platyrhyncha domestica* L. and *Nyroca fuligula* L. block 3 b excels in this over 4 b, in the remaining species, however, the proportions are reverse. In 2 c the corpuscles occur always rarer than in 4 c, and only in *Nyroca fuligula* L. their number is smaller in 4 c than in 2 c. In block 3 c the corpuscles appear in smaller numbers than in 4 c, with exception of *Nyroca fuligula* L., where their number is larger in 3 c than in 4 c.

From the comparison in the latero-median direction it results that in the second strip the number of corpuscles is smaller in 2 b than in 2 a, only in

Nyroca fuligula L. it is larger. The number of corpuscles in block 2 c exceeds that in 2 b, with exception of *A. crecca crecca* L., in which the proportions are the reverse. In the third strip I have found a greater frequency in 3 b than in 3 a, excepted *A. querquedula,* in which it is smaller. In *A. platyrhyncha platyrhyncha domestica* L. and *A. querquedula* L. the number is somewhat smaller in 3 c than in 3 b, being, however, larger in other species. In the fourth strip the number of Grandry's corpuscles is larger in block 4 b than in 4 a; in block 4 c in *A. platyrhyncha platyrhyncha domestica* L. and *Nyroca fuligula* L. it is larger than in 4 b, being smaller in the other species.

V. COMPARISON OF THE TOPOGRAPHY OF HERBST'S AND GRANDRY'S CORPUSCLES.

In *A. platyrhyncha platyrhyncha domestica* L. the number of Herbst's corpuscles exceeds in block 1 a of the anterior portion of the bill the number of Grandry's corpuscles, and the same might be said of blocks 2 a and 3 a; in 4 a, however, both kinds of corpuscles occur in equal numbers. In the direction from the tip of the bill towards the base the number of both diminishes in the marginal blocks. In block 2 b also the number of Grandry's corpuscles is smaller than that of Herbst's, in block 3 b, however, Grandry's corpuscles are predominant, and in block 4 b both are equal in number. The number of Grandry's corpuscles first increases in block 3 b, and diminishes in 4 b. In block 2 c Herbst's corpuscles are more frequent than Grandry's, on the other hand the latter are predominant in 3 c and 4 c. The number of Herbst's corpuscles diminishes gradually towards the base of the bill, that of Grandry's, on the contrary, increases. In the latero-median direction the number of Herbst's corpuscles first, in the second strip and block 2 b, diminishes, and increases again in block 2 c. Similar also is the distribution of Grandry's corpuscles. As to the third strip it can be observed that the distribution is much alike to that just described, only that the variations of the number of Grandry's corpuscles are very insignificant. In the fourth strip the number of Herbst's corpuscles first increases towards the middle, diminishing further on; the number of Grandry's corpuscles is much increasing, and in block 4 c exceeds that of Herbst's corpuscles by several times. (See fig. 2.)

In *A. platyrhyncha platyrhyncha* L. the number of Herbst's corpuscles exceeds that of Grandry's in block 1 a. In block 2 a the number of both increases, the number of Herbst's corpuscles predominating, similar as in 1 a. In block 3 a the number of both types diminishes, Grandry's corpuscles having the prevalence. In block 4 a the number of Herbst's corpuscles diminishes still more, whereas that of Grandry's considerably increases. In

block 2 b the number of Herbst's corpuscles is somewhat larger than that of Grandry's, but in 3 b and 4 b Grandry's are found in greater numbers. In general the number of Herbst's corpuscles diminishes gradually towards the base of the bill, that of Grandry's, on the contrary, increasing. In the blocks 2 c, 3 c and 4 c Grandry's corpuscles are throughout predominant. In analogy with the preceding case the number of Herbst's corpuscles diminishes towards the base of the bill, Grandry's, on the contrary, are here more abundant. In the latero-median direction the numerical proportions of both types of corpuscles are very variable. In the blocks 2 a and 2 b Herbst's corpuscles are more numerous, in block 2 c, however, Grandry's prevail. Herbst's corpuscles become considerably scarcer towards the middle, which is true also for Grandry's, only in block 2 c the latter increase again in number. In the blocks 3 a, 3 b, and 3 c Grandry's corpuscles are everywhere prevalent. The number of Herbst's corpuscles diminishes gradually towards the middle, that of Grandry's, on the contrary, increasing. In the blocks 4 a, 4 b, and 4 c the number of Herbst's corpuscles diminishes somewhat towards the middle of the beak. The maximum of Grandry's corpuscles is attained in block 4 b, but in 4 c already it diminishes again. Comparingly with Herbst's corpuscles Grandry's have a decided numerical preponderance in all blocks of the fourth strip. (See fig. 3.)

In *A. crecca crecca* L. in block 1 a the number of Herbst's corpuscles is larger than that of Grandry's. In block 2 a both diminish in number, but here also Herbst's are in numerical superiority. In block 3 a both types of corpuscles are still scarcer with a predominance in favour of Grandry's. In block 4 a the number of Herbst's corpuscles diminishes still more, whereas that of Grandry's strongly increases, surpassing that of Herbst's sevenfold. If we compare the blocks 2 b, 3 b, and 4 b, we see, that in block 2 b Herbst's corpuscles are predominant, in 3 b and 4 b, however, Grandry's. Towards the base of the bill Herbst's corpuscles become more rare, Grandry's, on the contrary, more frequent. A comparison of the blocks 2 c, 3 c, and 4 c shows that in 2 c Herbst's corpuscles are more numerous, but in 3 c and 4 c Grandry's. The number of Herbst's corpuscles is the same in all blocks mentioned, whereas that of Grandry's decidedly increases towards the base of the bill. Investigating the arrangement of the corpuscles in latero-median direction, one sees that in the second strip, in the blocks 2 a, 2 b, and 2 c, Herbst's corpuscles are more numerous, the number of both types diminishing gradually towards the middle. In the third strip, in the blocks 3 a, 3 b, and 3 c, excel Grandry's corpuscles. The number of Herbst's somewhat diminishes towards the middle, that of Grandry's, on the contrary, increasing. In the blocks 4 a, 4 b, and 4 c Herbst's corpuscles outweigh. The number of Herbst's corpuscles increases hardly perceptibly towards the middle. The

number of Grandry's corpuscles is largest in block 4 b, diminishes somewhat in 4 a and becomes still smaller in 4 c. (See fig. 4.)

In *A. querquedula* L. in block 1 a Herbst's corpuscles prevail; in block 2 a the number of both kinds diminishes, Grandry's gaining the advantage. In block 3 a the number of Herbst's corpuscles is still more reduced, that of Grandry's increasing in return. The same we see also in block 4 a, where the number of Grandry's corpuscles excels by several times that of Herbst's. In the blocks 2 b, 3 b, and 4 b Grandry's corpuscles are dominating. The number of Herbst's corpuscles first (in block 3 b) increases somewhat towards the base of the bill, but diminishes later (in block 4 b), whereas that of Grandry's gradually increases in this direction. In the blocks 2 c, 3 c, and 4 c it is also that Grandry's corpuscles prevail; the number of Herbst's first increases somewhat towards the base of the bill, in order to diminish afterwards. As to the distribution of the corpuscles in latero-median direction, Grandry's prevail in the blocks 2 a, 2 b, and 2 c. In block 2 b the number of both types of corpuscles diminishes somewhat in comparison with that in 2 a, but increases again in 2 c. In the third strip, in the blocks 3a, 3b, and 3c, Grandry's corpuscles are prevailing, the number of Herbst's increasing hardly perceptibly and gradually towards the middle. In the blocks 3 b and 3 c Grandry's corpuscles are equally frequent, without, however, attaining their number in block 3 a. In the fourth strip the number of Grandry's corpuscles considerably exceeds that of Herbst's; the number of the latter increases towards the middle; that of Grandry's is largest in block 4 b, whereas it is perceptibly smaller in 4 a and 4 c, both blocks showing the same density of corpuscles. (See fig. 5.)

In *Nyroca fuligula* L. the number of Herbst's corpuscles exceeds in block 1 a Grandry's by several times. In block 2 a the number of Herbst's corpuscles diminishes, that of Grandry's increasing, but nevertheless the former prevail. In block 3 a the number of both is smaller than in block 2 a, but here also Herbst's corpuscles are still prevailing. In block 4 a their number diminishes still more and Grandry's increase in number and obtain the prevalence. In the blocks 2 b, 3 b, and 4 b Grandry's corpuscles prevail throughout. In the blocks 2 b and 4 b Herbst's corpuscles occur as frequently and still more so in block 3 b. The number of Grandry's corpuscles is likewise the same in the blocks 2 b and 4 b, being somewhat larger in 3 b. In the blocks 2 c, 3 c, and 4 c Grandry's corpuscles prevail; both kinds attain their maximal frequency in 3 a, and are less numerous in 2 c and 4 c. The distribution in the latero-median direction is the following. In the second (2 a, 2 b, and 2 c) and the third (3 a, 3 b, and 3 c) strip the number of Herbst's corpuscles diminishes towards the middle, whereas that of Grandry's gradually increases. In the third strip Grandry's corpuscles attain their maximal number in block 3 c. In the fourth strip the number of Herbst's corpuscles

is smallest in block 4 a, largest in block 4 b, and diminishes again in block 4 c. The number of Grandry's corpuscles increases gradually towards the middle of the beak but does not attain the number in block 3 c. (See fig. 6.)

VI. TOPOGRAPHY OF HERBST'S AND GRANDRY'S CORPUSCLES IN THE EMBRYONIC BILL.

A brief description of the embryonic development of Herbst's and Grandry's corpuscles is found in FR. HESSE's paper "Über die Tastkugeln des Entenschnabels" (1878). After this author the development of both kinds of corpuscles takes place within a few days just preceding the eclosion of the duckling. The corpuscles begin to develop in numbers exceeding those of the corpuscles found in the adult state, but only those of them grow to be fully differenciated that find a contact with nervous fibres, all others getting reduced. Such corpuscles being in a state of reduction can be observed also in adult birds, but they must be strictly distinguished from small corpuscles that are capable of development.

A more detailed description of the development of the sensory corpuscles gives L. SZYMONOWICZ in his paper "Über den Bau und die Entwicklung der Nervenendigungen im Entenschnabel" (1897). His results are corroborated also by my investigations on this question.

The time of appearance of the first primordia of the corpuscles is depending on the height of the hatching temperature (and other external factors during the period of incubation) and becomes visible in 18 to 20 days old embryos. (See plate fig. 1, 2.) The corpuscles attain their full differenciation shortly before the hatching of the duckling, about the 26th day. Herbst's as well as Grandry's embryonic corpuscles differ from those in adult birds only by their smaller size. In certain opposition to HESSE, SZYMONOWICZ says the following: "The differenciation of the connective tissue to tactile cells of Grandry's and Herbst's corpuscles takes place under the influence of the nervous fibres." Thus, after SZYMONOWICZ, such corpuscles as are destined to reduction on account of lacking a contact with nervous fibres do not endure, because the differentiation of the cells of the connective tissue into primordia of tactile corpuscles is called forth by the approaching of fibre ends of tactile nerves. As to the number of tactile corpuscles, SZYMONOWICZ says: "It is probable that the number of nervous corpuscles in the duck-bill is towards the end of the embryonic period of life not smaller than in the adult bird." "It does not seem to me likely that nervous corpuscles originate also in the postembryonal life, and I must strictly emphasize that I have found them all in the embryonic life in the same state of develop-

ment. It must therefore be presumed that the primordia of all corpuscles originate at the same time."

In support of this presumption of SZYMONOWICZ's I am reproducing here the numerical tables of my countings of the tactile corpuscles in the cere. An exact counting can be effectuated only in older embryos, from 26 to 27 days old, because only by this time the primordia of the different corpuscles have separated. (See plate fig. 3, 4.) Comparing the numbers found in the embryos of the domestic duck with those in an adult bird, one sees that they are largely coincident. The distribution of both kinds of corpuscles in the cere is also the same in the embryo and the adult. (See tab. 6 and 7.)

Table 6. *Anas platyrhyncha platyrhyncha domestica* L., 26 days old embryo.

Antereo-posterior No.	Latero-median sign	Herbst's corpuscles	%	Grandry's corpuscles	%
	a	49	73	23	34
1	b	33	49	19	28
	c	31	46	15	22
	a	52	78	22	33
2	b	39	58	16	24
	c	26	38	15	22
	a	35	52	17	25
3	b	27	40	25	37
	c	18	27	27	40
	a	15	22	17	25
4	b	9	13	20	30
	c	7	10	18	27

Table 7. *Anas platyrhyncha platyrhyncha domestica* L., 27 days old embryo.

Antereo-posterior No.	Latero-median sign	Herbst's corpuscles	%	Grandry's corpuscles	%
	a	53	79	32	48
1	b	39	58	21	31
	c	28	42	18	27
	a	49	73	26	38
2	b	37	55	16	24
	c	24	36	14	21
	a	21	31	13	19
3	b	17	25	20	30
	c	18	27	23	34
	a	15	22	12	18
4	b	11	16	16	24
	c	9	13	26	38

1. *The density of the horizontal distribution of Herbst's corpuscles in the cere of a 26 days old embryo of the domestic duck.*

The number of Herbst's corpuscles attains its maximum in block 2 a, its minimum in block 4 c. Their number is larger in block 2 a than in block 1 a, but diminishes perceptibly towards the base of the bill. A similar distribution is found in the blocks 1 b, 2 b, 3 b, and 4 b. In the blocks 1 c, 2 c, 3 c, and 4 c Herbst's corpuscles diminish gradually in number towards the base of the bill. In the latero-median direction, i.e. towards the middle of the bill, there takes place a reducement in number of Herbst's corpuscles.

2. *The density of the horizontal distribution of Grandry's corpuscles in the cere of a 26 days old embryo of the domestic duck.*

The maximal number of corpuscles is attained in block 3 c, the minimal in block 1 c. In the blocks 1 a, 2 a, 3 a, and 4 a their number diminishes somewhat towards the base of the bill. In the b-series the relations are not quite the same. In block 2 b the number of corpuscles is smaller than in block 1 b, in the blocks 3 b and 4 b it is larger than in the former. In the blocks 1 c, 2 c, 3 c, and 4 c the number of corpuscles increases considerably up to the third strip, and diminishes again in block 4 c. In the latero-median direction a decrease of the corpuscles takes place in the two first strips towards the middle. In the third strip, however, their number increases towards the middle of the beak. In the fourth strip it first increases (in block 4 b), and then diminishes again in block 4 c.

3. *Comparison of the topography of Herbst's and Grandry's corpuscles in a 26 days old embryo of the domestic duck.*

In the 26 days old embryo of the domestic duck the number of Herbst's corpuscles in block 1 a is larger than that of Grandry's; the same we see also in the blocks 2 a and 3 a, and only in block 4 a Grandry's corpuscles are more numerous than the former. Similarly in the blocks 1 b, 2 b, and 3 b Herbst's corpuscles prevail and only in block 4 b the number of Grandry's surpasses considerably that of the former. In the blocks 1 c and 2 c Herbst's corpuscles prevail, in the blocks 3 c and 4 c Grandry's. In general it may be said that Herbst's corpuscles prevail at the tip and Grandry's at the base of the bill. (See fig. 7.)

4. *The denseness of the horizontal distribution of Herbst's corpuscles in the cere of the 27 days old embryo of the domestic duck.*

The maximal number of Herbst's corpuscles is attained in block 1 a, the minimal in block 4 c. In all rows of blocks their number decreases decidedly towards the base of the bill. In the latero-median direction the number of

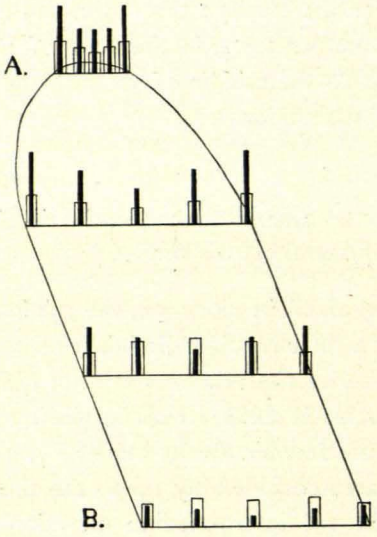

Fig. 7.

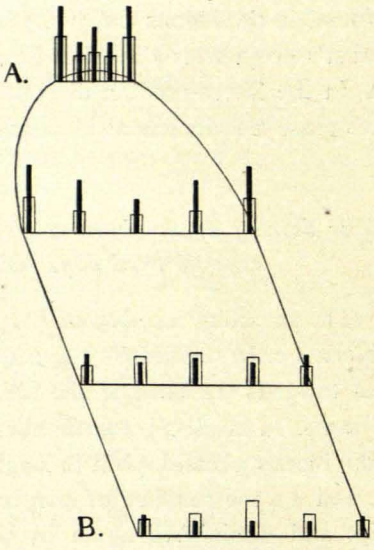

Fig. 8.

Fig. 7. *Anas platyrhyncha platyrhyncha domestica* L. 26 days old embryo. Lettering as on fig. 1.

Fig. 8. *Anas platyrhyncha platyrhyncha domestica* L. 27 days old embryo. Lettering as on fig. 1.

corpuscles diminishes in all strips towards the median sagittal plane, and the sole exception is found in the third strip, in which the number of Herbst's corpuscles is somewhat larger in block 3 c than in block 3 b.

5. *The denseness of the horizontal distribution of Grandry's corpuscles in the 27 days old embryo of the domestic duck.*

The number of corpuscles reaches its maximum in block 1 a, its minimum in block 4 a. In the blocks 1 a, 2 a, 3 a, and 4 a it diminishes towards the base of the bill. Within the b-group the number of corpuscles is smaller in block 2 b than in 1 b, in 3 b larger than in 2 b, in 4 b, on the contrary, it is smaller than in 3 b. In the c-group block 2 c contains less corpuscles than 1 c, whereas in the blocks 3 c and 4 c they are much more numerous than in 1 c. In the latero-median direction their distribution is the following:

in the two first strips the number of Grandry's corpuscles diminishes gradually towards the middle of the bill; in the fourth and third, however, it increases gradually in the same direction.

6. *Comparison of the topography of Herbst's and Grandry's corpuscles in the 27 days old embryo of the domestic duck.*

In the 27 days old embryo of the domestic duck Herbst's corpuscles are, as compared with Grandry's, prevalent in all blocks (1 a, 2 a, 3 a, and 4 a). A similar arrangement we see also in the blocks 1 b and 2 b, in the blocks 3 b and 4 b, however, the contrary is the case. Also in the blocks 1 c and 2 c Herbst's corpuscles prevail, in the blocks 3 c and 4 c, however, Grandry's. The distribution of both kinds of corpuscles corresponds with that already described in the adult bird. (See fig. 8.)

The results of my studies on embryonic material being incomplete, I do not venture at the present time to make any deductions from the data obtained.

VII. SUMMARY RELATING TO ADULT BIRDS.

1. The number of Herbst's and Grandry's corpuscles on 1 qmm is unequal in the same species of duck and, contrarily to HESSE's statements (1878), exceeds at the tip of the bill the number of 10 several times.

2. The immersion of Herbst's corpuscles in the cere varies much more considerably than that of Grandry's. When present in larger numbers Herbst's corpuscles are usually arranged in several layers one on top of the other. Grandry's corpuscles are mainly situated between Herbst's in the upper layer, their variation as to depth of immersion not being very great.

3. In all species of ducks studied the number of Herbst's corpuscles, not to speak of some exceptions, diminishes in the direction from the tip of the bill towards its base, and also in the latero-median direction with much proportionality.

4. At the margin of the cere the number of Grandry's corpuscles alters in the direction from tip to base differently in the several species of ducks. In most it first diminishes, and then increases considerably towards the base of the bill. At the anterior end their number diminishes in the latero-median direction, and increases again at the base of the bill.

5. At the tip of the bill prevail therefore Herbst's, at the base Grandry's corpuscles. Such topographic independance indicates that the physiological function of both kinds of corpuscles is evidently a different one.

The data obtained do not permit of deducting any laws as to the details in the topography of Herbst's and Grandry's corpuscles, and it remains un-

certain whether the variations described above are of specific value, or whether it is rather an individual character that must be attributed to them. It would therefore also be premature to form an opinion in how far these topographic types are correlated with the biology peculiar to each species and particularly with its feeding habits.

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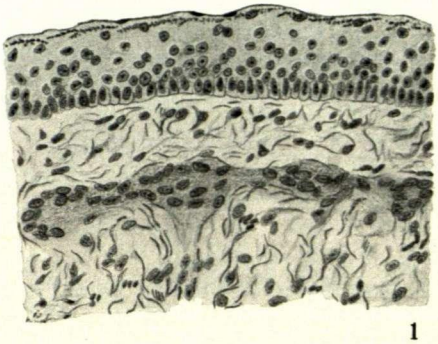

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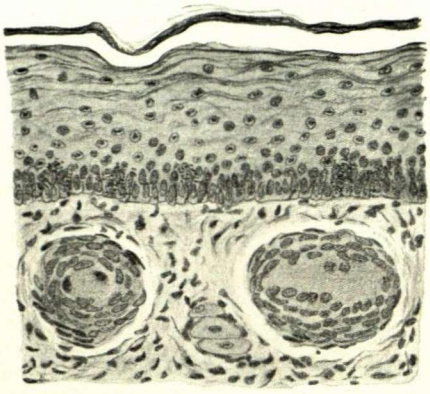

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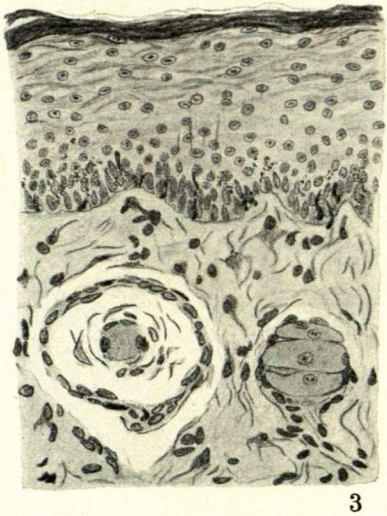

3

4

Fig. 1. *Anas platyrhyncha platyrhyncha domestica* L. Cross-section through the cere of a 21 days old embryo at the level of the middle of the bill. Thickness of section 10 μ, magnification 400 $\times$. Staining: iron hæmatoxylin + eosin. Rod-like primordium of sense corpuscles.

Fig. 2. *A. platyrhyncha plat. dom.* L. 24 days old embryo. Cross-section similar as on fig. 1, showing the separate sense corpuscles; the larger are Herbst's, the smaller Grandry's.

Fig. 3. *A. platyrhyncha plat. dom.* L. 26 days old embryo. Cross-section similar as on fig. 1.

Fig. 4. *A. platyrhyncha plat. dom.* L. 35 days old duck. Cross-section similar as on fig. 1.

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