A MORPHOLOGICAL STUDY OF AN EYE ANOMALY IN THE ALBINO RAT

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Prentice Alvin Caraway

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THESIS

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A MORPHOLOGICAL STUDY OF AN EYE ANOMALY IN THE ALBINO RAT

By

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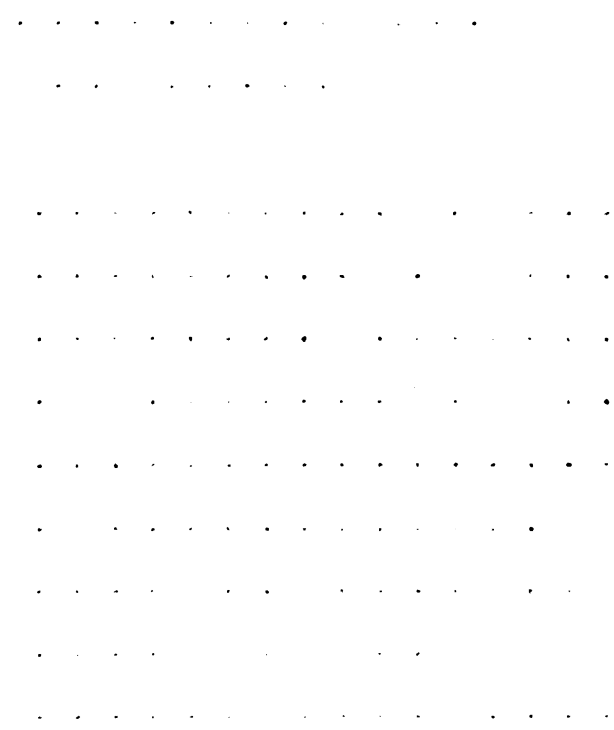

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A MORPHOLOGICAL STUDY OF AN EYE ANOMALY IN THE ALBINO RAT

INTRODUCTION

Two eye anomalies, anophthalmus and microphthalmus, in the albino rat were reported by King ('31). Opportunity, however, was not presented to continue the study embryologically due to the death of the stock. Quisenberry and Brown ('42) report a similar anomaly and from this strain individuals were selected for this study. Objectives were as follows: (1) to determine the morphological nature of the anomaly during stages of fetal growth; (2) to determine the fetal age of its occurrence and (3) to learn something of the nature of the factors causing the trait.

MATERIAL AND METHODS

A total of nineteen embryos from five pregnant rats were sectioned. The animals used were stock individuals from the colony of the Texas Agricultural Experiment Station and the personal stock of Dr. J. H. Quisenberry. The male was left with the female from 6:00 P.M. until 8:00 A.M. and matings were timed by the vaginal smear method. Long and Evans ('22) state that mating takes place in the early hours of stage two (oestrum). The timing of the embryos in these cases was accurate only to about twelve hours. Sizes of embryos were recorded from crown-rump (C/R) measurements in millimeters.

Embryos were collected by anaesthetizing the pregnant female and removing the complete uterus and fetuses. Following removal of the embryos they were fixed in Bouin's fluid and embedded in paraffin by use of the dioxan technique as reviewed by Mossman ('37). Serial sections were cut at 10 microns, stained in Delafield's hematoxylin, and counterstained in eosin.

Normal control animals were taken from a highly inbred strain that exhibited no similar eye defect. Embryos were prepared for examination by identical methods as those used in preparation of anomalous individuals.

DESCRIPTION OF DEVELOPMENTAL STAGES

Seven Millimeter Stage. Three anomalous embryos were obtained by mating a male (right eye anophthalmic, left eye normal) with a female (anophthalmic in both eyes).

The maximum diameters exhibited by the optic cup and lens in the control were 420u* and 150u respectively. A comparison of the data presented in Table 1 shows that the diameter of the optic cup and lens vesicle in the anomalous embryos varied from a minimum of 156u and 95u to a maximum of 370u and 180u respectively. It is also evident that there is significant difference between diameters of the optic vesicles and lens in right and left eyes of anomalous embryos.

The left eye of E0701 was in the lens vesicle stage; the diameter of the optic cup and lens were 156u and 95u respectively. The optic cup consisted of two undifferentiated layers which were separated by a well defined optic ventricle (fig. 2). It was also evident that the lens vesicle consisted of a single layer of columnar epithelial cells and that the lumen was circular.

The right eyes of E0701 and E0702 and the left eye of E0703 were approximately equal in size and exhibited striking similarities in degree of development. In all cases the lens structure was in the vesicle stage and closely resembled that of the control (fig. 1).

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* u = micron

Further, the distal portion of the optic vesicle had invaginated to reduce the cavity of the optic ventricle to a minimum. This inner layer displayed typical characteristics of the sensory layer similar to that in the control (fig. 1). The outer pigmented layer of the optic cup was very thin and in close proximity to the sensory layer.

The left eye of E0702 (fig. 3) and the right eye of E0703 (fig. 4) showed a degree of development very similar to that of the control. Both eyes exhibited a well differentiated sensory layer, pigmented layer, and lens vesicle. However, the lens vesicle of E0703 appeared to be further advanced due to the fact that the cells of the inner (proximal) wall had increased in height to produce a "crescent" shaped lumen (L, fig. 4).

Nine Millimeter Stage. Four anomalous embryos were obtained by mating a male (right eye anophthalmic, left eye normal) with a female (microphthalmic in both eyes).

In the control the maximum size of the optic cup and lens were 650u and 400u respectively. The invaginated portion of the optic stalk was in contact with the pigment layer of the retina and the two layers of the cup were well differentiated into an inner nervous layer and a thin pigmented outer layer (fig. 5). The data in Table[1] show that in the left eye of anomalous embryo E0901 the optic cup and lens vesicle exhibited

a maximum diameter of 280u and 170u respectively. The optic cup consisted of two very thin layers essentially the same in thickness. The lens vesicle consisted of a single layer of columnar epithelial cells arranged to form a circular lumen (fig. 6) while the epithelium in the proximal wall of the lens in the control (E0906) had elongated to such an extent as to almost obliterate the cavity of the original vesicle (fig. 5). In the control mesenchyme cells were present between the distal wall of the lens and superficial ectoderm, but in the anomalous embryo mesenchyme was absent and the two layers were in close contact (M, fig. 6). In general, the degree of development of the left eye of E0901 approximated that of five millimeter control series.

The left eye of E0902, the right and left eyes of E0903, and the left eye of E0904 (fig. 9) were very similar in structural development and size to the above described left eye of E0901 (fig. 6). However, in the left eye of E0903 the distal wall of the optic vesicle had invaginated only to a slight degree (fig. 8). This condition exhibited an optic vesicle cavity which resembled those of a very early control series (3 mm.). Another interesting feature was exhibited in the left eye of E0904. The layers of the optic cup were of equal thickness but were lying in close proximity, in contrast to E0903 above. In addition, the optic cup was folded or "crumpled" into a very irregular shape as shown in Fig. 9.

The right eye of E0904 (fig. 10) and E0902 very closely approximated that of the control in structural development. However, the right eye of E0904 displayed a slightly larger gross size.

Twelve Millimeter Stage. Four anomalous embryos were obtained by mating a male (right eye anophthalmic, left eye normal) with a female (anophthalmic in both eyes).

Anomalous structures of the right and left eye of E1201 (fig. 11) were essentially the same as those present in both eyes of E1204, the right eye of E1202, and the left eye of E1203. It is evident from Fig. 11 that in E1201 the optic cup and lens vesicle were entirely absent. However, a small optic nerve extended from the brain to the eye region where it terminated abruptly in a dense bundle of mesenchyme tissue (ON, fig. 11). Further study of anophthalmic embryos in this series revealed that the degree of development of the eyelid primordia was greater than it was in normal eyes. The eyelids of normal embryos were not fused but in anophthalmic embryos fusion of the eyelids was complete.

A study of the left eye of E1202 revealed a small lens vesicle and optic cup (fig. 12). The lens was in the early vesicle stage since the anterior and posterior walls were made up of a single layer of columnar cells. However, in control embryos of this age series cells of the inner wall of the lens vesicle had elongated to

obliterate the cavity of the lens vesicle (fig. 14). The walls of the optic cup in anomalous embryo E1202 consisted of a single layer of thin columnar cells and there was no indication of differentiation into a nervous layer or pigmented region (fig. 12). Mesenchymal cells had completely invested the space between the lens vesicle and the optic cup.

The right eye of E1203 exhibited several differences from those previously described. The size of the optic cup and lens approximated the normal eye in that the cavity of the lens vesicle was obliterated by the lengthening of the cells of the posterior wall. However, marked differances occurred in the arrangement of the lens fibers. This was especially evident in that the central lens fibers near the anterior epithelial layer were separated by large vacuoles (fig. 13). Lens fibers in the posterior (proximal) region of the lens were normally arranged. The optic stalk reached a maximum diameter of 30u in the optic foramen while the diameter of the optic stalk of the control at that point was 90u.

In the normal eye a well defined nerve fiber layer covered the inner surface of the cup. These fibers converged and passed inward through the optic stalk. However, in the anomalous eye (E1203) a well defined nerve fiber layer existed but the convergence of fibers took place in the ventral region of the cup (fig. 13) instead of in that region immediately adjacent to the optic stalk.

Eighteen Millimeter Stage. Five anomalous embryos were obtained by mating a male (both eyes anophthalmic) with a female (left eye anophthalmic, right eye microphthalmic).

Two embryos (E1802, E1805) displayed anophthalmia in both eyes. A comparison of the optic cup regions of these two embryos with that of an earlier embryo exhibiting anophthalmia in both eyes (E1201) showed that the two age groups differed in several respects. In E1201 the optic cup region of both eyes exhibited a small optic nerve (fig. 11) invested by a relatively heavy layer of mesoderm but in E1802 and E1805 both of these structures were absent. The latter embryos displayed another interesting feature. A crescent shaped mass of cells, essentially the same cytologically as those at the junction of the eyelids, was found in contact with the inner surface of the lids. The writer is led to believe that this crescent shaped mass of cells developed from an inpocketing of marginal epithelium found at the point of contact between the upper and lower lids.

A review of the data given in Table 1 shows that the degree of development in the right and left eyes of E1801 and the left eye of E1803 (fig. 18), 18 mm. embryos, and the left eye of E1202, 12 mm. embryo, is essentially the same since the diameters of both lens and optic cup in the 18 mm. embryos approximates that found in the left eye of the 12 mm. embryo. It was brought out in the preceding pages that in E1202 (fig. 12) the lens was in the vesicle stage and that the optic cup was made up of two undifferentiated layers. The chief difference between

the lens vesicle of the left eye of E1202 (fig. 12) and E1801 was that the epithelium of the former consisted of a single layer of short columnar cells while in the latter the epithelium had obliterated the lumen of the vesicle.

The left eye of E1804 (fig. 16) exhibited very similar conditions to those described above except for lens structure. An epithelial layer of loosely arranged columnar cells made up the wall of the spherical lens. The lumen of the lens vesicle was filled with poorly developed or degenerated lens fibers sharply separated from the epithelial layer. Several vacuoles were present between these fiber-like structures and the columnar cells.

The right eyes of E1803 (fig. 17) and E1804 showed striking similarities in structural development. However, the gross size of E1804 approximated that of the control in contrast to E1803 which was approximately one-half that of the control. Indication of cornea formation (fig. 17) was shown in both eyes by invasion of mesoderm cells between the epithelial layer of the lens and the superficial ectoderm covering the eye. The lens displayed considerable deviation from those of the control. The lens fibers in the proliferative zones appeared normally arranged and growth of the lens fibers from the posterior wall gave the appearance of a normally developed half of the lens. The anterior (distal) half of the lens was filled with very large vacuoles (fig. 17).

Twenty-one Millimeter Stage. Three anomalous embryos were obtained by mating a male (both eyes anophthalmic) with a female (both eyes anophthalmic).

The data given in Table 1 show that one embryo (E2102) was anophthalmic in the left eye and microphthalmic in the right eye. All others were microphthalmic in both eyes. Optic cup and lens structures were entirely absent in the left eye of E2102 (fig. 20). A very similar condition was noted in the left eye of E1201 in the twelve millimeter series (fig. 11). The size of the lens and optic cup in the remaining embryos varied from 290u to 180u and from 400u to 200u respectively. Very similar conditions have been described for E1801 and E1803 (fig. 18) in the eighteen millimeter series and E1202 (fig. 12) in the twelve millimeter series. However, the lens of E2102 and E2103 exhibited a more advanced stage of epithelial proliferation and as a consequence the lumen was almost obliterated. In addition, these elongated lens fibers were irregularily arranged within the lumen and were separated by numerous large vacuoles (fig. 19).

Table 1

Microphthalmia and Anophthalmia in Albino Rats

Description of Embryos			Control		Anomalous			
					left eye		right eye	
Number	Age, days*	C/R	optic cup diameter	lens diameter	optic cup diameter	lens diameter	optic cup diameter	lens diameter
E0706	12	7 mm.	420u (1)	150u				
E0701	12	7 mm.			156u	95u	240u	105u
E0702	12	7 mm.			370u	160u	300u	150u
E0703	12	7 mm.			240u	145u	350u	180u
E0906	13	9 mm.	650u	400u				
E0901	13	9 mm.			280u	170u	450u	250u
E0902	13	9 mm.			250u	155u	500u	270u
E0903	13	9 mm.			220u	110u	250u	110u
E0904	13	9 mm.			295u	170u	580u	340u
E1206	14	12 mm.	900u	500u				
E1201	14	12 mm.			absent	absent	absent	absent
E1202	14	12 mm.			250u	180u	absent	absent
E1203	14	12 mm.			absent	absent	800u	500u
E1204	14	12 mm.			absent	absent	absent	absent
E1806	16	18 mm.	1900u	1150u				
E1801	16	18 mm.			250u	190u	200u	220u
E1802	16	18 mm.			absent	absent	absent	absent
E1803	16	18 mm.			240u	150u	1000u	700u
E1804	16	18 mm.			450u	325u	1500u	1000u
E1805	16	18 mm.			absent	absent	absent	absent
E2106	18	21 mm.	2300u	1500u				
E2101	18	21 mm.			400u	270u	300u	210u
E2102	18	21 mm.			absent	absent	220u	180u
E2103	18	21 mm.			350u	290u	330u	250u

(1) : u = micron

* : approximate age

DISCUSSION

It has been shown in preceding pages that in the anomalous embryos optic cup development was always accompanied by development of a lens. In those embryos (E1201, E1202, E1203, E1802, E1805 and E2102) in which one, or both, optic cups failed to develop, there was no indication of lens development. These observations suggest that the lens may be induced by the optic cup. Induction of the lens in lower vertebrates has been ablely investigated by several workers. In certain amphibians Lewis ('07), Stockard ('07), and others, have shown that the formation of the lens depends directly upon the stimulation of the ectoderm by contact with the optic vesicle. Further, Lewis ('07) states: "the size of the early lens-structure is due in part to the area of contact or adhesion between optic vesicle and ectoderm, and in part to the length of time the optic vesicle or optic cup remains in contact by its retinal layers with the growing lens-structure." Le Cron ('07) augmented this by illustrating that the lens in Amblystoma punctatum was not self-differentiating but depended upon the continued influence of the optic cup for its normal development. Eigenman ('98) found that a lens structure was present in young embryos of Amblyopsis (a blind cave fish) but completely absent in old embryos. Stockard ('07), in his study of embryos of blind cave fish (Bdellostoma stouti), showed that

"the optic-vesicle may change into an optic-cup without the aid of the mechanical pressure of the lens." However, all anomalous embryos in this study that exhibited an optic cup, irrespective of the size, also displayed a lens. Spemann ('12) reported that the lens was capable of development in some amphibians without the stimulus of an optic vesicle. This controversial "lens-problem" is discussed by Werber ('18). Again, this series of anomalous embryos displayed no evidence of a lens present without the optic cup.

It has been illustrated in previous pages that expression of this anomaly varied from complete anophthalmia to near normal size eye. Eigenmann ('98, '99, '01) made extensive investigations on blind vertebrates and found that the degree of anomaly varied greatly. As to causes of this variation, he believes that development ceases at some ontogenetic stage and this is followed by a degeneration which is a continuous reduction of organs of the eye to the adult stage. In this study indications of degeneration of eye structures, especially the lens, were exhibited in several embryos (E1203, E1803, E1804, E1805, and E2101). Size of the lens ranged from near normal to microphthalmic; however, conspicuous vacuoles were present in all of the lenses as illustrated in figs. 13, 16, 17, and 19. The distal portion of the right lens of E1203 and E1803 presented extreme irregularity in arrangement of lens fibers. In addition, E1203 showed

evidence of shrinkage of the distal surface of the lens adjacent the heavily vacuolated area (fig. 13).

In contrast to Eigenmann's views, Stockard ('21) has presented the hypothesis that during embryogeny the faster growing regions are more inhibited by adverse conditions than the slower growing ones. In a study of anophthalmic mice, Chase and Chase ('42) concluded that after the optic vesicle formed there was an inhibition of the growth of the vesicle. The seven millimeter series of this study exhibited no major absences of structures; however, the gross sizes of these structures, in general, were less than those of the control. Individuals that exhibited microphthalmic eyes presented levels of development comparable to a much earlier embryo (five millimeter control). The nine millimeter stage revealed no anophthalmic eyes but exhibited a wide range in gross size of structures. Again, the size of the optic cups and lens vesicles of five of the eyes of this series appeared no further advanced than the five millimeter control stage. Similarly, the twelve millimeter, eighteen millimeter, and twenty-one millimeter groups presented microphthalmic eyes that exhibited a stage of development closely approximating that of five millimeter control series. The observations made in this study suggest that microphthalmic and anophthalmic eyes might be due to a factor (or factors) which inhibit early development rather than to a secondary degeneration or absorption of eye structures at some time after the onset

of development. In a study of fowl (homozygous Creeper) embryos, Landauer ('32) concluded that no sharp line could be drawn between the effects of extreme retardation and a complete inhibition of later development. He states: "The homozygous Creeper condition appears to be expressed chiefly by a retardation of growth in general but at a time when the extremities and the head are most susceptible to such influences."

Another interesting feature was noted in E0904. The optic cup was collapsed and folded as shown in Fig. 9. Beckwith ('27) states that "in all the eyes of Amblystoma punctatum in which the lens was not present the optic cup was variously folded or collapsed and the vitreous humor was absent." However, in E0904 a very small lens was present.

Twitty ('32) found that "following embryonic extirpation of the eye, the muscles fail to develop their typical arrangement. In extreme cases they may become condensed into a single mass so that their individual identity is obscured." In this study all embryos that exhibited complete anophthalmia revealed no ocular muscles.

SUMMARY

1. Degrees of expression in the anomalous strain ranged from complete anophthalmia in both eyes to both eyes near normal size. The highly inbred control strain gave all normal sized eyes.

2. Embryology and gross morphology of the anomaly are presented. Timed matings were utilized to obtain embryos in the two strains, and the eye regions were compared.

3. Optic cup development was always accompanied by development of a lens. No specimen showed lens development in the absence of an optic cup.

4. Observations suggest that there is an inhibition of growth in the early developmental stages rather than a degeneration or absorption of eye structures in the more advanced age groups of embryos.

5. Anophthalmic eyes revealed no ocular muscles.

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PLATES

PLATE I

Explanation of Figures

1 Left eye region of 7mm. control embryo (E0706). Frontal section through lens vesicle and optic cup. The two layers of the optic cup are differentiated into an outer, thinner (pigment) layer and an internal, thicker (nervous) layer. x 172.

2 Left eye region of 7mm. anomalous embryo (E0701) showing the two layers of the optic cup of equal thickness and separated by a well defined optic ventricle. x 172.

KEY TO PLATES

L V, lens vesicle

O N, optic nerve

O C, optic cup

L F, lens fibers

O C' folded layers of optic cup

O V, optic ventricle

E L, eye lid

V, vacuole

L, lumen

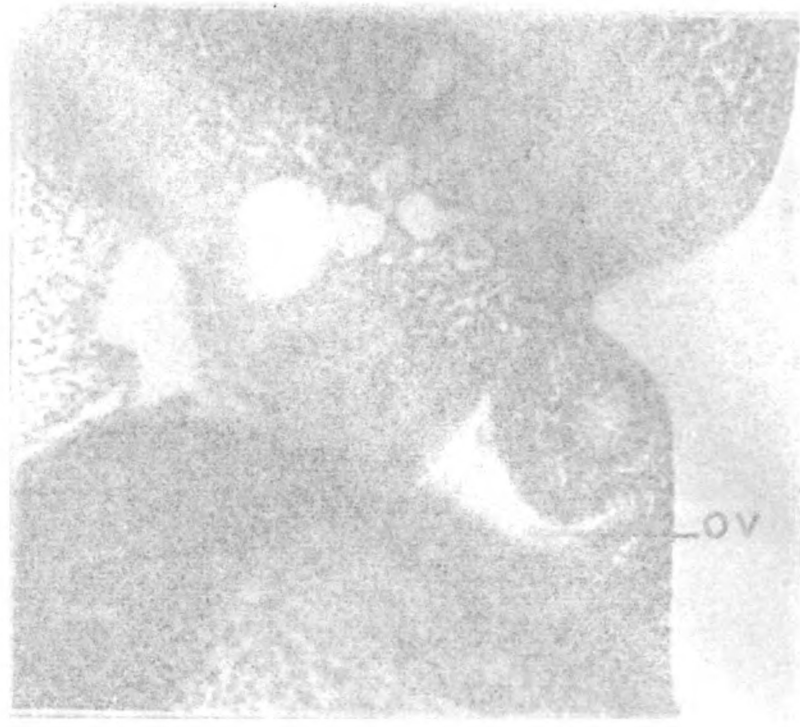
S, sensory layer of optic cup

P, pigment layer of optic cup

M, lens and superficial ectoderm in close contact

C, cornea

F, nerve fibers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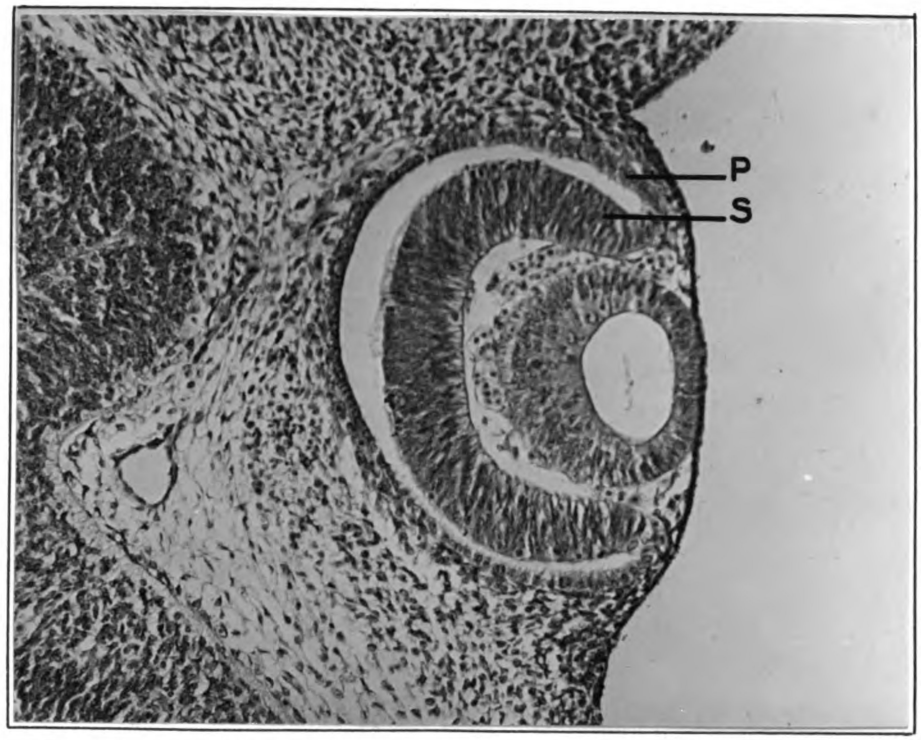
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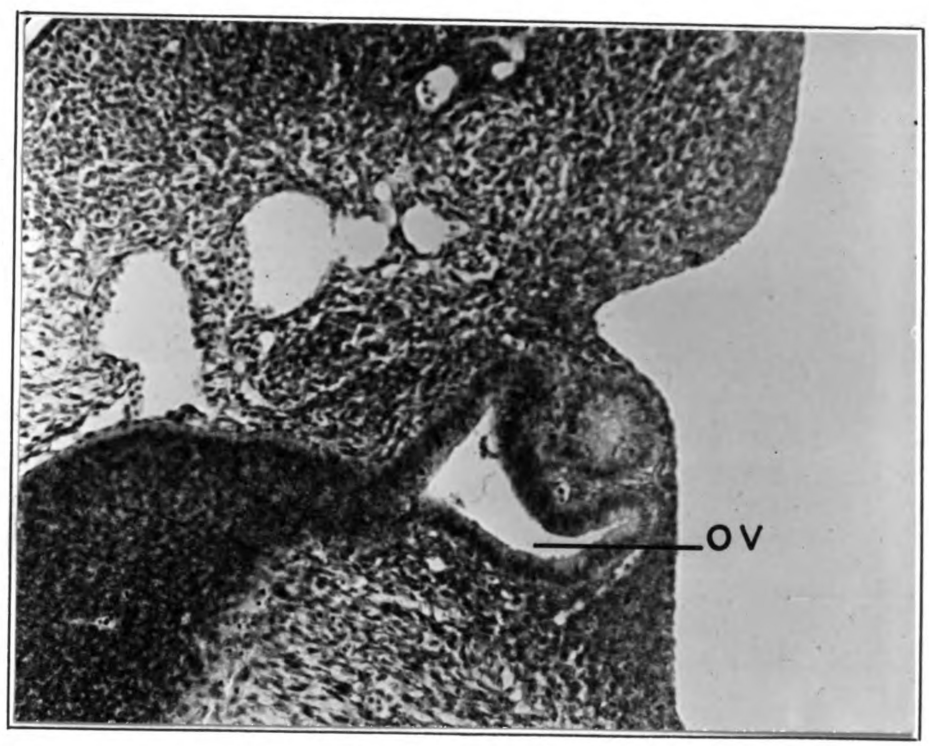
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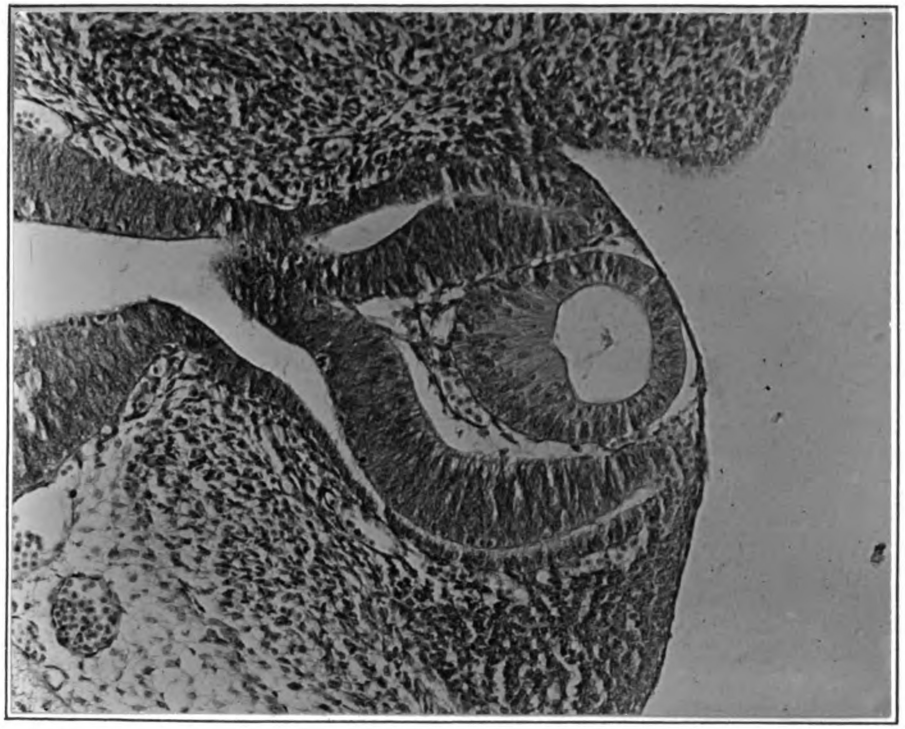
PLATE II

Explanation of Figures

3 Left eye of 7mm. anomalous embryo (E0702) showing a degree of development very similar to that of the control. x 172.

4 Right eye of 7mm. anomalous embryo (E0703). The "crescent" shaped lumen of the lens vesicle can be seen. x 172.



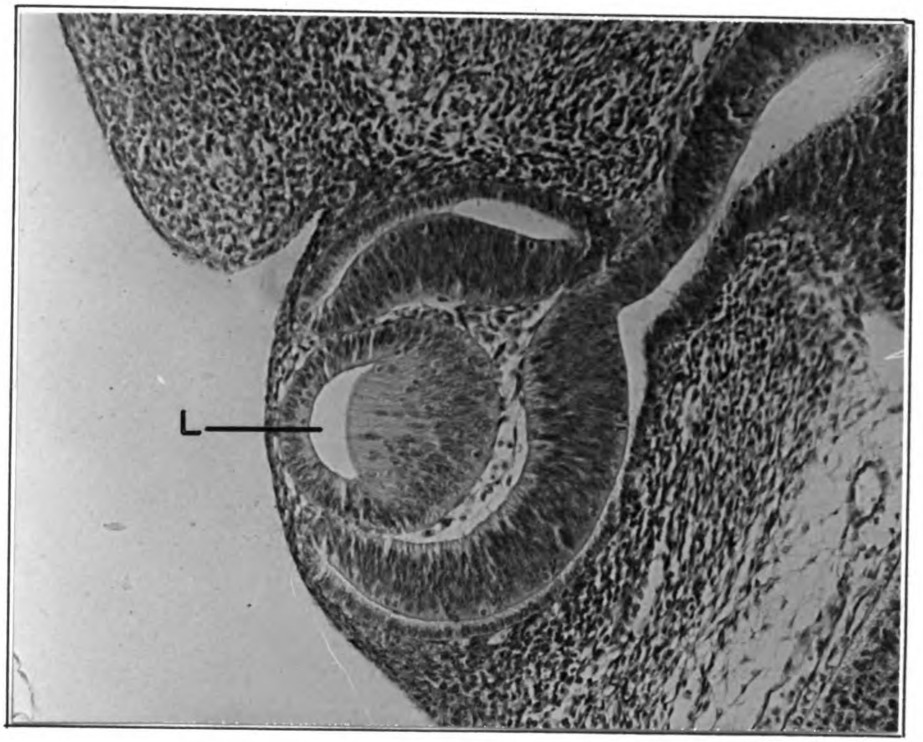

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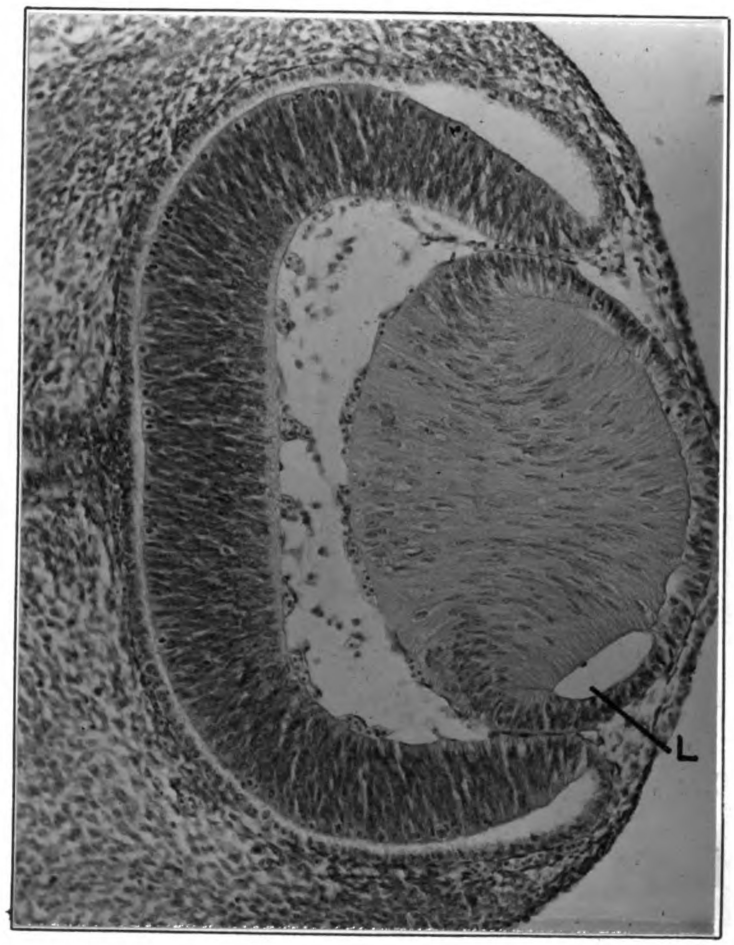
PLATE III

Explanation of Figures

5 Left eye of 9mm. control embryo (E0906). The inner layer of the optic cup is much thickened and the lumen of the lens vesicle is virtually eliminated. x 172.

6 Left eye of 9mm. anomalous embryo (E0901). The lens vesicle (L V) consists of a single layer of columnar cells which form a circular lumen. The distal wall of the lens vesicle and superficial ectoderm are in close contact at M. x 172.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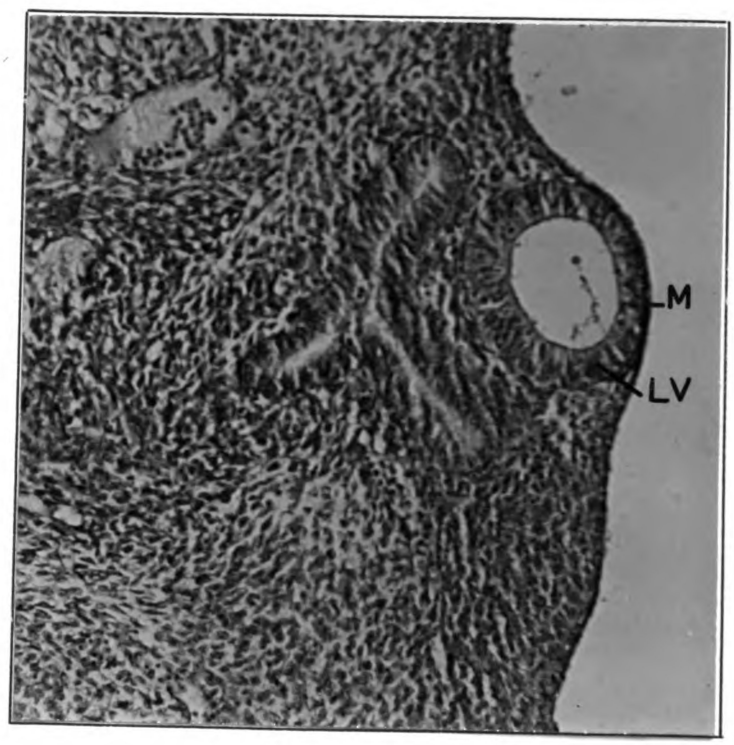
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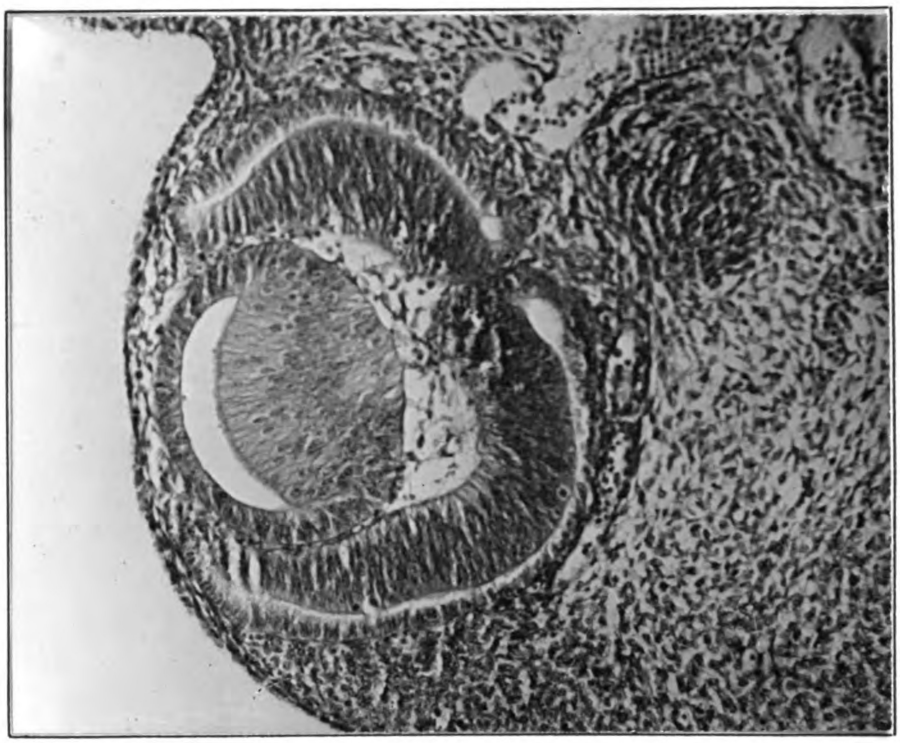
PLATE IV

Explanation of Figures

7 Right eye of 9mm. anomalous embryo (E0901). x 172.

8 Left eye of 9mm. anomalous embryo (E0903). The slightly invaginated optic vesicle can be seen. x 172,



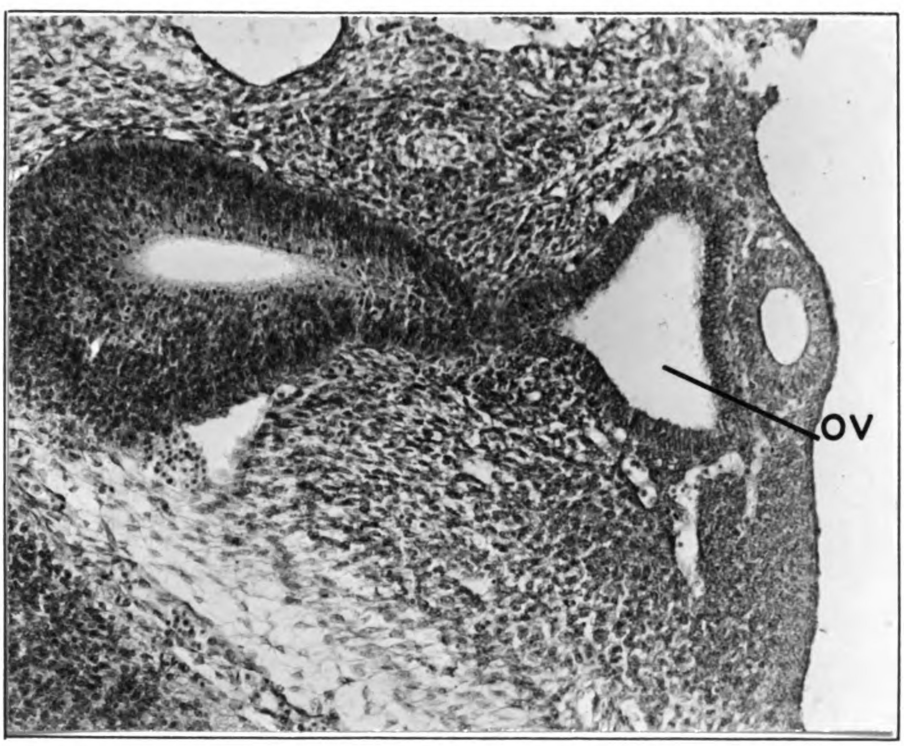

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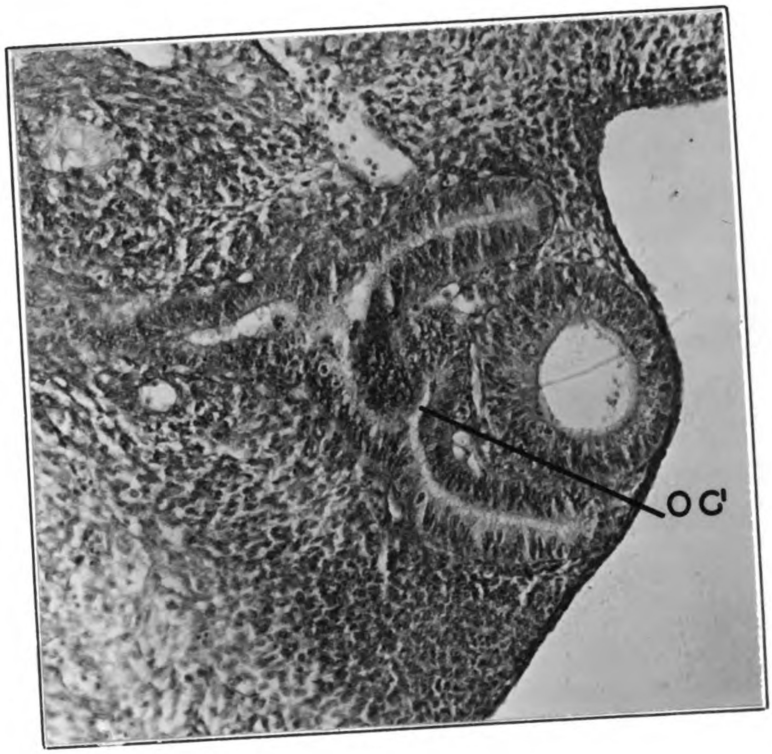
PLATE V

Explanation of Figures

9 Left eye of 9mm. anomalous embryo (E0904) showing extreme folding of the optic cup (OC'). x 172.

10 Right eye of 9mm anomalous embryo (E0904). The sensory layer (S) and the pigment layer (P) exhibit degrees of development similar to those of the control. x 172.


O C'

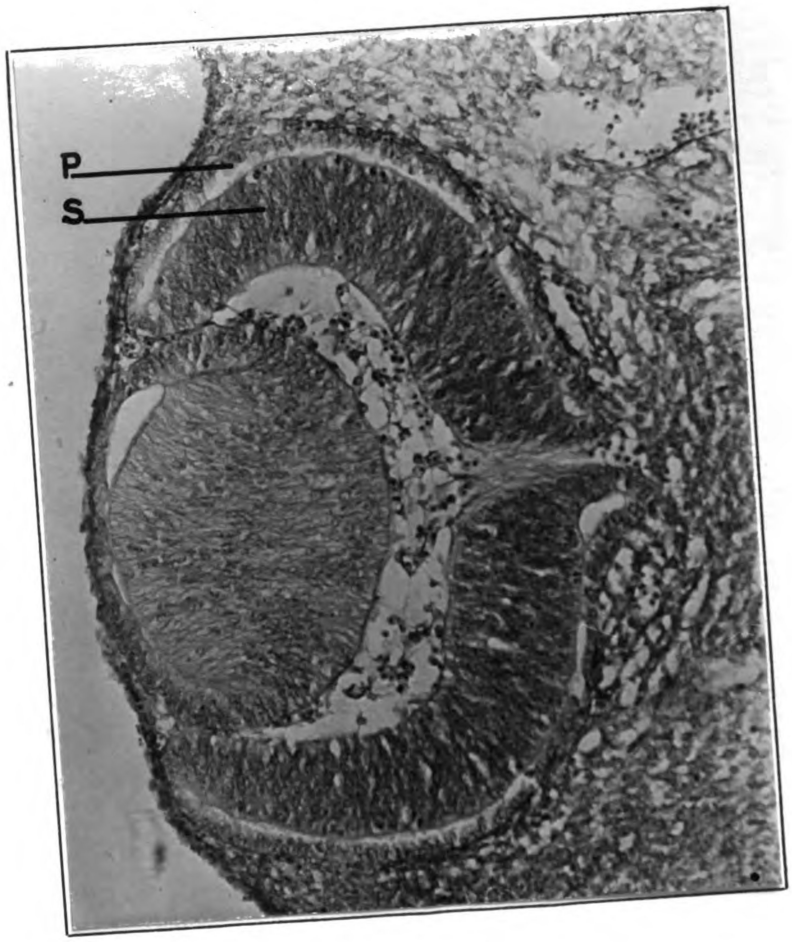
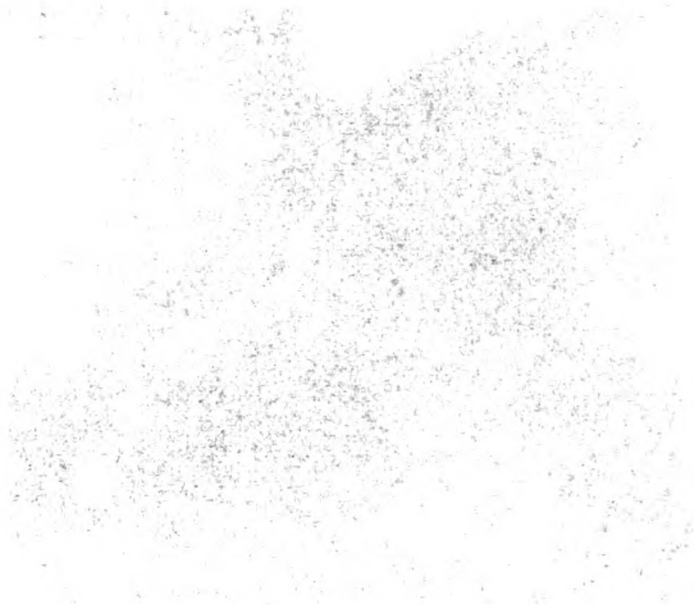

P
S

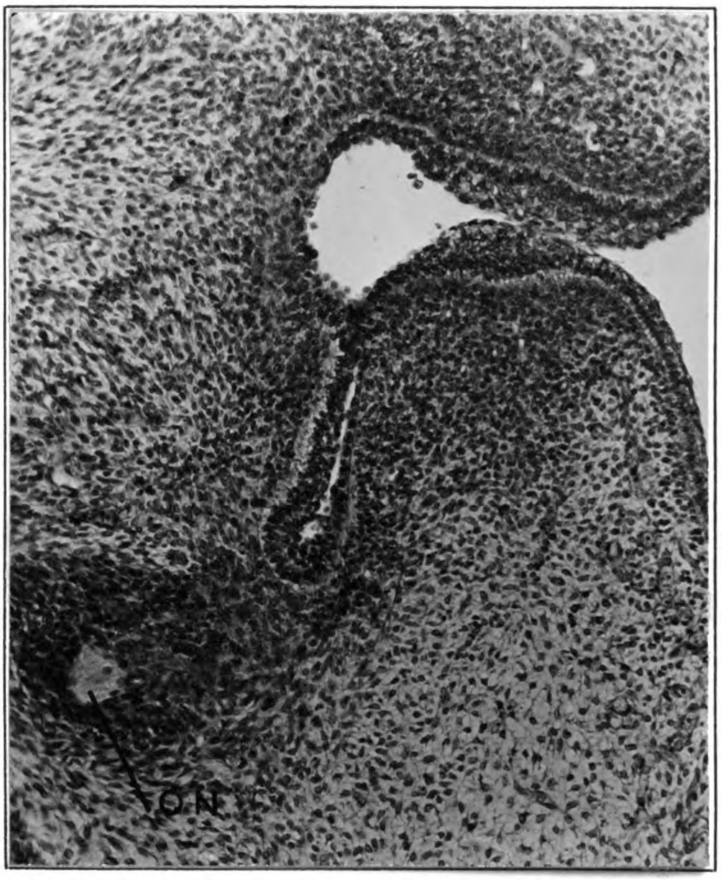
PLATE VI

Explanation of Figures

11 Left eye of 12mm. anomalous embryo (E1201). Optic cup and lens vesicle structures are entirely absent. However, the fibers of the small optic nerve (ON) can be seen. x 172.

12 Left eye of 12mm. anomalous embryo (E1202). The small optic cup (OC) and lens vesicle can be seen. Mesenchymal cells invest the space between the lens vesicle and the optic cup. x172.




ON

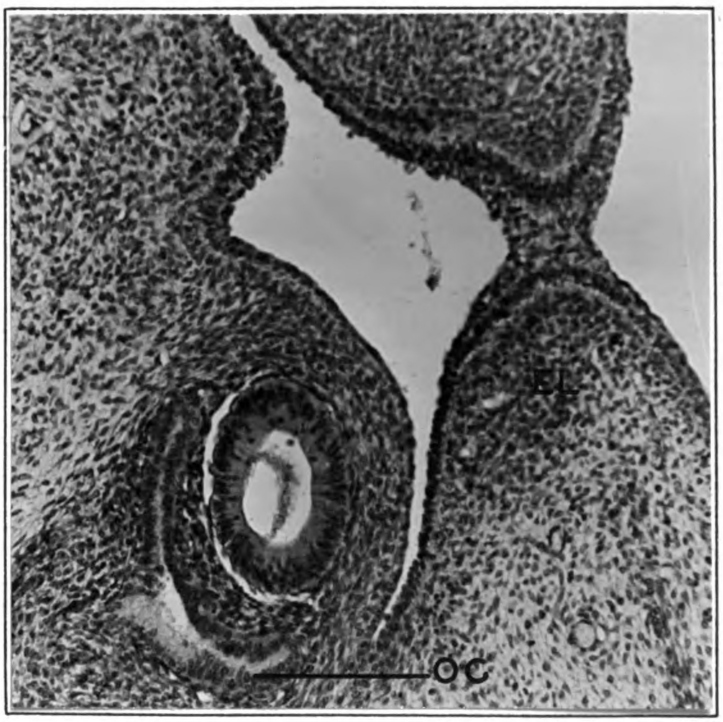
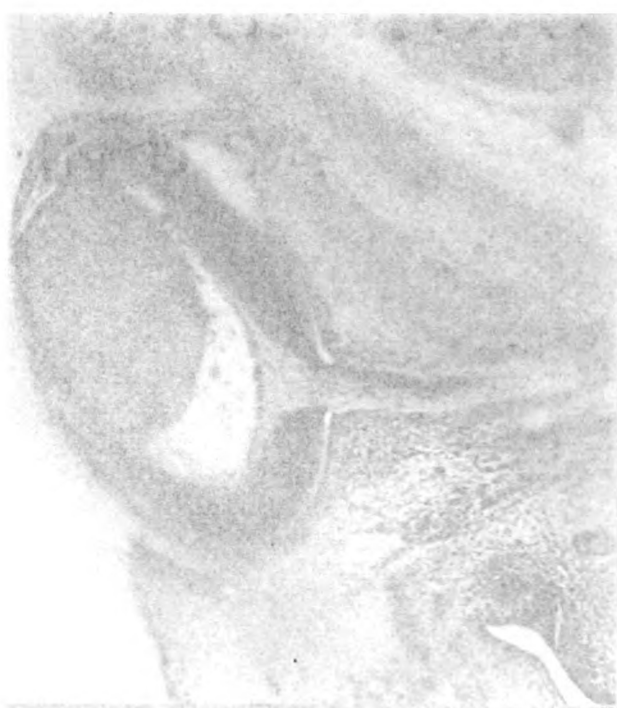

OC

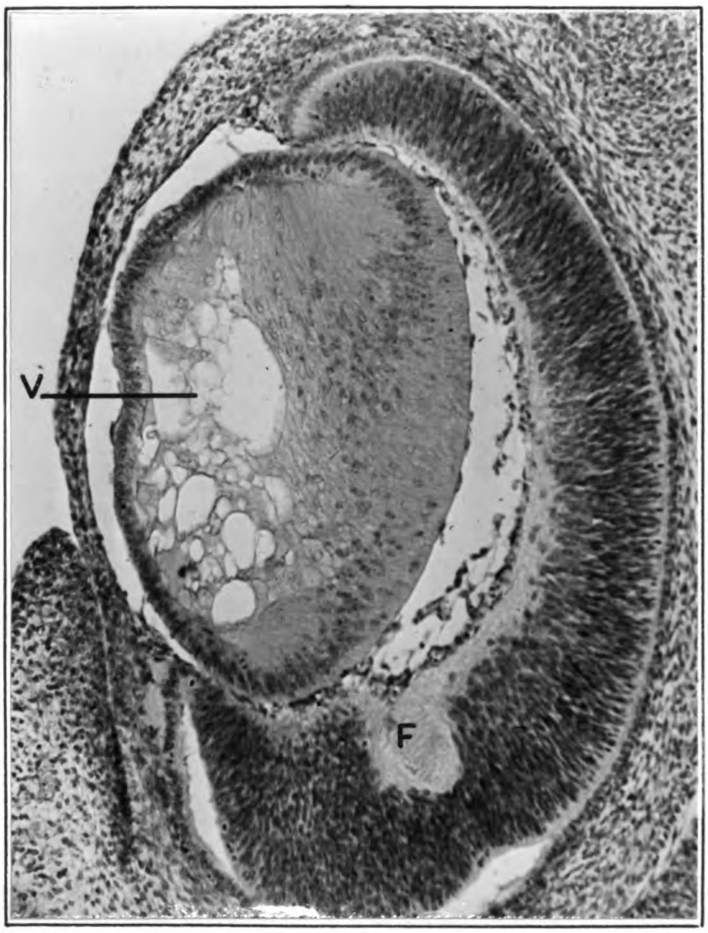
PLATE VII

Explanation of Figures

13 Right eye of 12mm. anomalous embryo (E1203). Conspicuous vacuoles (V) fill the distal half of the lens. Nerve fibers converge at a point (F) in the ventral region of the sensory layer. x 172.

14 Right eye of 12mm. control embryo (E1206). x 70.




V
F

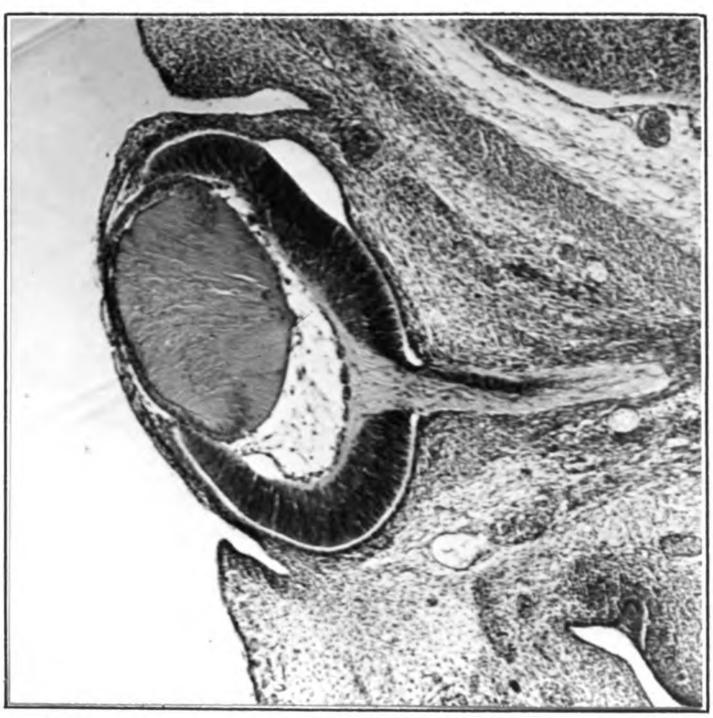
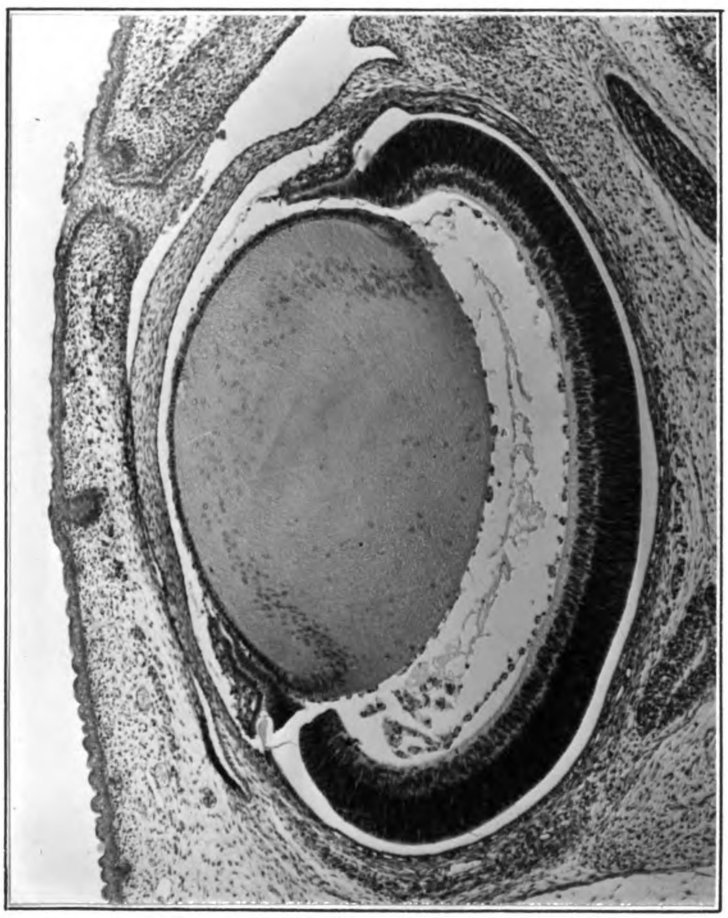


PLATE VIII

Explanation of Figures

15 Right eye of 18mm. control embryo (E1806). x 70.

16 Left eye of 18mm. anomalous embryo (E1804). Disarranged lens fibers (LF) fill the lens vesicle. x 70.



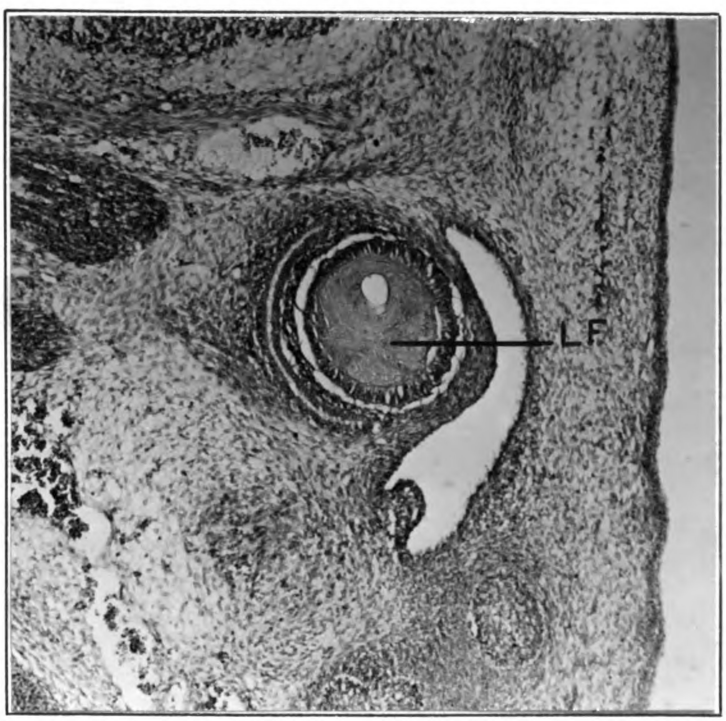
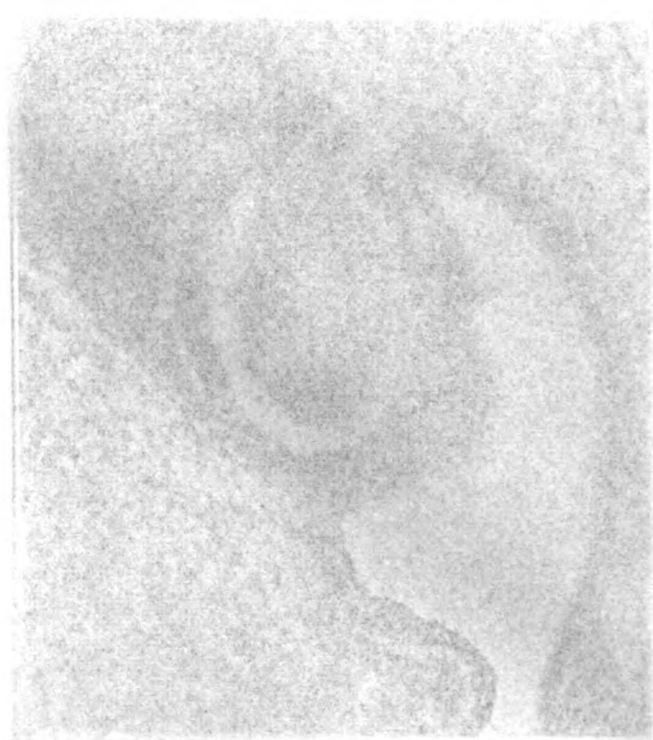

LF

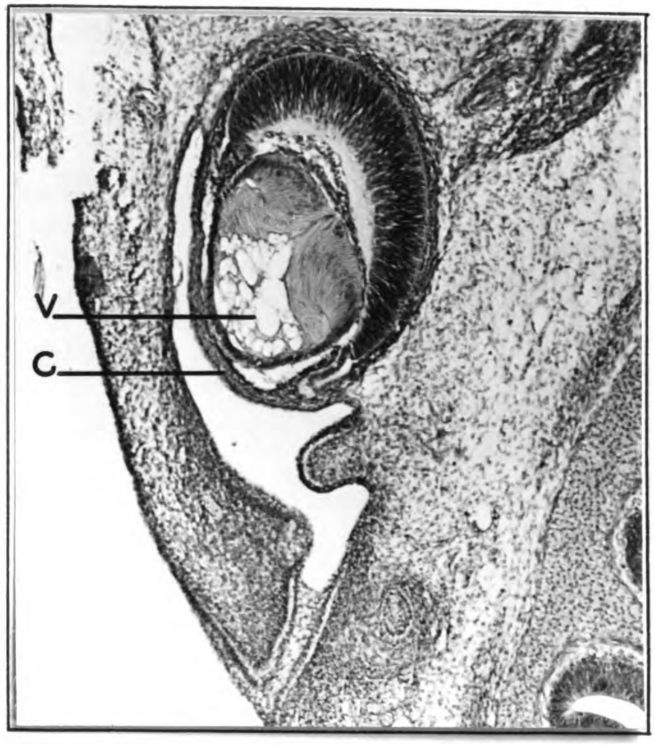
PLATE IX

Explanation of Figures

17 Right eye of 18mm. anomalous embryo (E1803). The distal portion of the lens exhibits extreme vacuolization. x 70.

18 Left eye of 18mm. anomalous embryo (E1803). x 172.




V
C

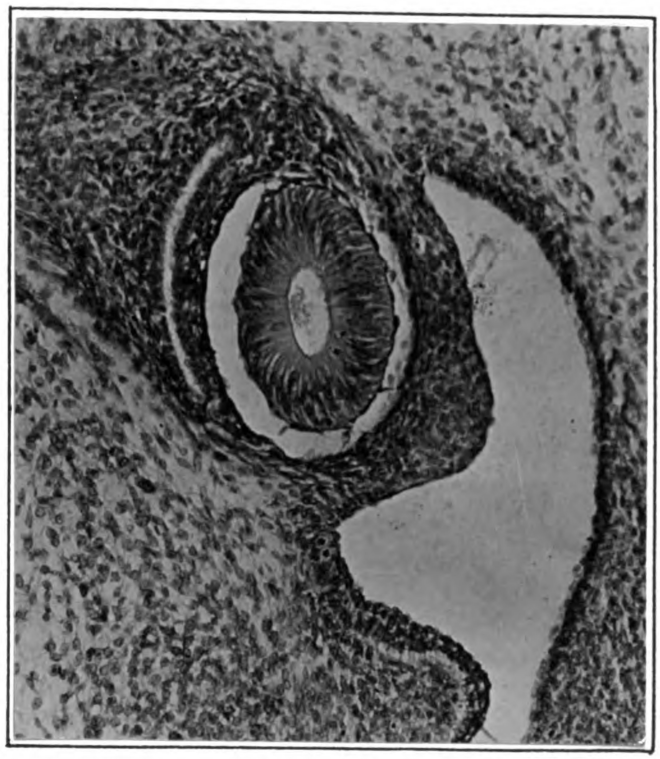
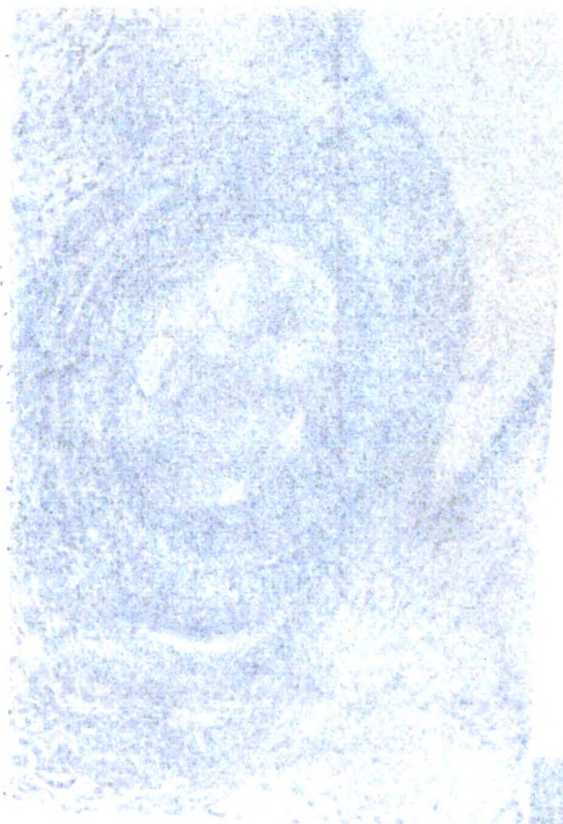


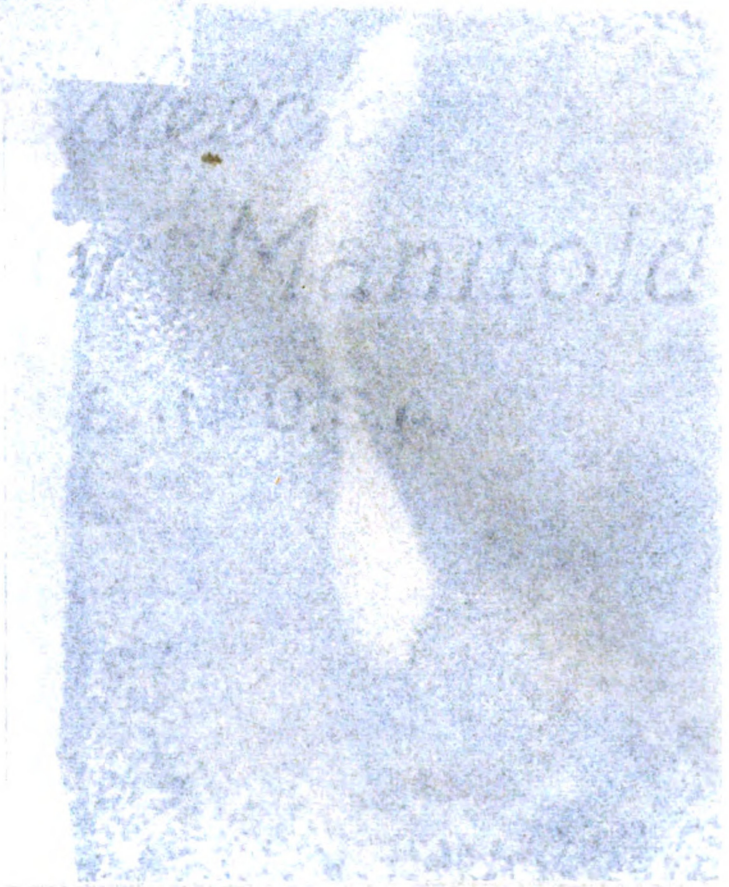
PLATE X

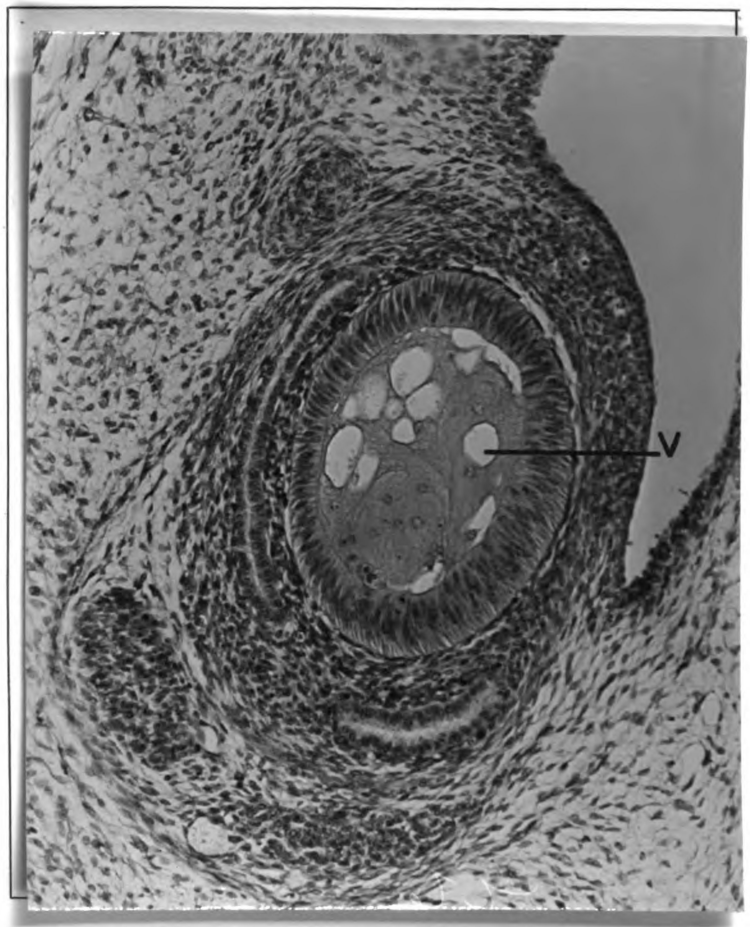
Explanation of Figures

19 Left eye of 21mm. anomalous embryo (E2101). Numerous vacuoles (V) are present within the lens vesicle. x 172.

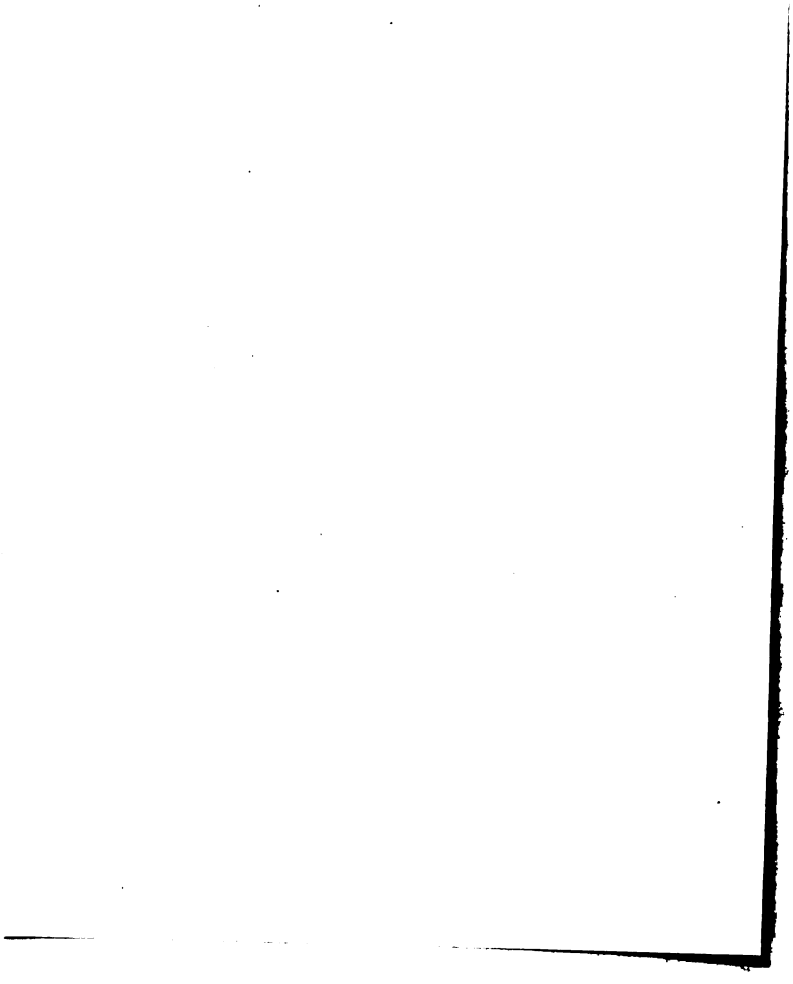
20 Left eye of 21mm. anomalous embryo (E2102). Optic cup and lens vesicle structures are absent; however, an extremely small optic nerve (ON) is present. x 172.






V


O.N



Caraway