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THE PECTEN OCULI OF THE PIGEON WITH PARTICULAR REGARD TO ITS FUNCTION

BY

KARL GEORG WINGSTRAND AND OLE MUNK

København 1965

Kommissionær: Ejnar Munksgaard

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Synopsis

The pecten of the avian eye was described by Olaus Borrichius in 1674. The numerous subsequent papers, though mainly morphological, include about 30 different theories on the function of the organ. Some of these theories are examined in the present morphological and experimental investigation of the pigeon's pecten.

The theory that the pecten, like the ciliary body, secretes intra-ocular fluid was mainly founded on the histological and histochemical similarity of the two organs. The similarity was critically re-investigated in the pigeon, but as the structural evidence proved to be short of conclusive, this particular line of approach was abandoned, especially after certain functional differences between the two organs had been brought to light.

Anatomical investigations revealed that it is possible to block the pecten arteries of the pigeon by surgery. The operation stops the pecten circulation and causes slow and progressive degeneration of the organ, until revascularization starts after some weeks. In eyes thus treated the retina shows ophthalmoscopical and histological symptoms of heavy degeneration, particularly in the ganglion cell layer and the layer of optic nerve fibres. In contrast, there was no degeneration in 31 eyes operated upon in the same way but with one or more of the pecten arteries left intact. It is concluded that the pecten is a nutritive organ, necessary for the maintainance of the inner retinal layers.

Investigations of the oxygen pressure in the bulb of normal pigeons by means of oxygen cathodes revealed a fall from about 100 mm Hg near the pecten to about 5 mm Hg near the retina. This shows that oxygen does diffuse from the pecten to the retina, and numerical estimates indicate that the amounts are large enough to be functionally significant. Blocking of the pecten arteries appears to result in almost complete anoxia in the corpus vitreum and the inner retinal layers. It is thus indicated that the inner retinal layers are dependent on the pecten for their oxygen supply.

The results support the theory that the pecten is a substitute for the absent intra-retinal vessels. It cannot be excluded that the pecten may perform other, subsidiary functions in the bulb, but this still remains to be shown.

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Introduction

The pecten oculi is a thin, folded membrane, rich in vessels and pigment, which projects from the papilla of the optic nerve far into the vitreous body of the bird's eye (Pl. I–III). Homologous structures are present in the eye of some reptiles and a few mammals, but these have the shape of a compact cone or are vestigial. Although the pecten has been known and discussed for about 300 years, there is still a great deal of uncertainty about its function. In the majority of papers, the function of the organ was discussed on the basis of morphological data only; this has resulted in about 30 theories, many of which are still accepted by different authors. More direct physiological experimentation with the pecten is difficult because of its inaccessible site, and this explains in part why experimental investigations have been few and insufficient for the making of definite conclusions.

When starting this work, the authors decided upon the classical way of approach. Experiments made by ABELSDORFF and WESSELY (1909) and by SEAMAN et al. (1962, 1963) indicated that the pecten, like the ciliary body, secretes intra-ocular fluid; thus attention was focused on the morphological and histochemical similarities of these organs in the hope of supporting this hypothesis. However, a few primitive experiments soon revealed physiological differences between the organs, and it was realized that the purely morphological way of approach was unlikely to lead to safe conclusions.

Consequently, a more direct way of attacking the problem was sought. To the authors' surprise it was found possible to eliminate the pecten functionally by blocking its vascular supply, and the retinal degeneration observed after such operations showed that the pecten is essential for the maintainance of the retina. In elaborating the method of operation, it was necessary to re-investigate the structure of the pecten in the domestic pigeon (*Columba livia* L.), the species used for the experiments, and to map out the vessels and nerves of the orbital region. Such morphological investigations are summarized in this paper as a basis for the understanding of operational procedure.

The results of the experiments mentioned above directed attention to the widely held idea that the pecten supplies the inner layers of the retina with oxygen by diffusion through the vitreous body (e.g. MANN 1924 a, b). The authors therefore decided to test this hypothesis by recording the oxygen pressure with oxygen cathodes in different parts of the vitreous body. The results obtained in normal eyes, as well as

in eyes with blocked pecten vessels, are in good agreement with the theory, and support it to a point not far from definite proof.

The series of investigations could not have been realized without the aid of specialists, who helped with technical problems, and gave advice in their own particular fields: Mr. TH. CHRISTENSEN (Latin text), Dr. E. FOX MAULE (Latin text), Dr. E. GREGERSEN (photo-coagulation), Mr. T. NORMAN and Mr. F. BJERRING (electron microscopy), Mr. H. RASMUSSEN (oxygen cathodes), and Dr. RY ANDERSEN (eye pathology). The authors are also indebted to the staffs of the Institute for Comparative Anatomy, Copenhagen, and the Institute for General Zoology, Copenhagen, for direct or indirect help. Technical assistance was made possible by a grant from the CARLSBERG FOUNDATIONS. The authors are aware that this help contributed greatly to the success of the work and wish to express their gratitude to all concerned.

Historical Note on the Discovery of the Pecten

The discovery of the pecten was formerly attributed to PERRAULT (1676), but SEAMAN and STORM (1963), rightly pointed out that STENO had mentioned the organ at an even earlier date. The publication referred to is STENO's famous description of the development of the chick in *Acta Medica Hafniensia*, vol. II for 1673, published in 1675.

This appeared to be the earliest record, but some remarks in the excellent description of the pecten in BLASIUS' "*Anatome animalium*" (1681, p. 136) indicated that the chapter was based on the work of the Danish scientist, OLAUS BORRICHIUS (OLE BORCH). The paper, copied by BLASIUS, is BORCH's "*Hermetis, AEgyptiorum et Chemicorum Sapientia*", printed in Copenhagen in 1674.

In this paper, BORCH criticizes a still older paper by PEIRESC in such a way that one has the impression that the pecten was actually described by PEIRESC. This may be the reason why COLE (1944, p. 322) quite definitely states that PEIRESC knew of the pecten. PEIRESC's investigations were published by the philosopher and physicist GASSENDUS in a book on PEIRESC's life (Latin edition 1641, English edition 1657). In this book, there is a long passage on the structure and function of eyes (pp. 274–283 in the Latin ed. for 1641), but no description of a structure identifiable with the pecten could be found, although remarkable features in the neighbourhood of the lens are mentioned.

The sequence of papers containing the first descriptions of the pecten is as follows, when the reports are arranged after the year of publication:

1674: OLAUS BORRICHIUS, in his "*Hermetis, AEgyptiorum et Chemicorum Sapientia*", pp. 258–259, describes the pecten of the eagle in a very accurate way and advances the first functional hypothesis: ". . . Membrana subnigricans et in plicas corrugata, nervoque optico in longum expanso continua, medium digitum lata erat, tota vasis distincta sangvineis secundum longitudinem rugarum. Margo singularis

humoris crystallini à *Peirescio* adesse creditus, observari hic nequit. Ex productis jam in medium non difficile, opinor, suerit, rationem reddere, cur oculi aquilae sine noxâ ferre qveant solare jubar".

(. . . There is a blackish membrane, wrinkled in folds, continuous with the greatly extended optic nerve, as broad as a middle finger, all over distinctly with blood vessels following the longitudinal course of the folds. The remarkable margin of the crystalline humour, which *Peiresc* believed to be present, cannot be observed here. On the basis of the extension (of the membrane) into the middle, I think it will not be difficult, now, to give a reasonable explanation why the eyes of the eagle can withstand the rays of the sun without being damaged).

1675: Nicolaus Stenonis (Steno), in his article on the development of the chick ("*In Ovo et Pullo Observationes*") in *Acta Medica Hafniensia*, vol. II for 1673, described the pecten of the 13 day old chick embryo in the following way: ". . . Optici nervi filamenta nigra, qvae per vitreum pergunt crystallinum . . ." (Black fibres of the optic nerve which advance through the vitreus to the crystalline humour . . .). Although the volume was printed in 1675, it is the "*Acta*" for 1673, and Steno's text was probably written 10 years earlier, in 1665, when he was working with Swammerdam at Iassy (see Maar 1910, Vol. II, p. 318).

1676: Claude Perrault, in the "*Mémoires pour servir a l'histoire naturelle des Animaux*", described the pecten in several birds (eagles, turkeys, bustards, and ostriches), but believed it was absent in the Numidian crane (*Anthropoides virgo*). He describes the pecten as a purse ("bourse"), attached to the papilla of the optic nerve. He considered that the "folded appearance" was an illusion, and believed the pecten to consist of a mass of fibres. He suggested that it has the same function as the uvea: "à prèparer la nourriture des humeurs de l'Oeil". This opinion was partly based on the black colour of both organs, and partly on the presumed absence of the pecten in the Numidian crane, which was said to have a particularly dark uvea (p. 334).

1680: Perrault, in the "*Essais de Physique*", repeats some of the earlier statements and his functional theory (1721, pp. 343–345).

1681: Geraldi Blasius, in his "*Anatome animalium*", quotes Borch's chapter on the anatomy of the eagle (pp. 136–138).

1682: Allen Mullen (Moulin) reports that he has seen in the chick the "little black bag" which Perrault had found in the eye of birds. This is mentioned on p. 63 in the small publication: "*An Anatomical Account of the Elephant, Accidentally Burnt in Dublin, on Fryday, June 17. in the Year 1681 (with an Appendix on the Eyes of Animals)*".

Of course, the question of the actual discovery of the pecten is not solved by merely filing the published statements after their date of publication. Communication between anatomical schools was very close in those days, as is shown by the almost simultaneous appearance of the pecten in scientific reports from Copenhagen (1674, 1675), from Paris (1676, 1680), from Amsterdam (1681) and from London (1682). It ought

to be mentioned also, that STENO visited Paris in 1664 and 1665, and may well have received certain hints from anatomists there before he and SVAMMERDAM dissected their chick embryos in 1665. The fact that STENO describes the pecten as "filamenta nigra" is suggestive of the way PERRAULT describes it: "fibres noires". BORCH could well have been inspired by STENO, but his description is entirely independent and actually includes all relevant morphological features which can be seen under low magnification. It is probable, therefore, that BORCH's description is based on very careful dissection. On the other hand, STENO and BORCH often worked together, and the actual dissection may have been performed by either of the two.

Theories on the Function of the Pecten

It is obvious that the beautiful morphological appearance of the pecten has greatly stimulated the imagination of investigators, as about 30 different functional theories have appeared in the pecten literature since the organ was discovered in 1674. In contrast, very few investigators have tried to control the theories experimentally. Consequently, only few theories have been definitely disproved, and none can be said to be so well supported by experimental evidence that it must be preferred to all the others.

This is admirably illustrated by the fact that theories advanced in the 17th century have survived happily to the present day. BORCH (1674) thought that the pecten protected the eye of the eagle from damage from the rays of the sun, and a similar function was accepted as being possible by, e.g., VERRIER (1936) and GRIFFIN (1953). PERRAULT (1676) suggested that the pecten serves to prepare nourishment for the eye. This basic idea, that the pecten is a kind of nutritive organ, has survived in different variations, including the ideas most widely held at present.

The theories on the function of the pecten have been reviewed more or less extensively by VIRCHOW (1901), WOOD (1917), v. SZILY (1922), KAJIKAWA (1923), MANN (1924 a), FRANZ (1934), WALLS (1942), and DUKE-ELDER (1958). The table below indicates the main lines of thought, together with references to the most important papers in which the theories are mentioned.

1. *The pecten is a nutritive organ* (PERRAULT 1676, 1680).
   a. *It supplies the inner eye in general:* MIHALKOWICS (1873), LEUCKART (1875), CARRIÈRE (1885), ABELSDORFF (1910), BLOCHMANN and v. HUSEN (1911), LEPLAT (1912), WOOD (1913, 1914, 1917), SLONAKER (1918), JOKL (1923), PLATE (1924), PASQUINI (1926), DUKE-ELDER (1958). *Contender:* WIEDERSHEIM (1909).
   b. *It supplies the vitreous body* (and, in some theories, also the lens): COLLINS (1900), LINDSAY-JOHNSON (1901), BÜTSCHLI (1912), MAWAS (1913), STRESEMANN (1927–1933).

c. *It secretes the fibrous material of the vitreous body:* v. Husen (1913), Plate (1924), Menner (1938).

d. *It is an enlarged ciliary or choroid process:* Hovius (1716), Haller (1768), Rosenthal (1811), Giraldés (1836), Bradley (1915).

e. *It produces intra-ocular fluid:* Leber (1903), Abelsdorff and Wessely (1909), Hess (1913), Kajikawa (1923), Verrier (1936), Menner (1938), Turchini (1933), Tanaka (1960), Seaman and Storm (1963), Seaman and Himelfarb (1963).

f. *It supplies the retina* (replaces intra-retinal and hyaloid vessels): H. Müller (1872), Beauregard (1876), Parreidt (1901), Rochon-Duvigneaud (1920, 1943, 1950), Mann (1924 a, b), Walls (1942), Leiner (1951), Kauth and Sommer (1953), Prince (1956), Polyak (1957), Pumphrey (1961), O'Rahilly and Meyer (1961). *Contenders:* Franz (1909, 1934), Griffin (1953).

g. *It supplies the retina through lymph vessels, supposed to run from the pecten to the retina:* Denissenko (1881).

2. *The pecten protects the eye from damage from strong light:* Borch (1674, 1681).

a. *Without specification of mechanisms:* Borch (1674, 1681), Desmoulins and Magendie (1825), Huschke (1827), v. Husen (1913), Wood (1914). *Contenders:* Leuckart (1875), Beauregard (1876), Kajikawa (1923), Mann (1924 a).

b. *Its blood stream carries away heat brought in by sunlight:* Griffin (1953).

c. *It is spread fan-like behind the pupilla and acts as a filter:* Treviranus (1820). *Contender:* Treviranus (1828), Barkow (1830).

d. *It is erected by the filling of its blood vessels, to catch the rays of the sun:* Ziem (1891, 1894).

3. *The pecten absorbs diffuse light in the eye, thereby contributing to a clear image:* Treviranus (1828), Thomson (1929), Verrier (1936).

4. *The pecten casts a shadow on the retina, facilitating vision in different ways.*

a. *Without specified mechanisms:* Desmoulins and Magendie (1825). *Contenders:* Kajikawa (1923), Mann (1924 a, b).

b. *It absorbs the rays from lateral and posterior directions in favour of binocular vision:* Petit (1738).

c. *It absorbs the rays from the dorsal and rostral fields in favour of monocular vision:* Treviranus (1820), Huschke (1827), Beauregard (1875). *Contender:* Beauregard (1876).

d. *It separates the binocular from the monocular field of vision:* Schleich (1896). *Contender:* Rabl (1900).

e. *The half-shadow cast on the retina increases sensibility:* Huschke (1827).

f. *The grid-like shadow cast on the retina increases resolution of movement:* Menner (1938), Croizier and Wolf (1944 a, b). *Contender:* Leiner (1951).

g. *The increased resolution of movement (point 4:f) is important for registering the sun-arc when the bird determines its latitude and longitude:* Griffin (1953), Matthews (1955).

5. *The pecten is a sensory organ.*
   a. *It is a thermoscope which registers radiating heat and prompts the bird when it is time to migrate:* Treviranus (1828).
   b. *It registers intra-ocular pressure changes during accomodation, so that distance to objects can be perceived:* Franz (1908 a, b, 1909, 1910, 1913, 1923, 1934), Kallius (1907), Wiedersheim (1909). *Contenders:* Blochmann and v. Husen (1911), Tretjakoff (1912), v. Husen (1913), Bütschli (1912), and most later authors.

6. *The pecten heats the eye, compensating for the cooling effect of air currents in arctic areas and at great altitude:* Kajikawa (1923), Bacsich and Gellért (1935).

7. *The pecten is a dark mirror, which casts images on the retina of objects in the sky* (e.g. birds of prey): Thomson (1928, 1929).

8. *The pecten has an active role in accommodation: Contenders:* Leuckart (1875), Th. Beer (1893), Abelsdorff (1910), Wood (1914), Mann (1924).
   a. *It is a muscle acting on the lens:* de la Hire (1701), Home (1796). *Contenders:* Home (1822), Leuckart (1875), Carrière (1885), Gadow (1891), Th. Beer (1893).
   b. *It can be erected by blood pressure, thus pushing the lens forwards:* Owen (1866).
   c. *It can be filled with blood and, by increasing intra-ocular pressure, acts hydraulically on the lens:* mentioned by Duke-Elder (1958), origin not known.

9. *The pecten smoothes out pressure variations.*
   a. *Its vessels are emptied when the pressure rises in connection with accommodation:* Rabl (1900), Hess (1909), Bütschli (1912), Leplat (1912), v. Husen (1913), Kajikawa (1923), Mann (1924 a, b), Rochon-Duvigneaud (1950). *Contenders:* Beauregard (1876), Abelsdorff (1910), Menner (1938).
   b. *It eliminates the pulse shock:* Mentioned by Duke-Elder (1958).
   c. *It regulates, by means of its blood content, the intra-ocular pressure during changes in altitude:* Mentioned by Duke-Elder (1958); origin not known (it is not Franz (1909) as quoted by Duke-Elder).
   d. *Like the corpus ciliare, it regulates the intra-ocular pressure by secretion of fluid* (compare point 1:e): Wood (1914), Seaman and Storm (1963), Seaman and Himelfarb (1963); compare Abelsdorff and Wessely (1909).

Experimental investigations, dealing with the pecten, were introduced by Beauregard (1875, 1876), who studied the organ with the ophthalmoscope. When the intact eye is stimulated to accommodate the pecten appears to make sudden movements,

but as these movements cease when the external eye muscles are removed, BEAUREGARD concluded that they have no connection with accomodation. In connection with these experiments it is of some interest that HESS (1909) found a small increase of intra-ocular pressure (1 mm. Hg), when the enucleated eye was stimulated to accommodate; he believed that the pressure changes in the intact eye are larger. Such pressure variations could possibly be eliminated by the pecten. ABELSDORFF (1910) re-investigated the problem. He stimulated the iris in situ to contract, after the external eye muscles had been immobilized with curare, and found no pecten movements during accommodation. As a whole, it seems unlikely from these experiments that the pecten has either an active or passive role in accomodation.

The most extensive experiments on the pecten are still those of ABELSDORFF and WESSELY (1909). These authors injected fluorescin into the blood and were able to show that the pecten is readily permeable to this dye and, probably, to other low-molecular substances as well. After extirpation of the ciliary body, the intra-ocular pressure could not be maintained; The bulb collapsed and the pecten was said to hypertrophy. Although crude, and subjected to justified criticism (FRANZ 1934, p. 1175), this experiment might indicate that the pecten helps the ciliary body to maintain intra-ocular pressure by secretion of fluid, and that the reported hypertrophy could be compensatory. ABELSDORFF and WESSELY (1909) also extirpated the pecten in owls, but the results of these experiments are difficult to evaluate, because the optic nerve, parts of the adjacent wall of the bulb, and, probably, the arteries to the chorio-capillaris were removed with the pecten.

KAUTH and SOMMER (1953) also experimented along these lines, destroying the pecten by cautherization. Within 8 days of the operation they observed by ophthalmoscope the development of a whitish reflex from the retina, but made no report of histological changes. According to the present authors' experience, rather much heat is needed to destroy the pecten, probably because of its abundant vascular supply. The retinal change could, therefore, perhaps be caused by damage to adjacent structures such as the optic nerve, to which the pecten is attached. On the other hand, the same symptom in the retina was observed by the present authors, after the pecten had been eliminated in a more selective way.

MENNER (1938) used an ophthalmoscopic method to map out the extreme limits of the pecten shadow on the retina in different bird species. In his opinion, the shadow is often complicated and foliated and serves to increase the resolution of movement. The theory was strongly supported by CROIZIER and WOLF (1944 a, b), who investigated the flicker response acuity both in man and in the sparrow. The resolution of small moving objects was much greater in the sparrow, but when a grid-like shadow was cast on the human retina, its resolution rose to a level comparable to that of the sparrow. They concluded that the normal, high resolution of movement in the sparrow-eye depends on the presence of such a shadow: the foliated pecten-shadow described by MENNER. However, the high resolution of the sparrow retina could also depend on retinal structure, and this explanation is made more attractive by certain doubts

expressed about the pecten shadow. Several authors (e.g., KAJIKAWA 1923, MANN 1924 a, b, LEINER 1951) have noticed that the pecten is directed towards the optic centre of the lens and cornea (Pl. I:1, compare WOOD 1917, CAMPELL, SMITH, and HARWARD 1962). This means that he pecten shadow is very small under favourable light conditions, when the pupilla is narrow, and falls mainly on the extended papilla of the optic nerve. Although the contours of the shadow can be uneven because of the pecten folds, it is hardly realistic to speak of the "grid pattern" required for the CROIZIER and WOLF theory. Only when the pupilla is wide open can there be a shadow effect on a somewhat wider zone of retina on each side of the pecten, but this zone cannot possibly be sharply contoured and will rapidly fade out to each side. This kind of shadow cannot produce the grid-effect necessary to substantiate the CROIZIER and WOLF theory. As it is realized that MENNER's lines do not represent sharp contours of a dark shadow but only extreme limits of the fading half-shadow under poor light conditions, the grid theory advanced by CROIZIER and WOLF is impossible to uphold.

KAUTH and SOMMER (1953) and LEINER (1951), found great carbonic acid dehydrase activity in the pecten of the fowl, twice as much as in the blood. Their interpretation favoured the hypothesis that the pecten is a respiratory organ for the inner layers of the retina. The enzyme would, in particular, facilitate the removal of CO_2 from the vitreous body.

Histochemical investigations by O'RAHILLY and MEYER (1961) and by SEAMAN and STORM (1963), show the presence of polysaccarid or mucoproteid membranes and alcaline phosphatase in the walls of the pecten vessels. They use these findings to support the theory of active secretion of fluid from the pecten. It is admitted that the said histochemical features indicate active transport through membranes, but it is open to doubt whether they reveal the specific function of the pecten. Positive PAS-reaction and alcaline phosphatase is a common feature in vascular walls, and can be seen in organs with very different functions.

The theory of active transport, particularly that of secretion of intraocular fluid, gains some support from electron microscopical studies (TANAKA 1960, SEAMAN and HIMELFARB 1963, SEAMAN and STORM 1963). It was found that the endothelial cells of the pecten capillaries have strongly folded, brush-border-like cell membranes both on the luminal and on the basal side. Similar membrane structures are familiar from other organs which are known to be concerned with active secretion of fluids, e.g. the ciliary body, the kidney, the choroid plexi, and the salivary glands. Although the analogy with these organs favours the hypothesis that the pecten is a secretory organ, the argument is far from conclusive.

Firstly, the folded membranes of the pecten are found in the endothelial cells of the vessels, whereas in the above-mentioned secretory organs, they are found in the epithelia outside the vessels. The structural similarity is thus restricted to the membrane folds as such and does not include the anatomical arrangement.

Secondly, it cannot be excluded that cell membranes of this type may be correlated with functions other than secretion or absorbtion. This is well illustrated throughout

the animal kingdom by the visual sense cells, which have folded membranes of different types, sometimes with the appearance of brush-borders (Röhlich and Török 1961), sometimes folded into the cell plasm (Eakin and Westfall 1962), and sometimes more elaborate, as in arthropods and vertebrates.

Finally, the brush-borders of actively secreting cells are associated with numerous mitochondria, important for the supply of energy to the transport process. In contrast mitochondria are not exceptionally numerous in the endothelial cells of the pigeon pecten (Pl. VI).

The question of water transport was recently attacked experimentally (Seaman and Storm 1963, Seaman and Himelfarb 1963). Injection of the drug Diamox into chickens caused a fall of intra-ocular pressure within an hour and was correlated with great changes of the ultra-structure of the pecten and the ciliary body. In both organs there was a general breakdown of the folded membranes. This was presumed to indicate that the pecten and the ciliary body are both concerned with the secretion of intra-ocular fluid and with the pressure regulation in the bulb. The pecten is believed to come into play only when the regulating mechanism is over-loaded. Although interesting, these experiments are not definitely conclusive, as the effect on the intra-ocular pressure would certainly be obtained after destruction of the ciliary epithelium alone, and the destruction in the pecten may or may not be significant in this respect. Moreover, the doses of Diamox used in these experiments were rather large, 100 times as large as those used for humans. The changes in the cell membranes of the pecten and the ciliary body could, therefore, be interpreted as unspecific destruction and should not necessarily depend on fundamental functional similarities. This possibility is made particularly attractive by the experiments with mammals, performed by Tormey (1963 a, b). His attempts to correlate the pressure fall after Diamox treatment with ultrastructural changes in the ciliary epithelium gave rather confusing results.

Nevertheless, when all arguments are taken into account, it appears possible and even probable that some fluid escapes from the pecten into the vitreous body. However, it has not been shown that this is an essential function of the pecten, important for the normal function of the eye.

The Structure of the Pecten in the Pigeon

Methods

The species used in the present investigation is the domestic pigeon (*Columba livia* L.). For light microscopical studies the eye was injected with Bouin's or Zenker's solution, or neutral formalin before dissection and final fixation in the same fluid. 5 μ paraffin sections were stained with Azan, hematoxylin-eosin, PAS-hematoxylin, alcian blue, or PAS-alcian blue. For electron microscopy, fixation was performed in ice-cold, collidin-buffered 2 % OsO_4 or in glutaraldehyde, followed by OsO_4. The cold fixative was in 3 cases perfused from the carotis, and fixation was continued in fresh ice-cold solution after the organs had been dissected out on ice. In 2 cases the organs were dissected out immediately after death and were put directly

into the cold fixative. Small pieces were embedded in methacrylate mixture, Westopal or Epon. Sections of about 500 Å were contrasted with uranyl acetate, permanganate or lead hydroxyde (NORMAN 1964) and were examined in a Siemens Elmiskop I.

External Shape, Orientation

In the pigeon, as in the majority of birds, the pecten has the macroscopic appearance described by BORRICHIUS in 1674: It is a thin, pigmented and very vascular membrane, wrinkled into transverse folds, and attached to the elongate, narrow papilla of the optic nerve (Pls. I–III). The folds give it the appearance of a comb, and this impression is strengthened by the thick, compact "bridge", which covers the inner ends of the folds and forms the free margin of the organ (Pl. I:2).

Only few birds differ from this general picture. The Kiwi (*Apteryx*) has instead a solid, pigmented cone resembling that found in lizards (LINDSAY-JOHNSON 1901, KAJIKAWA 1923). In the Ostrich (*Struthio*) and the Rhea, the pecten has the shape of a broad cone with a somewhat elongate base. It consists of branching lamellae, which are radially arranged around the axis of the cone, where they are attached to a more or less distinct central lamella (SOEMMERING 1818, BEAUREGARD 1876, CARRIÈRE 1885, KAJIKAWA 1923, VRABEC 1958). The Cassowary and the Emu have corrugated pecten membranes like the majority of birds, but an intermediate type is found in the Kingfisher (*Alcedo*), in which small supporting lamellae are attached to the normal pecten folds (KOLMER 1924, TANAKA 1938 b).

Variations in relative and absolute size, number of folds, proportions, and site have been reported for about 200 bird species (WAGNER 1837, GIEBEL 1857, BEAUREGARD 1876, VIRCHOW 1901, FRANZ 1909, 1934, WOOD 1917, ROCHON-DUVIGNEAUD 1920, 1943, 1950, KAJIKAWA 1923, STRESEMANN 1927–33, BACSICH and GELLERT 1935, and TANAKA 1938 a, b).

In the *domestic pigeon* the pecten membrane is wrinkled into 18–19 folds and is covered by a well-developed, compact bridge along the free margin (Pl. I:2). It stands on the narrow, elongate papilla of the optic nerve in the rostro-ventral sector of the bulb, and extends from a point 1.8 mm below the fovea out to a point 3 mm from the ora serrata (Pls. I–III). The maximal height is 3.3–4 mm, the length along the base is about 6 mm, and along the free margin 3–3.7 mm. The thickness between the culmen of the folds is 0.8–0.9 mm. The bridge is somewhat narrower than the folded part.

The pecten is orientated in such a way that its plane cuts the common optic centre of the lens and cornea. This is seen when the pecten is viewed with the ophthalmoscope through the pupilla. The bridge is then seen from the top and a series of low bulges on each side indicate the tops of the folds. The sides of the pecten cannot be seen when the pupilla is normally contracted (cf. figures in WOOD 1917 and in CAMPELL, SMITH, and HARVARD 1962). When the pupilla is wide open after treatment with curare, part of the sides can be seen, although from a very narrow angle. This

means that the pecten of the pigeon casts its shadow mainly on its own base, when the pupilla is normally contracted. Under poor conditions of illumination, when the pupilla is wide open, there may be some half-shadow with indistinct contours on a narrow strip of retina along each side of the pecten. For these reasons it is impossible to accept theories founded on the belief that the pecten casts a sharp, grid-like or foliate shadow on the retina (see p. 11). The organ is situated in such a way that it interferes as little as possible with the light coming in through the pupilla.

The Vessels

The folded pecten membrane is only 15–20 μ thick and consists mainly of densely packed capillaries which form two parallel rows in a cross section of the membrane (Pl. X:2, 4). The bridge contains a more irregular net of scattered capillaries. This vascular bed is supplied by 2–4 arteriae pectinis, which enter the bulb through the slit-like opening for the optic nerve, and by a vena pectinis, for which there is a separate foramen in the sclera (Figs. 6, 7, 8, Pl. V:2). After entering, these vessels turn longitudinally under the base of the pecten, emitting arterioles and venules to each fold (Fig. 8, Pl. V:2). Usually there is one arteriole and one venule in each fold. They pass in a fairly straight direction through the basal part of the organ, following the longitudinal course of the folds, and merge with the capillary bed before reaching the bridge. Often, a distinct vessel is seen following the culmen of each fold, whereas another distinct vessel is found in the centre of the organ. However, arterioles and venules may be found in both situations, so the arrangement appears to be very variable.

The Structure of the Folded Part of the Pecten

The thin wall forming the folds is covered on both surfaces by a superficial membrane, which can be identified in electron micrographs (Pls. IV, V:1, VII:1). This membrane is about 300 Å thick and shows the amorphous character and low density typical of basement membranes. The space between this membrane and the vessels is occupied by large intercellular spaces and by the scattered stroma cells and their processes (Fig. 1, Pls. IV, V:1).

The capillaries. As shown by Tanaka (1960), Seaman and Storm (1963), and Seaman and Himelfarb (1963), the endothelium cells of typical pecten capillaries are thin plates with brush-border-like fringes on both sides. In most sections the villi are seen as fairly regular, about 1 μ long and 4—600 Å thick processes, covered by the unit membrane of the cell surface (Pls. VI, VII:1). Tangential sections of the capillary wall show, however, that the villi are about 1 μ broad, tongue-like folds with the said height and thickness. The same sections show that the distal parts of the villi are unbranched and isolated from each other.

The villi on the luminal side of the endothelial cells end freely in the lumen of the vessel. Those on the outer or basal side also have well-defined ends with unbroken

membranes, in contact with and probably adhering to the fibrous perivascular membrane (Pl. VI). The villi are few and low in some of the vessels but are absent only in some of the larger vessels. The authors' methacrylate sections gave a poor picture of the villi on the basal side of the endothelium, particularly when the villi were cut parallel to their flat sides. However, in the Westopal and Epon sections, the villi could be distinctly seen in these places (Pls. VI, VII:1). The use of methacrylate is perhaps the reason why SEAMAN and STORM (1963) describe the basal villi as confluent with the fibrous perivascular membrane in some places in the pecten of the chick.

The cytoplasm of the endothelial cells contains small (0.3–0.7 μ) mitochondria and some ribosomes, many of which are bound to membranes. Small (200–300 Å) smooth-surfaced vesicles are common in the plasm. SEAMAN and STORM (1963) and SEAMAN and HIMELFARB (1963) observed formation of rows of such vesicles in connection with a general break-down of the villus system in chicks treated with Diamox. In the present material of normal pigeons, this was seen only in parts of a single pecten, which had been poorly fixed with osmic, and was clearly an artefact.

The fibrous perivascular membrane shows up in light microscopical preparations stained with PAS as a sharp, red-violet line, indicating carbohydrate compounds. In the electron micrographs it is seen as a 0.3–0.5 μ thick zone, consisting of a homogeneous ground substance with low electron density and numerous collagen filaments with distinct periodicity. The inner limit of the zone is undefined and the villi of the endothelium appear to dip into the amorphous ground substance. The outer limit is sharp, formed by a 400 Å thick condensation of amorphous substance, similar to the basement membrane of normal epithelia (Pl. VII:1). This membrane forms the outer surface of the vessels. SEAMAN and STORM interpret the entire fibrous perivascular sheath as being the counterpart of the basement membrane of other capillaries.

Intramural cells are common in light microscopical sections, situated in the thick fibrous perivascular membrane. In electron micrographs they were found in the same site, splitting the perivascular membrane into an inner and an outer lamella (Fig. 1). Their flattened cell body was often seen to contain a well developed endoplasmic reticulum with numerous ribosomes. Parallel filaments, indicating a contractile function, could not be discovered in the pigeon, and SEAMAN and STORM were unable to find them in the chick. The authors also found occasional cells of this type outside the perivascular membrane on the outer surface of the vessel.

The stroma cells are scattered in the space between the vessels and the superficial membrane of the pecten. Their angular, irregular cell body with the large nucleus is often in direct contact with a capillary wall on one or two sides, whereas the major part of the cell membrane is bordered by the intercellular spaces (Fig. 1, Pls. IV–VI). The cell body sends numerous ramified processes out to the superficial membrane and to the walls of the vessels. The finest ramifications of these stroma cells are very numerous in some parts of the intercellular space and may be as thin as 600–700 Å. When reaching the superficial membrane these processes usually end with rounded

tips and do not form a closed plasmatic surface (Pls. V–VII). When ending on the surface of vessels they are often, though not always, inflated to vascular feet (Pl. VI).

The plasm of the stroma cells and their processes is dense in electron micrographs. All stroma cells appear to contain several spherical pigment granules with a diameter

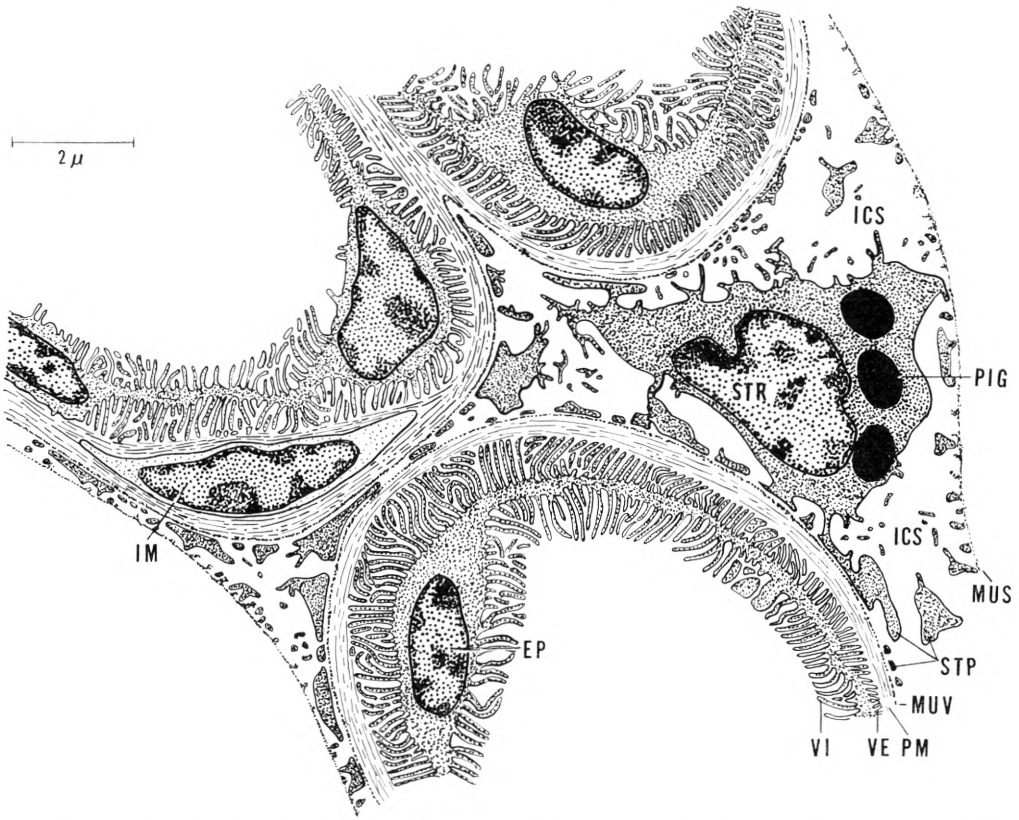


Fig. 1. Diagram showing the folded wall of the pecten in the pigeon, based on an electron micrograph of a cross section. The drawing illustrates the relations of capillaries, stroma cells and the mucopolysaccharid membranes; of the cytoplasmic organellae only pigment granules are shown. — EP = endothelial cell nucleus, ICS = intercellular space, IM = intramural cell nucleus, MUS = superficial mucopolysaccharid membrane, MUV = mucopolysaccharid membrane covering outer surface of capillary, PIG = pigment granules, PM = perivascular membrane of capillary, STR = stroma cell nucleus, STP = stroma cell processes, VI = inner villi of endothelium, VE = outer villi of endothelium.

of 1–2 μ. The mitochondria of the stroma cells are particularly large (1.5–2 μ) and are usually rounded with beautiful, parallel cristae. There are a few ribosomes and scattered endoplasmic vesicles. Small, smooth-surfaced vesicles and bundles of thin filaments are sometimes seen in the plasm, but these are more typical of the bridge, as described below.

Connective tissue strings, which are fairly few and scattered, are distinct in light microscopical sections, stained in Azan. The counterpart in the electron micrographs

is cross sections of tubules, filled with collagen filaments and surrounded by a thin amorphous membrane of the mucopolysaccharid type (Pl. V:1). The collagen is often disposed peripherally within the tube, as was expected from the tube-like appearance of the strings in the light microscope. As there is an almost continuous layer of stroma cell processes outside the membrane, the collagen-filled space is separated from the surrounding intercellular space.

The intercellular space is an important system of cavities and clefts in the pigeon (Fig. 1, Pls. IV, V:1). It forms a continuous cavity under the superficial membrane and extends between the stroma cells and vessels of the interior. The cavity is traversed by the numerous processes of the stroma cells, but as these are slender rods, there is no reason to believe that the intercellular space is divided into separate compartments. The space must therefore be looked upon as a continuous cavity, extending from the superficial membrane to the wall of the vessels and surrounding all stroma cells and their processes. TANAKA (1960) describes this space in different bird species, but SEAMAN and STORM (1963) and SEAMAN and HIMELFARB (1963) did not find intercellular spaces in the chick. It may therefore be of interest that the same general morphology was found in the pigeon both after fixation in OsO_4 and after fixation in glutaraldehyde, and there was no difference between specimens fixed by perfusion from the carotis and those fixed by putting the organ directly into the fixative after dissection. As it is unlikely that the pigeon and the chick are fundamentally different with regard to intercellular spaces, it is probable that the difference rather depends on the method used. It is possible that the fluid in the intercellular space had escaped and that the spaces themselves had collapsed in SEAMAN's and STORM's preparations, as these authors cut the fresh organ into small pieces before the fixation.

The superficial membrane, covering the free surface of the wall, may be supposed to have covered a continuous cellular surface on the embryonic pecten as a basement membrane. In adult pigeons, however, the stroma cells have retracted and the large intercellular space begins directly under the membrane. The stroma cells are only in contact with the membrane by means of the tips of the fine processes, which are rather far apart. Large areas of membrane have no contact at all with the stroma cells (Fig. 1, Pls. IV, V:1, VII:1). The amorphous substance of the membrane is often seen to project inwards, between the tips of the stroma cell processes, as strings (Figs. 1, Pls. V:1, VII:1).

The Bridge of the Pecten

The bridge is a fairly compact structure, consisting mainly of strongly pigmented stroma cells, which give it a black colour. The intercellular spaces are small but fairly numerous, and it has not been possible to ascertain whether they are continuous or not. The surface is covered by the same superficial membrane as that seen on the folded part, but in the bridge it rests on a continuous cellular surface formed by the stroma cells. Capillaries are fairly rare and their endothelium is of the common type, without the brush-borders seen in the folded part of the pecten.

The stroma cells are not so extensively ramified as in the folds but often send long processes to the external surface. In addition to pigment granules, large mitochondria and a moderately developed endoplasmic reticulum with ribosomes, the stroma cells contain numerous small, parallel filaments (100 Å thick), plus numerous smooth-surfaced vesicles with ± 500 Å diameter. The bundles of filaments occur regularly in the long processes, but may also be seen in the cell body proper (Pls. VII:2, VIII).

The outer surface of the bridge attaches itself firmly to the vitreous body during dissection, and in electron micrographs the collagen filaments of the vitreus can be seen immediately outside the basement membrane of the surface (Pl. VIII). In light microscopical preparations, stained in Azan, thin strands of blue-staining vitreous substance can be seen penetrating from the surface deep into the tissue of the bridge. This was noted by Kajikawa (1923, p. 320). In electron micrographs these narrow, ramified channels, filled with collagen filaments, are seen throughout the tissue of the bridge. They are surrounded by stroma cells and lined by a basement membrane, and are completely separated from the empty intercellular spaces. At the opening on the surface, the basement membrane is continuous with the membrane on the surface of the bridge, and the collagen is continuous with that of the vitreous body.

No distinct nerve fibres or sensory cells could be identified in the bridge or in the folded part, and although the negative statement has a rather limited value, it can be concluded with safety that there is no appreciable innervation. This negative result, which is also supported by Seaman and Storm (1963), makes it impossible to accept any theories of the pecten being a sensory organ (Franz 1908–1934).

The Nature of the Stroma Cells

Most recent authors agree with Bernd (1905), Mann (1921, 1922, 1924 b) and Lindahl and Jokl (1922 a), who regard the stroma cells as being ectodermal, because the pecten appears to receive contributions from the retina in later embryonic stages. The stroma cells would, then, be a kind of glia cells, but up to now little to support this idea has been gained from morphological studies of the adult pecten.

In the present study two cytological features were revealed which speak in favour of the glial nature of the stroma cells: 1) The way the processes ramify and end with inflated vascular feet on the capillaries in the folded part of the pecten, and 2) The presence of bundles of thin filaments and of numerous small vesicles in the plasm, particularly in the stroma cells of the bridge. Although present in other cell types as well, such vesicles and filaments are typical of the Müller cells in the retina (Fine and Zimmermann 1962, Pedler 1963, Cohen 1963); the filaments also appear to be typical of fibrous astroglia (Luse 1956) and of ependyma (Fleischauer 1958). As, moreover, the stroma cells have no significant features in common with fibrocytes, the glial nature appears to be well supported by their cytological appearance.

Vessels and Nerves of the Orbital Region of the Pigeon

The following notes on the vascular supply and innervation of the orbital region in pigeons are reported here because they form the basis of the operational procedure in the following chapter and are necessary for critical evaluation of the results. In many respects, the vessels and nerves of the pigeon eye agree with those of the sparrow, described in detail by SLONAKER (1918), but the differences are large enough to be of essential importance during the operations.

Methods

Routine examination of vessels was made by different methods of injection. In one series of animals, the arteries of the head were injected from the carotis with starch-vermilion, after the animal had been killed with ether (See WINGSTRAND 1951, p. 15); the head was fixed with 80 % alcohol, formalin and acetic acid (90:5:5), decalcified in nitric acid (conc. acid, 7 parts : water, 93 parts), bleached in 2 % hydrogen peroxide, and cleared over 96 % and absolute alcohol in benzyl benzoate. Another series was, in addition, injected from the v. jugularis with the same starch solution, in which cobalt blue had been substituted for vermilion. Some of these preparations were also used for dissection, and some were cut into smaller pieces or thick sections before being cleared to allow detailed study. A third series of pigeons was injected with Tensol Cement No. 7 (Imp. Chem. Indust. Ltd.). The injection took place from the carotis. First, a thin plastic solution stained with Sudan III was injected until the entire vascular system was filled, followed by plastic with vermilion and cobalt blue, which filled the arteries and could not pass the capillaries. After polymerization, the soft parts of the head were removed with hypochlorite (BUGGE 1963), which left the skeleton intact, or with strong hydrochloric acid, which left the plastic clean. Additional information was drawn from some series of celloidin sections through the head of pigeons, injected from the carotis with starch-vermilion or India ink-gelatine.

The Vascular System of the Pecten

As shown already by ANDRE and BEAUREGARD (1874), BEAUREGARD (1876), and DENISSENKO (1881), the vascular bed of the pecten is almost completely isolated from the vessels of the surrounding parts. In the authors' preparations of pigeons, injected with plastic or India ink, there were no vessels connecting the base of the pecten with the choriocapillaris. One or a few small capillaries were usually seen to connect the innermost end of the pecten with the capillary net in the optic nerve. As the pigeon, like other birds, has neither hyaloid nor intra-retinal vessels, the plastic casts of the vascular beds show the pecten vessels entering through a clean opening in the choriocapillaris, through which the optic nerve entered. It thus appeared possible to eliminate the pecten experimentally by blocking its arteries and veins.

Arterial System of the Orbital Region

(Figs. 2–8, Pls. II–III)

1. The *a. ethmoidalis* (Figs. 2, 4) is a branch of the ramus anterior of the carotis cerebralis. It leaves the brain cavity and enters the orbit through a foramen just above the foramen opticum (cf. HOFMANN 1900, HAFFERL 1933, CORNELIAC 1935,

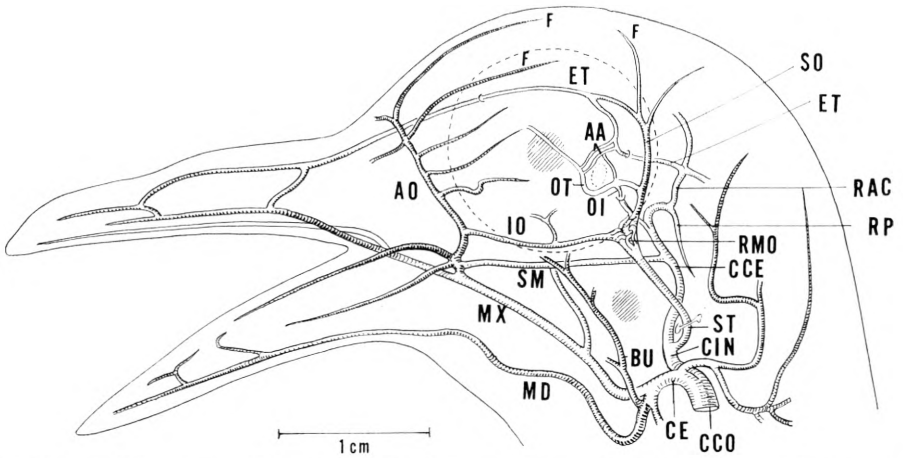


Fig. 2. The arterial system of the pigeon's head, drawn from a cleared specimen, injected with starch-vermilion. — AA = anastomotic arteries in front of the optic nerve, AO = a. antorbitalis, BU = a. buccalis, CCE = a. carotis cerebralis, CCO = a. carotis communis, CE = "a. carotis externa", CIN = a. carotis interna, ET = a. ethmoidalis, F = arteries to frontal skin, IO = a. infraorbitalis, MD = a. mandibularis, MX = a. maxillaris, OI = a. ophthalmica interna, OT = a. ophthalmo-temporalis, RAC = ramus anterior of the carotis cerebralis, RP = ramus posterior of carotis cerebralis, RMO = rete mirabile ophthalmicum, SM = a. spheno-maxillaris, SO = a. supraorbitalis, ST = a. stapedia.

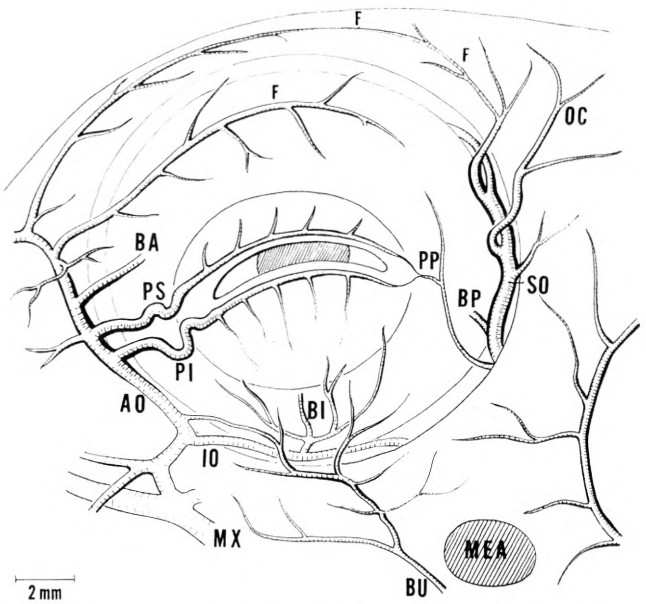


Fig. 3. Superficial arteries of the eye region of a pigeon, drawn from a cleared specimen injected with starch-vermilion. — AO = a. antorbitalis, BA, BI and BP = bulbar arteries from the antorbital, the infraorbital, and the postorbital arteries, resp., BU = a. buccalis, F = arteries to the frontal skin, IO = a. infraorbitalis, MEA = meatus acusticus externus, MX = a. maxillaris, OC = arteries to the skin behind the eyes, PI and PS = inferior and superior palpebral arteries coming from the antorbital, PP = palpebral artery coming from the supraorbital, SO = a. supraorbitalis.

Wingstrand 1951). The artery passes forwards along the interorbital septum above the optic nerve to the rostro-medial corner of the orbit, where it fuses with the ramus supra-orbitalis of the a. stapedia and passes into the upper beak near the median plane. It is connected with the ramus ophthalmo-temporalis of the a. stapedia by one or, what is more usual, two arteries in front of and one behind the optic nerve. The main branches of the a. ethmoidalis are arteries to the m. rectus superior, the m. quadratus, and the m. obliquus superior. The a. ethmoidalis was called a. ophthalmica interna by Slonaker (1918), but since a true a. ophthalmica interna does exist, there is no reason to use this name.

2. The *a. maxillaris*, when passing forwards under the orbit, emits a branch, which the present authors call *a. antorbitalis* (Figs. 2–5). This branch passes medial to the jugal arch into the orbit. It follows the anterior margin up to the "lacrymal" (prefontal) bone, which it passes on the posterior side. At the dorsal margin of the lacrymal it leaves the orbit and sends branches to the skin above and in front of the eye. When passing medial to the jugal, it anastomoses with the infra-orbital branch of the a. stapedia and, sometimes, with the small buccal artery described below. In some specimens, the antorbital artery is fed exclusively by the a. maxillaris, in others, by the a. infra-orbitalis, but it is always present and emits the following branches: a) two arteries to the lower beak, b) an a. palpebralis inf. to the lower eyelid, c) an a. palpebralis sup. to the upper eyelid, d) an artery to the dorsal part of the anterior eye segment, and e) skin branches, two of which usually pass backwards to the skin above the orbit, the lateral one following a course lateral to the superior margin of the orbit (Figs. 3, 5).

3. The "*a. buccalis*" is a small artery coming from the carotis externa near the point of division into the a. maxillaris and a. mandibularis (Figs. 2–3). The artery passes out to the skin in front of the meatus acusticus externus and below the lower eyelid. It may communicate with the antorbital artery in some specimens (see above).

4. The small *a. ophthalmica interna* s. str. leaves the carotis cerebralis near the intercarotic anastomosis on each side of the pituitary, passes forwards in the sella turcica and enters the orbit together with a small v. ophthalmica interna below the optic foramen (Fig. 2). The artery joins the a. ophthalmo-temporalis below the optic nerve or connects with the post-optic anastomotic artery (Fig. 8).

5. The *a. stapedia* (Hafferl 1921), syn. a. ophthalmica externa (Slonaker 1918) is emitted from the carotis interna in the quadrate region, passes through a canal in the cranial base behind the stapes and emerges through a foramen in the postero-ventral wall of the orbit, where a large rete mirabile temporale (ophthalmicum) is formed by this artery and the corresponding veins (Fig. 2). The three main arteries emitted from this rete are:

a) The *a. supraorbitalis*, which passes dorso-lateral to the posterior margin of the orbit (Figs. 3–5). From here, it turns more medially and passes over the dorsal surface of the bulb to fuse with the a. ethmoidalis. The a. supraorbitalis emits branches from behind into the lower and upper eyelid; one branch goes to the temporal sector of the anterior bulb segment, and two or more branches pass out to the skin behind

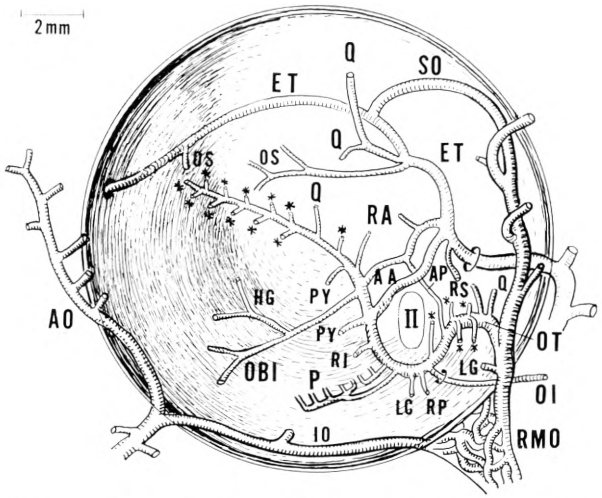


Fig. 4. Deep arteries of the orbit of the pigeon, seen in the orbit after removal of the bulb. Drawing combined from studies of plastic casts, cleared and injected specimens, and from dissection of injected specimens. — AA = anastomotic arteries in front of the optic nerve, AO = a. antorbitalis, AP = anastomotic artery behind the optic nerve, ET = a. ethmoidalis, HG = arteries to Harderian gland, IO = a. infraorbitalis, LC = a. ciliaris longa, LG = artery to lacrymal gland, OBI = artery to m. obliquus inferior, OI = a. ophthalmica interna, OS = arteries to m. obliquus superior, OT = a. ophthalmo-temporalis, P = pecten arteries, PY = arteries to m. pyriformis, Q = arteries to m. quadratus, RA, RI, RP, RS = arteries to mm. recti (anterior, inferior, posterior, and superior, resp.), RMO = rete mirabile ophthalmicum, SO = a. supraorbitalis: "II" marks the entrance of the optic nerve, and the asterisks* mark the short posterior ciliary arteries.

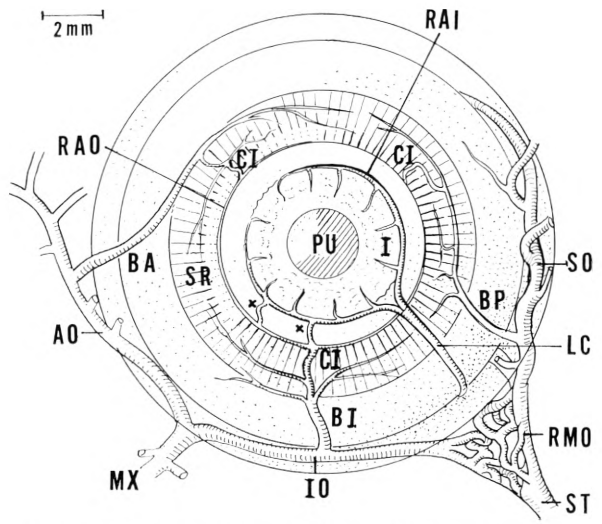


Fig. 5. Arteries of the anterior bulb segment in the pigeon. Combined as fig. 4. — AO = a. antorbitalis, BA, BI, and BP = arteries to the anterior surface of the bulb from the antorbital, the infraorbital, and the supraorbital artery, resp., CI = anterior ciliary arteries, passing round the edge of the ossicular ring, I = iris, IO = a. infraorbitalis, LC = a. ciliaris longa, MX = a. maxillaris, PU = pupilla, RAI = ring artery of iris, RAO = ring artery on the inner side of ossicular ring, RMO = rete mirabile ophthalmicum, SO = a. supraorbitalis, SR = ossicular ring, ST = a. stapedia.
The asterisks* mark arteries, crossing over to the iris in the ligamentum pectinatum.

and above the orbit. These skin branches are usually smaller than those from the antorbital artery.

b) The *a. infraorbitalis* passes forwards from the rete temporale along the bottom of the orbit and fuses with the above-mentioned branch of the a. maxillaris to form the a. antorbitalis (Figs. 2–5). In some specimens it is smaller, and fails to contribute to the a. antorbitalis. On its way it emits two or three smaller branches to the ventral sector of the anterior bulb segment and to the conjunctiva under the lower lid. One or two of these branches are the source of anterior ciliary arteries, whereas one or two additional anterior ciliary arteries are emitted from the branches of the antorbital and supraorbital arteries.

c) The *a. ophthalmo-temporalis* (SLONAKER 1918) is the main artery of the posterior bulb segment and supplies most of the eye muscles and the glands of the orbit (Figs. 2, 4, 6–8). After leaving the rete temporale, the artery passes along the wall of the orbit, making a loop below the optic nerve. From the optic nerve onwards it is attached to the horizontal meridian of the eye, emitting short posterior ciliary arteries to the choriocapillaris. The a. ophthalmo-temporalis anastomoses with the a. ophthalmica interna just below the optic nerve and is connected with the a. ethmoidalis by two or three anastomotic arteries, one of which runs behind the optic nerve, whereas the others run in front of it. Above the nerve the vessels often fuse into two before joining the a. ethmoidalis. In this way, the entrance of the optic nerve into the orbit is surrounded by an arterial ring which often consists of several vessels and is more or less plexus-like (Figs. 6–8, Pl. V:2).

The post-optic part of the a. ophthalmo-temporalis emits arteries to the m. rectus superior, m. quadratus, and 4–5 short posterior ciliary arteries to the bulb (Fig. 4). The m. rectus superior may also receive an artery from the a. ethmoidalis. The infra-optic loop of the a. ophthalmo-temporalis emits branches to the m. rectus posterior and m. r. inferior, and, in addition, the long ciliary artery and 2–3 aa. pectines to the pecten. The pre-optic part of the artery supplies the m. pyriformis, m. obliquus inferior and the Harderian gland, and emits smaller arteries to m. quadratus and m. rectus anterior. The latter muscle also receives an artery from the anastomotic vessel in front of the optic nerve. In addition, the pre-optic part of the a. ophthalmo-temporalis emits about 13 short ciliary arteries, which may branch one or a few times before entering the bulb at approximately the horizontal meridian.

Details of the Arterial Supply of the Bulb Proper

(Figs. 4–8)

In an operation of the kind described in the following pages, it is essential that the pecten arteries should be completely blocked, but it is also essential that vital arteries to other parts of the bulb are not damaged in any way liable to impair the results. For this reason, the vessels of the bulb proper are considered in detail.

The pecten arteries, 2, 3, or even 4 in number, are emitted from the infra-optic

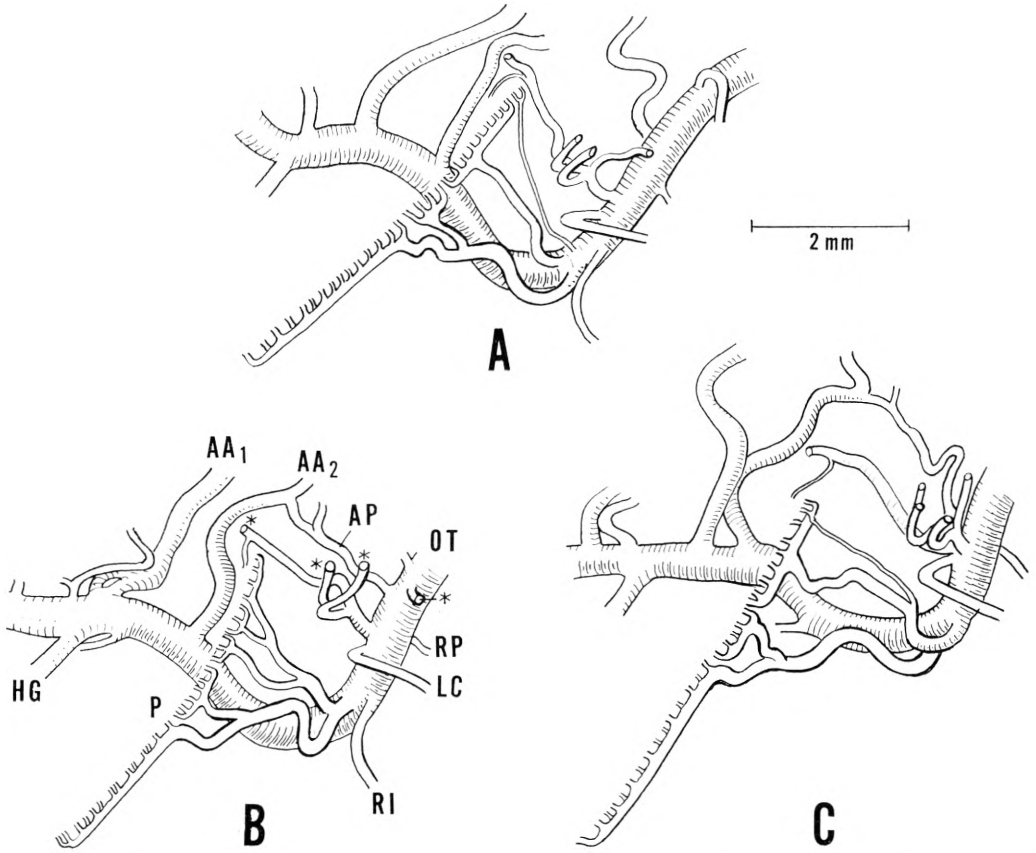


Fig. 6. Variations of the arteries around the entrance of the optic nerve. All figures based on photographs of the orbital bottom in cleared specimens, injected with starch-vermilion, after removal of anterior eye segment. — AA^1 and AA^2 = anastomotic arteries in front of the optic nerve, AP = anastomotic artery behind the nerve, HG = artery to m. obliquus inferior and Harderian gland, LC = a. ciliaris longa, OT = a. ophthalmo-temporalis, P = pecten arteries, RI = artery to m. rectus inferior, RP = artery to m. rectus posterior. The asterisks * mark the short ciliary arteries. The anterior (left) artery often sends a small vessel to the pecten.

loop of the a. ophthalmo-temporalis (Figs. 4, 6–8, Pl. V:2). In the pigeon they do not form a rete mirabile pectinis (cf. Barkow 1829, 1830). They pass along the ventral side of the optic nerve to the bulb and enter it through the elongate, cleft-like opening of the sclera, where the nerve itself enters. Two or three large arteries enter along the posterior aspect of the nerve, but there is a small and variable artery which passes down on the rostral aspect of the nerve. The latter vessel is usually a branch of one of the short ciliary arteries (Fig. 6), but in one pigeon it was emitted by the artery of the pyriform muscle (Fig. 8). Many attempts to eliminate the pecten surgically failed bacause this small anterior artery had been left intact. Although small, it is large enough to prevent degeneration of the pecten even after cautherization of all other pecten arteries.

The short posterior ciliary arteries, about 18 in number, are emitted by the a. ophthalmo-temporalis. They often branch a few times before entering through the foramina in the scleral cartilage. They supply the choriocapillaris and are, therefore, of vital importance for the retina, particularly as adult birds lack intra-retinal and hyaloid vessels. Fortunately, as these short arteries are situated far from the exposed area of the bulb, they are never in danger during the operations. In theory, the a. ophthalmo-temporalis could be severed, as it passes across the field of operation below the optic nerve. Such accidents are easily discovered, however, because of the uncontrollable bleeding which follows, and because, with the technique used, the pulsations of the artery can be directly checked in the wound. Moreover, the anastomotic arteries in front of the optic nerve will secure the supply of the retina, if accidental blocking of the ophthalmo-temporal artery below the optic nerve should pass unnoticed (Fig. 4).

The supply of the anterior eye segment. The antorbital, infraorbital, and supraorbital arteries emit branches which supply the superficial parts of the anterior eye segment, including the 2–3 anterior ciliary arteries (Figs. 3, 5). The ciliary artery from the infraorbital vessel is the largest, and is present in all investigated specimens. These anterior ciliary arteries pass around the inner margin of the ring of scleral ossicles and enter a ring artery, situated on the inner side of the ossicles, parallel with the canal of Schlemm. One or two rather important arteries branch off from this ring and cross the ligamentum pectinatum to the iris, where they enter a large ring artery in the peripheral part of the stroma iridis (Fig. 5). This annular iris artery also receives the long ciliary artery. The latter leaves the a. ophthalmo-temporalis just behind the pecten arteries, enters the bulb along the postero-ventral aspect of the optic nerve together with the long ciliary nerve, and passes out to the iris in the choroid coat without emitting any branches on the way (Fig. 8).

The annular artery of the iris supplies the abundant capillary plexus of the stroma and sends radial vessels out to the ciliary folds and processes. As the ciliary body is known to be of essential importance in maintaining intraocular pressure, its blood supply via the ring artery of the iris requires particular attention during the operation. One of the affluents to this arterial ring, viz., the long ciliary artery, is often damaged when the pecten vessels are blocked. It is possible, though difficult, to save the long ciliary artery, but in most experiments no attempt was made to keep it intact. The reason for this was that the cutting of this artery in control experiments did not cause damage to the retina or other essential intraocular structures, except for immobilization of the iris caused by the simultaneous cutting of the long ciliary nerve. Obviously, the anterior ciliary arteries and the extensive communications between the ciliary folds and the choriocapillaris are enough to secure sufficient circulation in the region. To ensure that the iris circulation was in order, the iris in pigeons which had been operated upon, was viewed through a dissection microscope. In this way the capillary tufts, which protrude into the anterior eye chamber from the corneal surface of the iris, can be studied in detail through the transparent cornea.

Fig.7

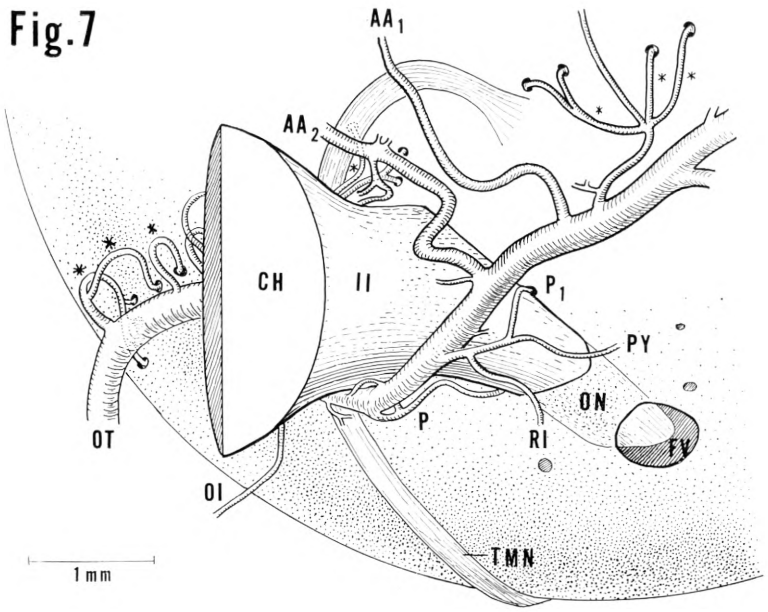
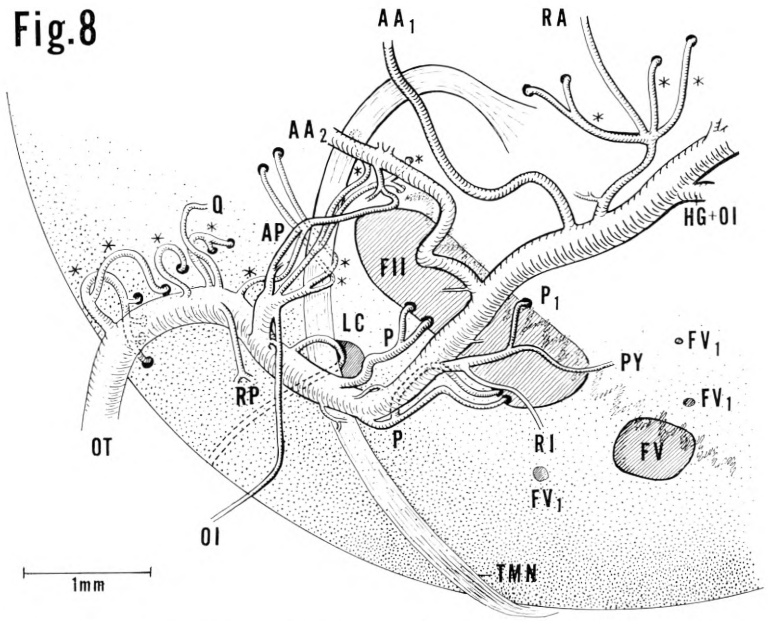


Fig.8



Figs. 7 and 8. The arteries around the entrance of the optic nerve into the left bulb of a pigeon, viewed from the median plane. Anterior direction right. The stippled area is the scleral cartilage, the openings of which are darkly shaded. The zig-zag shadow in fig. 8 is the projection of the base of the pecten. The optic nerve is removed in fig. 8 to show details. Graphic reconstruction from celloidin sections. — AA_1, AA_2 and AP = anastomotic arteries in front of and behind the optic nerve, resp., CH = median section through chiasma, FV = foramen of the ventral posterior ciliary vein and pecten vein, FV_1 = foramina for small veins, F II = foramen for the optic nerve, HG + OI = artery to Harderian gland and m. obliquus inferior, LC = a. ciliaris longa, OI = a. ophthalmica interna, ON = optic nerve extension below the scleral cartilage, OT = a. ophthalmo-temporalis, P = pecten arteries, P_1 = exceptional pecten artery entering in front of the nerve, PY = artery to m. pyriformis, Q = artery to m. quadratus, RA, RI and RP = arteries to mm. recti (anterior, inferior and posterior, resp.), TMN = tendon of the membrana nictitans.
II = nervus opticus. The asterisks* mark the short posterior ciliary arteries.

The Venous System of the Orbit and Eye

(Figs. 9–11)

Because of the extensive anastomoses in the venous system of the orbit of birds, complications in the drainage of the eye are not anticipated if the operation is performed carefully. The veins are therefore dealt with in a more cursory manner, and for more details the reader is referred to the diagrams (Figs. 9–11). However, the orbital veins of the pigeon differ so much from those of the sparrow (SLONAKER 1918), the turkey, and the duck (NEUGEBAUER 1845), that a few comments are necessary.

A. *The inner parts of the orbit* are drained by three main outlets: the v. ophthalmica, the rete mirabile temporale (ophthalmicum), and the sinus cavernosus.

1. The *v. ophthalmica* branches off from the v. facialis interna (NEUGEBAUER 1845) at a point where this vein runs above the pterygoid, behind the palatinum and lateral to the rostrum sphenoidale. The vena ophthalmica follows the medial wall of the orbit upwards, forms the anterior part of the venous ring around the optic nerve and continues upwards to the point where the anterior end of the hemisphere is in contact with the orbital wall (Figs. 9, 10). Here it pierces the bone and communicates with the annulus venosus cerebri antiquus (NEUGEBAUER 1845), which is a venous sinus around the olfactory lobes.

2. *The rete mirabile venosum temporale* (ophthalmicum) is interdigitated with the rete mirabile arteriosum temporale in the postero-ventral part of the orbit (Figs. 9–11). It is drained by two veins: a laterally situated one which follows the a. stapedia to the v. facialis externa, and a more medial one, which independently passes through the bone to the v. facialis interna (Fig. 9). The rete receives three veins, which follow the branches of the a. stapedia and are named like the arteries:

V. supraorbitalis (v. temporalis, NEUGEBAUER 1845) follows the a. supraorbitalis over the bulb and ends in an anastomosis with the v. ophthalmica at the point where this vein pierces the orbital wall (Figs. 10, 11, Pl. II).

V. infraorbitalis passes below the bulb along the a. infraorbitalis to the rostro-ventral margin of the orbit, where it communicates with the v. maxillaris (Figs. 10, 11, Pl. III).

V. ophthalmo-temporalis, which is a large vein, following the a. ophthalmo-temporalis from the rete to the optic nerve (Fig. 11, Pl. III). Here it turns dorsally and forms the dorsal part of the venous ring around the nerve before joining the v. ophthalmica. The ventral part of the ring around the optic nerve is formed by rather small vessels.

3. *The sinus cavernosus* around the pituitary in the sella turcica communicates with the venous ring around the optic nerve by several vessels, of which the "v. nervi III" (WINGSTRAND 1951) is particularly large in the pigeon. The sinus cavernosus is drained by the "v. carotis" which follows the carotis cerebralis through the bone to its junction with the v. facialis externa in the quadrate region.

B. *The veins of the anterior eye segment and the eyelids* (Fig. 10). The drainage of eyelids, anterior eye segment, and surrounding structures is effected by the v.

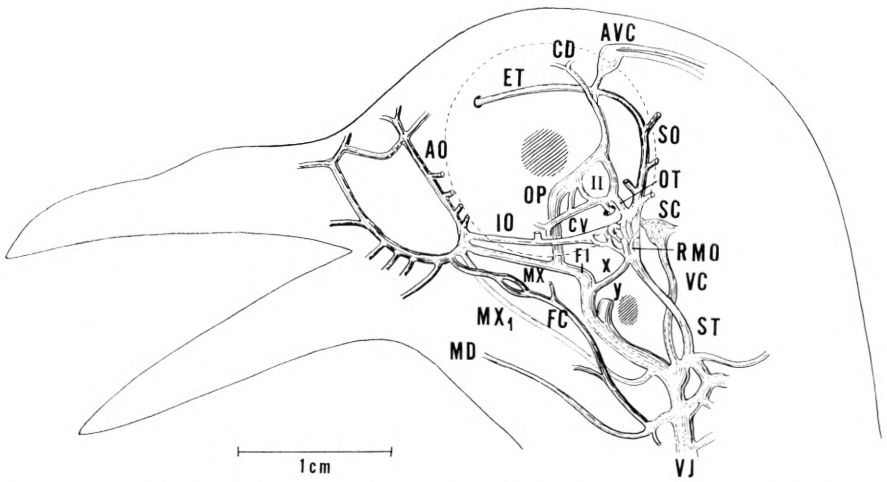


Fig. 9. Main veins of the head of a pigeon. Diagram combined from dissection of injected specimens, cleared specimens, and plastic casts. — AO = vena antorbitalis, AVC = annulus venosus cerebri antiquus (NEUGEBAUER), CD and CV = dorsal and ventral posterior ciliary vein, resp., ET = v. ethmoidalis, FC = v. facialis cutanea, FI = v. facialis interna, IO = v. infraorbitalis, MD = v. mandibularis, MX = v. maxillaris, MX_1 = vein along the a. maxillaris, OP = v. ophthalmica, OT = v. ophthalmo-temporalis, SC = sinus cavernosus, SO = v. supraorbitalis, ST = v. stapedia, VJ = v. jugularis, X = vein from the rete mirabile ophthalmicum to v. facialis interna, Y = transverse anastomosis of the jugular vein.
II = entrance of optic nerve into the orbit.

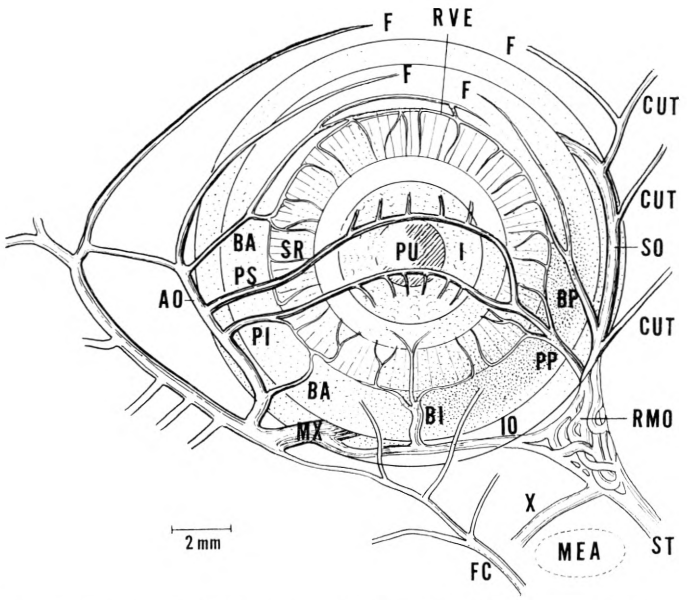


Fig. 10. Veins of anterior bulb segment and superficial parts of eye. Technique as fig. 9. — AO = v. antorbitalis, BA, BI and BP = veins from the anterior bulbar surface to antorbital, infraorbital and supraorbital veins, resp., CUT = veins from the skin behind the eye, F = veins from frontal skin, FC = v. facialis cutanea, I = iris, IO = v. infraorbitalis, MEA = meatus acusticus externus, MX = v. maxillaris, PS, PI, and PP = superior, inferior and posterior palpebral veins, PU = pupilla, RMO = rete mirabile ophthalmicum, RVE = external ring vein of limbus, SO = v. supraorbitalis, ST = v. stapedia, SR = ossicular ring with numerous small anterior ciliary veins passing around the inner margin, X = vein from rete mirabile ophthalmicum to v. facialis interna.

infraorbitalis, the v. supraorbitalis, the v. maxillaris, and the v. facialis cutanea (NEUGEBAUER 1845). The two first-mentioned are described above and their branches follow closely those of the corresponding arteries. The *v. maxillaris* is the direct forward continuation of the v. facialis interna, from the point where the v. ophthalmica branches off (Fig. 9, P. III). When passing forwards under the orbit, this vein turns laterally, emits a small suprapalatine branch, passes under the rostral end of the jugal arch to a superficial position at the rostro-ventral corner of the orbit, and ends with several branches in the upper and lower beak. One of these branches runs in front of the orbit and supplies approximately the same parts as the antorbital artery (v. antorbitalis, Figs. 9–11). When the maxillary vein emerges under the jugal arch it communicates with three main veins: the v. infraorbitalis, the v. cutanea facialis, and a vein which follows along the a. maxillaris.

The *v. cutanea facialis* (NEUGEBAUER 1845) is a branch of the v. mandibularis. It passes upwards in front of the ear opening just under the skin, and turns rostrally under the orbit to fuse with the v. maxillaris (Fig. 9).

The anterior ciliary veins are branches of the antorbital, supraorbital, and infraorbital veins, which, like the arteries, also supply the eyelids, the conjunctiva, and the surrounding skin. The anterior ciliary veins are very numerous and pass round the inner margin of the ossicular ring (Fig. 10). They drain the ciliary muscle and the canal of Schlemm. The ciliary folds and the iris are probably drained into the large marginal veins of the ora serrata as connections between the iris veins and the anterior ciliary veins are very small and few.

C. *Veins of importance for the operation.* The drainage of the anterior eye segment cannot be seriously interfered with during the operation. Nor is it necessary to consider in detail the drainage of the eye muscles and glands, which is effected by the extensively anastomozing veins of the orbit (Fig. 11). However, the drainage of the posterior bulb segment with the choriocapillaris and the pecten appears to be more critical, and will therefore be considered separately.

The choriocapillaris is fed by the short posterior ciliary arteries which enter along the horizontal meridian. The drainage takes place through a dorsal and a ventral posterior ciliary vein. The dorsal vein is a branch of the upper part of the v. ophthalmica, whereas the ventral vein bifurcates after leaving the bulb and connects both with the v. ophthalmica and with the venous ring below the optic nerve in somewhat variable ways (Fig. 11). The dorsal vein enters the bulb through a foramen in the scleral cartilage, about half-way between the fundus and the dorsal equator. It passes through the choroid coat to the ora serrata, where it bifurcates into two arms which continue to each side in the large marginal ring sinus of the ora. The ventral vein enters the bulb at the level of the outer part of the pecten, bifurcates early, and the two rami pass out to the ora and continue as the marginal ring sinus (Seen in pl. III). At its entrance into the bulb it receives the veins from the pecten. On their way out to the ora, both the dorsal and the ventral ciliary veins receive numerous small vessels from the cho-

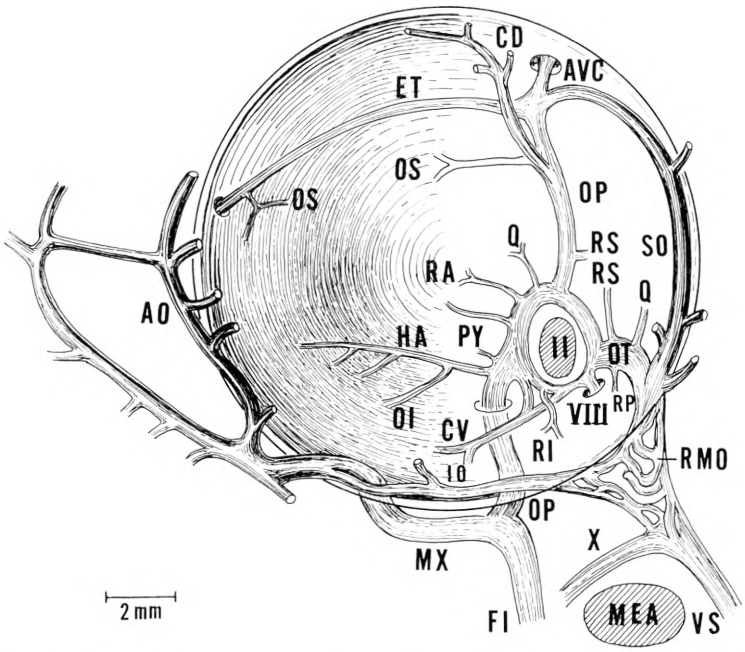


Fig. 11. Veins of the bottom of the orbit, seen from a lateral direction after the bulb had been removed. From plastic casts and dissections of injected specimens. — AO = v. antorbitalis, AVC = anastomosis to the annulus venosus cerebri antiquus (NEUGEBAUER), CD and CV = dorsal and ventral posterior ciliary veins, ET = v. ethmoidalis, FI = v. facialis interna, HA = vein from Harderian gland, IO = v. infraorbitalis, MEA = meatus acusticus externus, MX = v. maxillaris, OI = vein from m. obliquus inferior, OP = v. ophthalmica, OS = vein from m. obliquus superior, OT = v. ophthalmo-temporalis, Q = veins from m. quadratus, RA, RI, RP and RS = veins from mm. recti (anterior, inferior, posterior, and superior, resp.), RMO = rete mirabile ophthalmicum, SO = v. supraorbitalis, VS = v. stapedia, V III = v. nervi III from sinus cavernosus, X = vein from rete mirabile ophthalmicum to v. facialis interna.
II = entrance of n. opticus.

riocapillaris. Other veins from the choriocapillaris connect with the ring sinus along the ora, and are thus indirectly drained by the posterior ciliary veins. The ring sinus also receives radial veins from the ciliary folds and processes.

The operational procedure introduced in the present paper includes blocking of the ventral ciliary vein at the point where this emerges from the bulb at the level of the outer part of the pecten (Figs. 7, 8). This is necessary because its extra-bulbar parts cover the pecten arteries. At the same time, the veins of the pecten are blocked, as they connect with the ciliary vein at its emergence from the bulb. This blocking of the ventral ciliary vein does not appear to cause any severe disturbance of the choroidal circulation, probably because the extensive anastomoses via the ring sinus of the ora offer abundant possibilities for the blood to escape. This is shown by the fact that the blocking of the vein alone, in numerous controls, had no significant effect on the retina, as long as one or more of the pecten arteries were left intact.

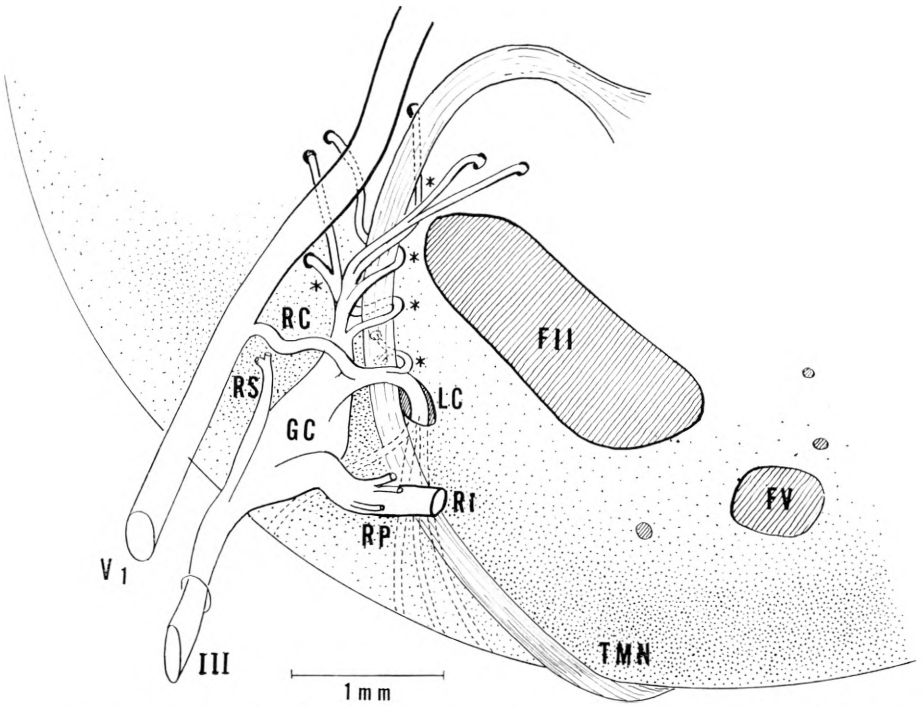


Fig. 12. Nerves of the left bulb in the pigeon, seen from the median plane. Anterior direction right. Compare fig. 7 and 8. Graphic reconstruction from celloidin sections. — FV = scleral foramen for ventral posterior ciliary vein and pecten vein, F II = foramen for the optic nerve, GC = ganglion ciliare, LC = n. ciliaris longus, RC = n. ciliaris longus, perhaps including radix longa, RS = ramus superior III, RP = nerves to the m. rectus posterior, RI = ramus inferior III, TMN = tendon of the membrana nictitans. III = n. oculomotorius, V_1 = ramus profundus of n. trigeminus, The asterisks* mark the short ciliary nerves.

The Nerves of the Orbital Region

The nerves of the orbit of the pigeon do not differ very much from those of the sparrow, which were excellently described by SLONAKER (1918). As, moreover, only few nerves need to be safeguarded during surgery, this part of the anatomy is dealt with briefly.

As the branches of the n. trigeminus present in the orbit either pass further to the upper beak or are concerned with the sensorial innervation of eyelids and skin, they are of little interest in the present case. Of these nerves, the ramus infraorbitalis of the n. maxillaris may be damaged in some cases, as it passes across the field of operation together with the a. and v. infraorbitalis, but for the said reasons this cannot interfere with results obtained in the bulb.

Most nerves to eye muscles and glands are never approached. Only the oculomotorius branch to the m. rectus inferior, m. rectus anterior, m. obliquus inferior and the Harderian gland can be damaged in some cases, but this nerve has no connection with the bulb proper (Fig. 12).

The innervation of the bulb proper is effected by the long and short ciliary nerves (Fig. 12). The short ciliary nerves originate in the ciliary ganglion, which is attached to the posterior side of the optic nerve. The ganglion appears to receive a radix longa from the n. profundus V, but in microscopical sections the nerve fibres can be followed as a distinct bundle along the surface of the ganglion into the long ciliary nerve, as shown in fig. 12. The branch from the m. profundus is, therefore, a n. ciliaris longus, perhaps including a. radix longa. The short ciliary nerves, about 8 in number, are emitted from the dorsal pole of the ciliary ganglion. They follow the sheaths of the optic nerve to the bulb, where they enter through separate foramina in the scleral cartilage in the region dorsal, or dorso-caudal to the opticus (Fig. 12). In the specimen, reconstructed in fig. 12, one of the short ciliary nerves appears to follow the long ciliary nerve before entering the bulb close to this nerve. The short ciliary nerve in question may be cut together with the long ciliary nerve in operations, but the other nerves and the ciliary ganglion are not in the zone of danger.

The long ciliary nerve follows the long ciliary artery into the bulb just behind the pecten arteries. Inside the choroid coat it divides into 4–6 separate branches, which pass straight out to the iris and ciliary body. Being situated near the pecten arteries, the long ciliary nerve can be damaged during the operation, when the pecten arteries are cautherized. Possible damage to this nerve cannot interfere with the experiments, however, for the cutting of this nerve in numerous control experiments did not cause any visible changes in the eye beyond immobilization of the iris.

Comparison between the Pecten and the Ciliary Body

Originally, the present work was intended to illuminate functional similarities between the pecten and the ciliary body and was inspired by the experiments of Abelsdorff and Wessely (1909). These authors showed that the ciliary body secretes intraocular fluid, and as the pecten was said to hypertrophy after extirpation of the ciliary body, there was some reason to believe that it has a similar function. It was hoped that the histological and histochemical properties of the two organs would indicate whether they could have the same function or not.

In some preliminary histological and histochemical studies, the pecten was compared with the ciliary body and with the anterior, vascular surface of the iris. Certain features were common to all three organs: a rich vascularization, strongly PAS-positive perivascular membranes, presence of alcaline phosphatase. Alcaline phosphatase was shown to be abundant in the pecten and the iris, whereas the large amount of pigment made quantitative estimates difficult in the ciliary body.

Tanaka (1960), and Seaman and Storm (1963), simultaneously studied the organs in electron microscope and found the remarkable, brush-border-like cellular membranes of the endothelial cells in the pecten. This was compared with the folded cell membranes found in the epithelium of the ciliary folds. Moreover, Seaman and Storm

(1963) and SEAMAN and HIMELFARB (1963) showed that the drug Diamox caused similar changes in the cell membranes in both organs, and that these changes in structure were simultaneous with a fall of intra-ocular pressure. The pressure change could, of course, depend on interference with one or both of these organs.

It soon became evident, however, that simple comparison of the two organs was not a promising way of approaching the functional problem, as the structural similarities were found to be too little specific (cf. pp. 12–13), and a primitive experiment revealed a distinct functional difference.

This experiment was arranged to check whether the pecten becomes permeable to large molecules when the pressure in the bulb is decreased by corneal puncture. ABELSDORFF and WESSELY (1909) had shown that this is a typical feature of the ciliary body. Four pigeons received 4 subcutaneous injections of 3 ml 0.5 % trypan blue with 48 hour intervals. After this treatment, the blood and the urine were distinctly blue-stained, but no trypan blue could be seen ophthalmoscopically in the vitreous body or the camera anterior. This is in accordance with experience in the case of mammals, in which the ciliary body of the normal eye is impermeable to trypan blue. Repeated puncture of the cornea some hours after the last injection resulted in strong blue-staining in the camera anterior and posterior. This was evidently due to leakage through the ciliary body and, perhaps, through the capillary tufts of the iris surface. No staining was seen in the vitreous body or around the pecten, a result confirmed by subsequent fixation and sectioning of the specimens. The pecten thus remains impermeable to the dye, whereas the ciliary body becomes permeable when the pressure is decreased in the bulb.

As the functional properties of the pecten and the ciliary body could be shown to be different, it appeared futile to argue in favour of identity by means of structural comparison.

Operative Elimination of the Pecten by Coagulation of Its Vessels

As the function of the pecten could not be revealed with certainty by histochemical and histological investigations, a more direct experimental approach to the problem had to be found. In many analogous cases, operative elimination of the organ provided valuable information. If such an operation could be performed in the case of the pecten without damage to other relevant structures, the function would, probably, be revealed by the post-operative symptoms.

ABELSDORFF and WESSELY (1909) tried surgical extirpation of the pecten, but since the optic nerve and, probably, the vascular supply of the choroid had been destroyed, the experiments were not very informative. KAUTH and SOMMER (1953) cautherized the pecten, but do not describe the method or the results in detail. The present authors attempted a similar method in collaboration with Dr. E. GREGERSEN, Rigshospitalet, Copenhagen. The light beam from a photo-coagulator, used for coagulation in the human eye, was concentrated on the pecten of an anaesthetized pigeon.

Although maximal effect was used, no damage was inflicted on the pecten, probably because the heat of the beam was transported away by the blood of this extraordinarily vascular organ. In contrast, the retina was easily damaged by the light beam. It was realized that coagulation of the pecten would require so much heat that damage to surrounding parts by heat-spreading would be unavoidable. This would ruin the experiments, particularly as heat coagulation by any method would damage the optic nerve head, to which the pecten is attached.

The anatomical analysis of the vessels, briefly summarized in the preceding chapters, gave some hope that coagulation of the pecten vessels at their entrance into the bulb would lead to degeneration of the organ. This finally led to the method employed.

Methods

Operations on domestic pigeons were undertaken on a table covered with plastic which allowed for easy cleaning and firm adherence of plaster tape. Holes were bored for the strings which were to fix wings and legs.

The pigeons (common domestic breed) were placed on the back with wings spread, and fixed by a string between the primaries and secondaries. The wing tips were fixed onto the table by plaster tape, and the legs were held in position by strings. During the whole operation the body of the pigeon was covered with cotton wool to avoid heat loss.

The pigeons were anaesthetized with 6 % nembutal in 0.7 % NaCl, injected into the vena basilica (Neugebauer 1845) at the point where this runs over the volar side of the elbow joint. The vein is particularly distinct after the skin has been washed with ether. 0.15 ml was given as an introductory dose, and this was slowly increased by 0.02 ml at a time until the animal was completely relaxed. The syringe was fixed with plaster tape to the table with the needle in situ, so that additional injections could be performed without delay. The final dose, necessary for preventing twitches in the neck musculature during operations in the eye region, was between 0.18 and 0.25 ml for normal-sized pigeons.

A glass tube was introduced into the mouth and fixed by plaster tape around the beak. This secured free respiration and facilitated the fixing of the head to the table. The head was turned with the left side up, and attached to the table by plaster tape over the occipital region and the tube (Pl. IX:1).

The area around the eye was washed with 70 % alcohol, and the feathers above and below the eye were carefully cut to avoid contamination. It was not possible to perform an aseptic operation, but the wound was rarely infected, probably because the pigeons were treated prophylactically with penicillin.

The operation was performed under a Zeiss binocular operation microscope with illumination through the objective lens. The magnification was varied between 15 and 50 times. An ordinary dissection microscope and a separate spot-light were used in the first experiments but did not operate well, as the incision is deep and narrow.

In the operation proper, the wound was held open with small metal hooks made of fairly large insect needles with a bent tip (Pl. IX:2–3). The needles were connected by a string to a lead load (10–50 g), which was left hanging over the margin of the table and secured a constant pull in the hook. After the first incision had been made, the bulb was pulled dorsally by a broad hook, made by bending a 8 mm metal strip, and connected with a 45 g lead load (Pl. IX:5). During the operation, bleeding must be avoided as much as possible, as even small vessels can fill the narrow wound with blood in a short time. When this occurs, it is very difficult to drain the wound and stop the vessel under the particular conditions of control required by a critical experiment. Therefore, all visible vessels which had to be cut, were first coagulated with a small platinum loop. This was made of 0.15 mm platinum wire, bent to a sharp point, which could be introduced into the narrow wound without touching the walls. The loop was heated to dark red by a controllable current and was applied slowly, so that the vessels were coagulated and not opened.

The operation was performed by the following steps and took about 1.5 to 2 hours. In some cases individual variation made it impossible to block the pecten vessels without extensive bleeding or damage to larger vessels. Such specimens had to be discarded.

1. As the eye fits firmly into the orbit, a piece of the supraorbital crest of the frontal bone must be cut loose to allow the slight upward dislocation of the bulb which is necessary for operations taking place along the bottom of the orbit. The skin incision is made along the edge of the supraorbital crest between the two parallel skin arteries over the eye (Fig. 3). After exposure of the frontal, the supraorbital crest is cut free with iris scissors from a transverse cut behind the lacrymal to another transverse cut in front of the level where the brain cavity begins (Pl. IX:2). No important vessels or nerves are damaged by this operation, but some caution is necessary when cutting longitudinally through the bone to ensure that the a. ethmoidalis in the medial wall of the orbit is not damaged (Fig. 4). The wound is kept moist with saline, and the skin is provisionally closed over it.

2. A skin incision is cut with small scissors along the lower margin of the featherless lower eye-lid as shown in Pl. IX:2–3. The skin flaps are drawn to the side with hooks, whereby the whitish ligamentum orbitale inferius can be seen to extend from the lower margin of the orbit in front of the bulb. If the incision is performed as described, no larger vessels or nerves are cut.

3. The ligamentum orbitale inferius is cut through along the lower margin of the orbit (Pl. IX:3–4). The incision is made cautiously, under careful microscopic control, with small scissors, in order that the branches of the infra-orbital vessels and nerves, some lying directly under the ligament, are not damaged. A hook is attached to the bulbar flap of the ligament and is connected with a 50 g load which pulls the bulb dorsally. A cleft then appears between the bulb and the bottom of the orbit (Pl. IX:4).

4. The musculus depressor palpebrae inferioris, which forms a thin membrane on the ventral surface of the bulb behind the bulbar branches of the infra-orbital

vessels, is split (Pl. IX:4–5). The broad metal hook is inserted through the incision to press directly on the bulb and pull it dorsally. The membraneous muscle is freed from the bulb, so that access is obtained to the angle between the inferior and posterior rectus muscles (Pl. IX:5). If necessary, small cotton pellets can be inserted on each side to lift the membrane from the surface of the bulb.

5. Small cotton pellets are carefully inserted under the posterior and inferior rectus muscles in order to elevate the muscles from the bulb. The fat obscuring the vessels under the optic nerve is removed in small pieces with watchmaker's forceps. It often contains small veins, and some caution is necessary to avoid bleeding. The larger vessels first exposed are the ventral ciliary vein and the veins below the optic nerve (Fig. 11). These veins usually cover the pecten arteries and the a. ciliaris longa and n. ciliaris longus, which become visible after the ventral ciliary vein has been blocked. The long ciliary artery and nerve are situated posteriorly, where the tendon of the membrana nictitans disappears between the posterior rectus and the optic nerve.

6. The ventral ciliary vein is coagulated at the point where it emerges from the bulb, and coagulation is continued along the vein, shrinking it up to the neighbourhood of the optic nerve proper. Together with the other sub-optic veins, it is then elevated from the bulb with a needle, thus revealing the underlying arteries and the long ciliary nerve (Pl. IX:6). The two or three pecten arteries are then coagulated and the a. ophthalmo-temporalis is raised from the bulb with a needle, so that the entire ventral and ventro-caudal margin of the optic nerve is exposed, and all vessels passing down here are blocked. As the innermost, often minute, pecten artery may run close to the long ciliary artery and nerve, it is often difficult to save these structures without running the risk that the operation will be incomplete. When the ventral and ventro-caudal border between the whitish optic nerve and the dark bulb is clear of vessels entering the bulb, attention is turned to the anterior side of the optic nerve above the rectus inferior. The a. ophthalmo-temporalis is carefully lifted from the bulb and any vessels entering the bulb here are coagulated. Coagulation in front of the nerve must always take place under optic control. If not, the v. ophthalmica will most probably be damaged, and the space filled with blood.

7. The pellets of cotton wool are removed, the wound is filled with 6 % penicillin in 0.7 % NaCl, the hooks are removed, and the skin incisions are sutured with silk. A compress is fixed over the eye with adhesive plaster.

8. The pigeon is given a prophylactic injection of 1 ml of 6 % penicillin in one pectoral muscle and 0.2 ml of 0.2 % picrotoxin solution in the other pectoral muscle to counteract the nembutal anaesthetic. The animal is left under a layer of cotton wool until it wakes up.

The pigeons are usually active and have a good appetite 6–12 hours after the operation. They were carefully watched in the following days and conjunctivitis, which was seen in some cases, was treated with penicillin.

Control operations were performed in the same way, but one or two pecten arteries were left intact, whereas the other vessels were blocked.

The right, unoperated eye was always used as a normal reference when the left, operated eye was examined ophthalmoscopically or histologically.

Ophthalmoscopy was performed after mydriasis had been produced with 0.225 % tubocurarine chloride in 0.025 % benzalkonium chloride, applied directly on the cornea (CAMPELL et al. 1962 a, b). The pupilla of the operated side was often large enough for ophthalmoscopy without treatment because of damage to the long ciliary nerve.

Results

With two exceptions, the first 27 attempts to block the pecten arteries failed. The pecten remained normal ophthalmoscopically as well as histologically, and dissection of some specimens, injected with vermilion-starch from the carotis (p. 20) revealed a fairly large pecten artery. This had probably regenerated from the small and variable vessel to the pecten, which enters in front of the optic nerve (p. 25). As these birds had been operated upon with the same aim in view as the birds with a degenerate pecten, they must be regarded as particularly valuable controls. These 25 birds were grouped with the 4 animals in which one or two pecten arteries had been left intentionally, and the group was later increased by 2 additional, unintentional controls.

After the importance of the small anterior pecten artery had been realized, 11 out of 16 operations were successful. Two of these animals were used for oxygen measurements within the bulb before degenerative symptoms had developed in the pecten, and were then killed. In these cases the oxygen values near the pecten showed that the operation had been successful. The remaining 9 birds, like the first two successful specimens, were allowed to survive for periods varying from 7 to 317 days, and the changes in the bulb were observed ophthalmoscopically until the birds were killed and examined histologically (for technique, see p. 13).

Controls. The intended controls, in which pecten arteries had been purposely left during the operation, did not show any ophthalmoscopic or histological changes in the pecten. The unintentional controls had, by definition, a normal pecten after the operation. In all these controls, a degenerated patch of retina developed just temporal to the base of the pecten. Within a strictly delimited area with a diameter of 2–3 mm, total destruction of the retina followed within a few days of the operation. The fundus, like all other parts of the retina in these controls, remained normal, both as regards the ophthalmoscopical picture and the histological appearance. The patch behind the pecten is, therefore, an effect of the operational technique, and is probably due to prolonged pressure of the broad hook on the bulb during the operation. As the patch is present in all the eyes operated upon, it will not receive special attention in the following.

The degeneration of the pecten could be seen *ophthalmoscopically* as a slight shrinkage of the folds 2–7 days after a successful operation. The change was often incon-

spicuous during the first week and could be recognized only after comparison with the normal, right eye. A week or more after the operation, the change could always be distinctly observed in the ophthalmoscope. During the second week, white patches developed and tended to spread over most of the folds, but the bridge remained normal.

When examined *histologically*, the pecten did not show any striking symptoms in animals killed on the 1st and 4th day after the operation, although oxygen records showed that the operation had been successful. The vessels were distended with blood which had been trapped there because the pecten vein was blocked earlier than the pecten arteries.

In 8 animals killed 7–38 days after the operation, different stages of progressive degeneration could be seen. After 7 and 10 days some of the vessels contained many macrophages and small necrotic loci. Macrophages were also seen between the vessels among the stroma cells. Lysis of the endothelial cells was already seen in some specimens on the 7th day. In specimens killed 15 days or more after the operation, large areas of the folds were reduced to the PAS-positive, perivascular membranes, whereas endothelium cells, intramural cells and stroma cells had disappeared (Pl. X:1–4). These heavily degenerated parts of the folds are probably identical with the white patches seen in the ophthalmoscope. In one specimen, the spaces between the folds were filled with pigmented cells of the retinal type. This tissue had probably invaded the pecten from the retinal pigment layer, which, in this specimen, showed heavy pathological proliferation (Pl. X:6). The bridge did not show any striking changes in any of the pigeons operated upon.

Degeneration of the pecten never led to complete elimination of the organ. It was progressive during the first two or three weeks after the operation, but then came to a stop. Animals fixed 165, 300 and 317 days after the operation, still had a pecten, but this was shrunken and distorted, with large patches consisting of perivascular membranes only. Other parts of these pectens contained scattered vessels with normal blood corpuscles, indicating that some regeneration had taken place (Pl. X:5). The slow degeneration of the devascularized pecten probably depends on its isolated situation in the non-vascular vitreous body. White blood cells can, therefore, only reach the pecten by active migration over large distances. Necrosis develops slowly and is restricted to a few small loci in the larger blood clots. Most parts of the folds break down slowly without formation of necrotic masses.

The revascularization of the pecten probably starts during the second week in most of the pigeons, for some vessels with normal, non-necrotic blood are always found in the pecten, even in birds fixed two weeks or more after the operation. This is borne out also by the oxygen recordings in the bulb (p. 53), which revealed low oxygen values in the neighbourhood of the pecten during a week or more after the operation but indicated some oxygen supply to the organ later. This revascularization will, of course, prevent further degeneration.

The retina of the successfully operated pigeons. Striking symptoms developed in

the retina of all eyes with an atrophic pecten when the animals were kept alive for more than 4 days.

Ophthalmoscopically, the first changes were seen on the 3rd or 4th day as a distinct whitish or yellowish reflex from the entire retina. The choroidal vessels, which can be seen through the retina in the normal eye, were completely hidden. In this respect, the present observations agree with those of KAUTH and SOMMER (1953), who saw a whitish reflex from the retina after they had destroyed the pecten by cautherization.

In three pigeons which were kept alive for 165, 300, and 317 days, this change was found to be transitory. After some months the retina again looked practically normal, the only recognizable difference between the operated and the non-operated eye being the absence of the fine radial striation in the former. Histological examination of these specimens showed strong or almost total reduction of the optic nerve fibre layer and reduction of ganglion cells on the operated side.

The earliest *histological* changes in the retina were noted 7 *days* after the operation, whereas the retina of pigeons killed on the 1st and 4th days appeared to be normal. In the 4 pigeons killed on the *7th and 10th days,* the retina, particularly the nerve fibre layer along the inner surface, had been invaded by numerous macrophages (Pl. XII:1, 3). A narrow zone along the membrana limitans interna lacked nerve fibres in many places, indicating shrinkage of the nerve fibre layer. No conclusive evidence of oedema was recognized, although the whitish reflex seen in the ophthalmoscope indicated that an oedema had developed.

In the 4 pigeons killed after *15 to* 38 *days* the thickness of the retina was strikingly reduced in comparison with the control eye (Pl. XI and XII). The number of macrophages in the retina was considerable, particularly in the nerve fibre layer. The number of cells in the ganglionic layer was distinctly reduced. Two of the pigeons, killed 2 and 3 weeks after the operation, showed particularly heavy degeneration. The outer and inner segments of the visual cells were atrophic or completely absent, so that the outer surface of the retina resembled that of an ordinary epithelium (Pl. XII:4). The two nuclear layers and the ganglionic layer were strikingly reduced. Local cystoid degeneration and proliferation of the cells of Müller were noted. Needle-shaped pigment granules of the retinal type were found in the retina proper; these were partly free, partly within macrophages. The latter were common also in the layer of rods and cones. The retinal pigment layer was pathologically proliferated locally.

The pigeons killed after *165, 300, and 317 days* had obviously recovered from the acute effects of the operation, and the ophthalmoscopic picture of the retina was nearly normal. Histologically, the outer layers including rods and cones, nuclear layers and plexiform layers appeared normal. In one pigeon (165 days), the inner nuclear layer was even thicker than normal in some places. However, in all three specimens, the nerve fibre layer was strongly reduced and was completely absent over large areas of retina (Pl. XII:2). In two of these specimens, the number of cells in the ganglionic layer was strikingly reduced, but changes in this layer were less distinct in the third specimen.

Conclusion. Complete blocking of the pecten vessels caused progressive degeneration of the organ during the first weeks after the operation, followed by slow and incomplete revascularization. In all eyes with a degenerate pecten the retina developed degenerative symptoms, sometimes restricted to the nerve fibre layer and the ganglionic layer, sometimes including the entire retina. The innermost layers of the retina were the first to show symptoms after the operations. The effect on the retina in 11 experimental animals was not caused by irrelevant factors inherent in the operative technique, as shown by the normal retina in the 31 control eyes. These eyes had a normal pecten and one or two pecten arteries preserved, but had been treated in the same way as those of the experimental animals in all other respects.

It may therefore be concluded that an intact pecten is necessary for the maintainance of a normal retina.

The most simple explanation of this result is that the internal retinal layers are dependent on the pecten for their supply of substances which diffuse through the vitreous body. This is supported by the fact that the innermost layers of the retina, which face the pecten, are the first to degenerate after operations, and may be the only layers which show changes. The old idea that the pecten serves as a nutritive organ for the inner retinal layers and is a substitute for internal retinal vessels is, thus, supported to a point little short of definite proof.

As the distance from the pecten to the retina is considerable, it is plausible that the supply primarily includes easily diffusible substances with small molecules such as oxygen. Removal of carbon dioxyde from the inner parts of the eye may also be an important function of the pecten and is, of course, usually coupled with the oxygen supply. The authors' attention was directed to oxygen supply by the whitish or yellowish colour of the retina in pigeons with degenerate pectens. This could indicate anoxia; it looks very much like the cotton-wool exudate seen in the human retina after occlusion of the arteria centralis (see Hogan and Zimmermann 1962, p. 495).

The Intra-Ocular Oxygen Pressure of Normal Pigeons

The operations described in the preceding chapter show that the presence of a normal pecten is necessary for the maintainance of the inner layers of the retina. This dependence as such is well established, but the physiological mechanisms responsible for it are not definitely revealed by the post-operative symptoms. For reasons given above, the supply of oxygen from the pecten to the retina may be one of the decisive factors. If this is true, oxygen must diffuse through the vitreous body of normal pigeons, and a gradient in oxygen pressure must be expected from the surface of the pecten to the surface of the retina. A possibility of checking the theory was thus presented, as the oxygen pressure can be measured in different parts of the vitreous body by means of oxygen cathodes.

Methods

The pigeons were fixed to the operating table and anaesthetized as for operations (see p. 35). For recording in one eye only, the head was fixed with one eye facing upwards, but for simultaneous recordings in both eyes it was placed in a holder in a vertical position so that both eyes were accessible. Mydriasis was produced by corneal application of a few drops of 0.225 % tubocurarin in 0.025 % benzalkonium chloride solution (CAMPELL et al. 1962). The disposition of holders and electrodes must be such as to allow good ophthalmoscopic control of the electrode tip when inserted into the bulb.

Recording of oxygen pressure was made with the oxygen cathodes devised by DAVIES and BRINK (1942, 1957), CONELLY (1957), CATER et al. (1957) and DAVIES (1962). The electrodes were made of 0.1 mm glass-isolated platinum wire and were ground obliquely at the tip like hypodermic needles (Fig. 13). The exposed platinum surface was coated with collodium ad modum CONELLY (1957). The cathode was connected to an amplifier like the one described by CATER et al. (1957) and was given a charge of -0.6 V, as measured against a calomel electrode which was placed in contact with a saline-soaked piece of cotton wool on the head of the pigeon. Under these conditions, the current is roughly proportional to the oxygen pressure around the tip of the electrode (see CONELLY 1957).

The authors made a series of experiments with different types of coated electrodes, but found the syringe-like ones to be most suitable for the purpose; they slide in easily through the wall of the eyeball and the vitreous body and are automatically cleaned of fibres and debris. Conical electrodes with the point formed by platinum are easily inserted, but the coating of the exposed platinum point is easily damaged. Blunt electrodes are difficult to push through the wall of the bulb and tend to collect fibres and membranes on the free platinum surface.

The capillaries for glass isolation were drawn from 5 mm glass tubing; 100 mm of this tubing formed a handle for the electrode, while the platinum wire was melted into the capillary. The handle was mounted in a somewhat shorter piece of thicker tubing, in which the electrode could slide without rocking. This made the forward movement of the electrode precise and stable when inserted.

Before insertion of the electrode, the supraorbital crest of the anaesthetized pigeon was exposed as for operations (p. 36), and the crest was removed. The point of insertion was chosen at the exposed dorsal pole of the bulb, behind the ring of scleral ossicles and approximately in the equator. The main branches of the posterior dorsal ciliary vein, seen with a dissection microscope, were avoided. Under microscopic control a small hole was made with the heated platinum loop described on p. 36. The scleral cartilage and the choroid were perforated and coagulated to avoid bleeding and damage to the coating when the electrode was inserted. The electrode was usually aimed at the pecten, and recordings were made at five different levels on the way down (Figs. 14 and 15), viz.: 1) near the insertion in the dorsal part

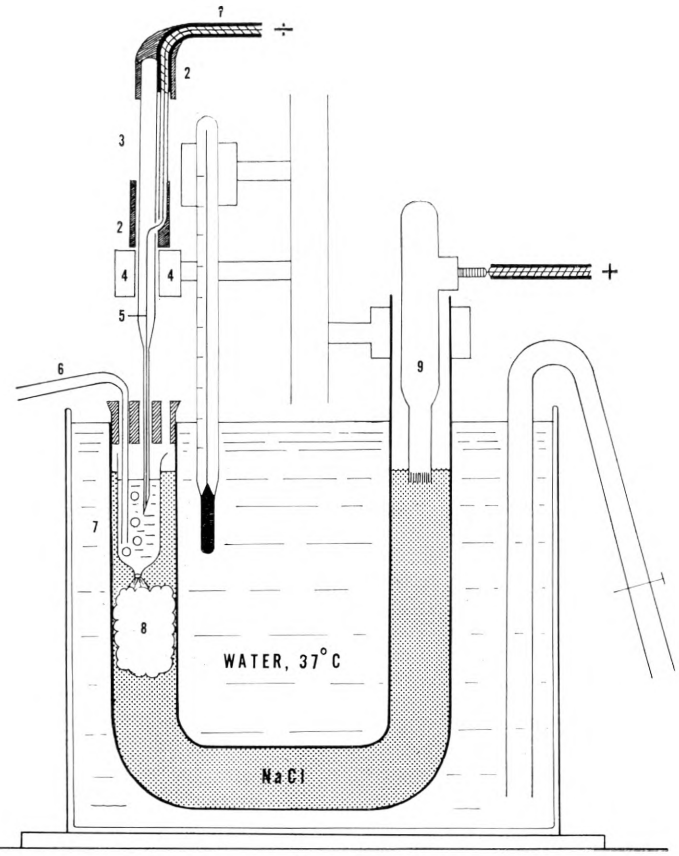


Fig. 13. Apparatus for calibration of electrodes. — 1 = shielded wire, 2 = isolation tape, 3 = glass tubing acting as shaft of electrode, 4 = glass tubing acting as holder for electrode, 5 = platinum wire, 0.1 mm, 6 = glass capillary for introduction of air or N_2, 7 = bag of dialysis tubing containing vitreous body, 8 = cotton wool, 9 = calomel electrode.

of the vitreus, 2) behind the upper part of the iris, 3) centrally, 4) behind the lower part of the iris, and 5) close to the pecten. The position of the electrode tip was checked with the ophthalmoscope. In some cases the electrode was re-aimed in order that recordings could be made near the fundus retina or in other parts of the vitreus.

Readings of the current were made 30 and 60 secs after the voltage had been switched on, and the current was interrupted after the second reading to avoid unnecessary polarization of the electrode. After 30 secs the current is approximately stable, and this value was used for calculations. The somewhat lower value at 60 secs was used as a check only.

Calibration of the electrodes was made immediately before and after each series of readings. If the calibration had changed more than 10 $^0/_0$ during the experiments, indicating damage to the coating, only the relative values were of any use, and absolute values were not calculated. Calibration was made in the apparatus shown in

Fig. 13, with the electrode tip in the fresh vitreous body of the pigeon. The vitreous body was saturated first with nitrogen, then with air, and kept at 37°C, the same temperature as that recorded with thermocouples in the vitreous body of ananaesthetized, normal pigeons. The current recorded in nitrogen and air gave the two points on the graph μA/mm O_2, necessary for calculation of the oxygen pressure.

Whereas the double calibration shows whether the electrodes have operated safely or not, there are a few other sources of error which must be considered and, if possible, avoided, in experiments of this kind. Small air bubbles may be introduced together with the electrode and may spoil the results completely, and a similar effect is produced by bleeding from the point where the electrode penetrates the wall. These complications are avoided by careful coagulation before insertion and by the use of the sharp, syringe-like electrodes, which slide in easily. In spite of all precautions the oxygen pressure is sometimes high near the point of insertion, probably because of diffusion through the opening, but it usually sinks to normal values after some time. The freshly inserted electrodes show too high values during the first few minutes, probably because an amount of atmospheric oxygen is introduced with the coating. Values near the pecten or the retina are dependent on the orientation of the electrode: whether the platinum surface faces the wall or not.

Results

Good *relative values* of oxygen concentration in different parts of the vitreous body were obtained from 15 normal pigeons. In all cases the values from the neighbourhood of the pecten were the highest, and a fall in oxygen pressure was registered when the electrode tip was moved to the dorsal parts of the eye or to the fundus region. The values at the pecten were usually 10–15 times as large as those obtained near the retina of the fundus, and 6–10 times as large as those obtained in the dorsal part of the vitreous body.

An electrode in contact with the pecten always showed regular pulsations of the oxygen pressure, following the rhythm of the respiratory movements. This obviously depends on variations in the oxygen saturation of the arterial blood, caused by the intermittent renewal of air in the air capillaries of the lung.

The *absolute values* of oxygen pressure, obtained from 6 normal pigeon eyes, are given in Table 1. In spite of good calibration there is a good deal of variation from one animal to another, and repeated recordings in the same site during the experiment also gave some rather considerable variations, especially in the neighbourhood of the pecten and the retina. Part of this variation certainly depends on differences in the location of the electrode, as the technique used does not give greater accuracy than 0.5 to 1 mm. However, the main cause of the variation of values, recorded in the same site, is the varying depth of the anaesthesia. This was demonstrated in control experiments, in which the electrode was left with the tip fixed near the pecten of the anaesthetized pigeon, which received an injection of 0.2 ml of 0.2 % picrotoxin

TABLE 1.

Oxygen pressure in mm Hg, recorded in different parts of the vitreous body of normal pigeons. A–E shows recordings at different levels along a straight line from the pecten to the insertion of the electrode near the dorsal equator. F and G are values in the neighbourhood of or in contact with the retina of the fundus. The asterisk * denotes that the higher values were obtained after picrotoxin injection.

Pigeon nr.	Vitreous body, level of					Fundus retina	
	A Pecten	B Lower iris	C Centre	D Upper iris	E Dorsal bulb	F Ca. 1 mm from	G Contact with
1.	44–94	22–25	14–23	9–18	4–11	6–7	3–7
2.	26–58*	15–24	14–17	10	7	4–7	4–7
3.	31–86*	30–38	17–30	8	7–9	13	1
4.	49–77	32	16–24	12–16	8–14	–	3–12
5.	52–70	36–41	14–25	10–13	6–13	–	4–7
6.	70–76	42–51	19–33	14–19	8–13	–	–

in the pectoral muscle. The drug counteracts the nembutal anasthesia and stimulates the pigeon, which has to be killed when it begins to move. In one such experiment the recordings of the fixed electrode rose from 39 to 86 mm Hg in 14 minutes after the injection, in another from 26 to 58 mm Hg in 19 minutes. Thus, the anaesthesia can lower the values to about 50 % of the normal ones in the neighbourhood of the pecten, and the higher values recorded here are, therefore, likely to be most reliable.

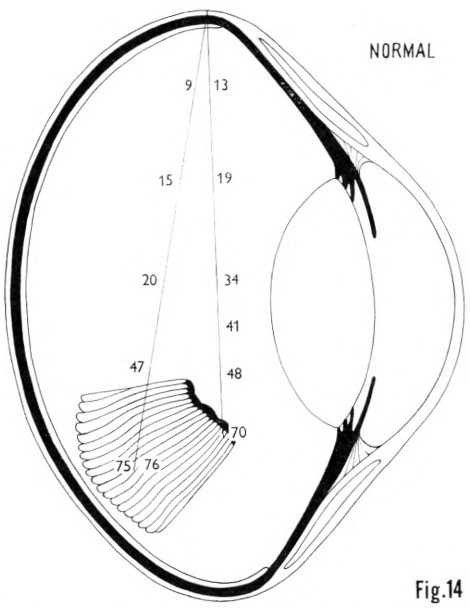


Fig.14

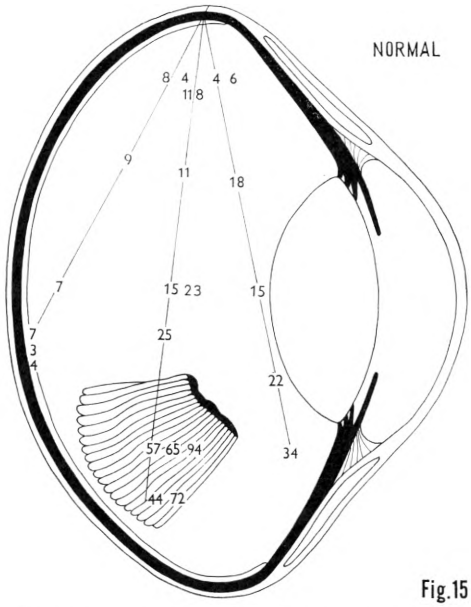


Fig.15

Figs. 14 and 15. Oxygen pressure in mm O_2, recorded in different parts of the bulb of two normal pigeons, anaesthetized with nembutal.

The oxygen pressure recorded in the neighbourhood of the pecten varies between 70 and 94 mm Hg, if the lowest values are excluded for reasons given above (see Table 1, Figs. 14, 15). Somewhat lower values were regularly recorded when the electrode surface was facing the bridge, and the highest values were obtained near the folds. In the latter case, the pulsations of the oxygen pressure were most pronounced. This strongly indicates that the oxygen pressure around the pecten of normal, non-anaesthetized pigeons is very close to the arterial oxygen tension, which appears to be about 100 mm Hg in the pigeon (WASTL and LEINER 1931), and in other birds (Duck, WASTL and LEINER 1931, Fowl, MORGAN and CHICHESTER 1935).

As shown in the Table 1 and in the diagrams (Figs. 14–15) the oxygen pressure in the vitreous body of normal pigeons with moderate anaesthesia is 22–51 mm behind the lower iris margin, 14–33 mm in the centre, 9–19 mm behind the upper iris margin, and 4–14 mm in the dorsal part of the bulb near the point of insertion. The variations seen in these figures undoubtedly depend both on the varying position of the electrode and on differences in the anaesthesia. Nevertheless, the fall of oxygen pressure from the pecten up to the dorsal part of the bulb is distinctly shown.

The values at the retinal surface are of particular importance for calculations of diffusion rates. They could not be recorded with the necessary accuracy near the insertion, where contamination with atmospheric oxygen from the wound could be expected. Therefore, in some experiments, the electrode was re-aimed, the tip approaching the wall of the fundus with the platinum surface facing the retina. In all cases values as low as 3 or 4 mm Hg were obtained when the electrode was close enough to the retina (Table 1). Higher values up to 12–13 mm were recorded before it had come close enough. In such cases, the electrode tip could well be 1 mm from the surface as the ophthalmoscopic control did not allow greater accuracy. Thus, the peripheral parts of the vitreous body in contact with the retina have a very low oxygen concentration, about 3–5 mm only. In the authors' calculation of diffusion rates, 5 mm was chosen as a basis to compensate for the effect of the anaesthesia. These values, which must hold good also for the inner layers of the retina, are in good agreement with DAVIES' and BRINK's (1957) recordings from the cerebral cortex of the cat, where values between 2 and 10 mm Hg were obtained.

A distinct rise up to 25 mm Hg or more was always recorded when the electrode tip was pushed into the retina. In such cases the recording space around the electrode tip obviously included deeper retinal layers, where oxygen diffusion from the choriocapillaris comes into play. The minimum oxygen concentration in the bulb is thus found in the inner layers of the retina. This means that the oxygen coming from the choriocapillaris is consumed in the outer layers and does not reach the inner layers in any significant amounts. The method used is not accurate enough to determine exactly how far into the retina the gradient from the choriocapillaris extends.

A few recordings indicate a slight increase of the oxygen values when the electrode tip is placed close behind the ciliary body (Fig. 15). This probably means that some

oxygen is given off from the ciliary folds, but as the gradient system dominated by the pecten is not significantly disturbed, the amounts must be fairly small.

The measurements of oxygen pressure in the vitreous body of normal pigeons thus show that there is a fall of oxygen pressure from about 100 mm around the pecten to about 5 mm along the inner surface of the retina. Such a gradient cannot exist in a homogeneous, non-consuming medium like the vitreous body without diffusion taking place. *It is thus shown that oxygen does diffuse from the pecten to the retina. This result satisfies the basic requirement of the theory, according to which the pecten is a substitute for intraretinal vessels and supplies the inner layers of the retina with oxygen.*

Quantitative Considerations on the Basis of the Recorded Oxygen Pressure

The oxygen gradient found by recording with oxygen cathodes shows definitely that oxygen diffuses from the pecten out to the retina. However, it still has to be discussed whether the oxygen supply from the pecten is large enough to have a functional significance in the retina, i. e., whether interruption of this supply could have been the reason for degeneration of the retina after the pecten vessels had been blocked. This is not immediately shown by the recorded values, for oxygen gradients will probably be found around many well-vascularized organs and need not necessarily have a specific functional significance. In the present case it is only shown that the pecten is over-supplied with blood with regard to its own oxygen consumption.

The Amounts of Oxygen Supplied to the Retina by the Pecten

In calculating the rate of diffusion of oxygen the folds of the pecten are not taken into consideration, but the organ is regarded as a compact plate with plane, parallel side walls tangential to the folds on each side. The total surface of this organ is around 42 mm^2, and the oxygen pressure on its surface is about 100 mm Hg. The retina is considered to be a half-sphere with 7 mm radius and an oxygen pressure of 5 mm along the inner surface. The complicated geometrical configuration of the pigeon's eye does not allow simple, exact calculations. Therefore, a few models were introduced which give an idea of the amount of oxygen transferred to unit area of retina per time unit.

1. In the first model, the surface of the pecten (42 mm^2) is spread on the surface of a half-sphere (radius 2.58 mm), concentric with another half-sphere with 7 mm radius, representing the retina. The former surface is given the oxygen pressure 100, the latter 5. The amount of oxygen passing half-spherical surfaces concentric with and lying between the two, must obviously always be the same and independent of the radius r. It is proportional to $\frac{dp}{dr} \cdot 2\pi r^2$, where dp is the fall of pressure over

the thickness dr of the half-sphere. This gives $\frac{dp}{dr} = \frac{k}{r^2}$, and $p = -\frac{k}{r} + a$, where k and a are constants. If the values for the "pecten" ($p = 100$, $r = 0.258$ cm) and the "retina" ($p = 5$, $r = 0.70$ cm) are inserted, it is found that $k = -38.82$. The pressure fall/cm at the surface of the retina is then easily found: $\frac{dp}{dr} = -79.22$ mm Hg/cm. This model is presumed to give values which represent conditions in the dorsal parts of the bulb, far from the pecten.

2. The pressure fall at the dorsal retinal surface can be calculated in a second way. If it is assumed that the ventral parts of the vitreous body around the pecten are saturated with oxygen, they may be considered as a "lake" of oxygen with a 70 mm pressure, and with the surface at the level of the bridge of the pecten. The diffusion from this surface along the posterior surface of the lens to the dorsal retina may be considered as diffusion between two parallel surfaces, 9 mm apart (See Fig. 14–15). The fall of pressure will then be linear and its numerical value: $\frac{70-5}{0.9} = 72$ mm Hg/cm, which is in reasonable agreement with the above value.

3. Using method 1 for a model, in which the radius of the retina is reduced to 4.5 mm, the value for $\frac{dp}{dr}$ along the retinal surface increases to 283.7 mm Hg/cm. This model will probably fit conditions in the central parts of the fundus, which are less than 4.5 mm from the pecten.

4. The fovea is situated about 1.8 mm from the side of the pecten. A retinal surface here, parallel to the side of the pecten, would receive oxygen corresponding to a fall in pressure at the retinal surface of $\frac{100-5}{0.18} = 530$ mm Hg/cm.

A fall of oxygen pressure of 75 mm Hg/cm at the most distant retinal surface in the dorsal part of the bulb, and 300 mm Hg/cm in the central fundus appear, therefore, to be realistic estimates.

The supply of oxygen per unit time to each cm² of retina under these conditions can be calculated approximately by using KROGH's (1918) "diffusion constant" for oxygen in water: 0.34 ml O_2 passes 1 cm² of surface per minute, if the fall in pressure is 1 athm. per μ and the temperature is 20° C. If it is supposed that the constant increases 1.4 % for 1° C increase of temperature, the constant at 37° C, expressed in ml/cm² surface, per hour, and in mm Hg/cm, will be about $0.33 \cdot 10^{-5}$. Diffusion in the eye takes place in the vitreous body, which contains 1–2 % of solids. The diffusion constant may therefore be somewhat lower than in pure water, but the difference will probably not be of fundamental importance for the result.

A diffusion constant of $0.33 \cdot 10^{-5}$ gives the following values for the oxygen supply per cm² and hour to the areas of retina dealt with:

The dorsal retina: $0.33 \,.\, 10^{-5} \cdot 75 = 2.5 \cdot 10^{-4}$ *ml/hour.*
The fundus retina: $0.33 \,.\, 10^{-5} \cdot 300 = 9.9 \cdot 10^{-4}$ *ml/hour.*

The Pecten's Role in Oxygen Economy of the Retina

A comparison between the amounts of oxygen supplied by the pecten and the total amount of oxygen consumed by the retina would give an idea of the pecten's role in the metabolism of the retina. This comparison can only be made as a rough estimate, however, as the normal oxygen consumption of the retina is unknown in pigeons. Comparisons must therefore be made with values obtained in experiments with the mammalian retina, which is better known in this respect. Another source of error is introduced with the assumption that the percentage of oxygen supplied by the pecten should express its functional importance in the retina. The innermost layers of the retina, which are of interest as potential recipients of the pecten oxygen, probably have a much lower metabolism than the rod and cone layer, which is supplied by the chorio-capillaris. Therefore, the pecten may supply a much thicker layer of tissue than expected from simple calculations on the percentage of retinal oxygen coming from the pecten.

1. In Wahrburg experiments, the mammalian retina consumes 10–20 ml oxygen per g dry weight and hour (Spector 1956). Using the 20.8 ml per g per hour found in dogs as a basis for calculations, the value for 1 cm^3 of wet retina will be about 4.2 ml/hour. According to the estimate on p. 48, the oxygen supply from the pecten to each cm^2 of retina is $2.5 \cdot 10^{-4}$ in the dorsal part of the eye, and $9.9 \cdot 10^{-4}$ in the fundus. If it is assumed that the oxygen consumption is the same throughout the retina, the thickness of the layer, supplied by the pecten, would be:

$$\frac{2.5 \cdot 10^{-4}}{4.2} \text{ cm} = 0.5\,\mu \text{ in the dorsal part of the bulb, and}$$

$$\frac{9.9 \cdot 10^{-4}}{4.2} \text{ cm} = 2.4\,\mu \text{ in the fundus.}$$

If reliable, these values would indicate that the oxygen from the pecten plays no particular role in the supply of the ganglion cell layer which lies 10 μ (periphery) to 20 μ (fundus) from the inner surface of the retina. However, the values are probably much too low for the following reasons: 1) In the Wahrburg experiments, the oxygen consumption of the retina was determined under atmospheric oxygen pressure, and may therefore be much higher than in the living animals, where the oxygen pressure may be as low as 5 mm Hg. 2) The oxygen consumption in the inner retinal layers, which receive the pecten oxygen, is necessarily much lower than in average retinal tissue, as these layers mainly consist of nerve fibres. These two factors taken into consideration it is not excluded that the pecten oxygen may be essential for the innermost 10–20 μ of the retina, which primarily degenerate when the pecten is blocked.

2. The normal brain substance of man consumes 2.1 ml of oxygen per cm^3 of tissue under normal conditions of blood supply (Lassen 1959). If this is assumed also for the internal layers of the pigeon retina, only 1 μ (dorsal retina) and 5 μ (fundus) deep layers can be supplied by the pecten. However, the nerve fibre layer of the retina

probably consumes less oxygen than the average brain substance, so the layer supplied from the pecten may well be much deeper.

3. The following calculation approaches the problem from a quite different angle. The uveal oxygen consumption in the dog was calculated by PILKERTON, BULLE and O'ROURKE (1964 a) to 4 μl/g · min (cf. also ELGIN 1964). The weight of the uvea is 340 mg (PILKERTON et al. 1964 b), and the radius of the retinal half-sphere is about 10.5 mm. If it is supposed that half of the uveal oxygen is used by the retina, each cm² of retina will consume $59 \cdot 10^{-4}$ ml/hour. In the following calculation it is assumed that the oxygen consumption per cm² retina is of the same order of size in the pigeon. In this animal, the oxygen supply from the pecten was estimated above (p. 48) to be $2.5 \cdot 10^{-4}$ ml/hour in the dorsal part of the bulb and $9.9 \cdot 10^{-4}$ ml/hour in the fundus. This makes about 4 % and 15 % of the total retinal supply respectively.

When it is remembered that the optic nerve fibre layer and the ganglion cell layer occupy about 13 % of the cross section of the pigeon retina, and that 4 – 14.5 % of the retinal oxygen is supplied from the pecten according to the calculation above, it appears reasonable to assume that the said two layers are supplied mainly by the pecten. The weak points of this calculation are (in addition to the somewhat daring transfer of values from dog to pigeon): 1) The possibility that more than half of the uveal oxygen is used by the retina in the dog, and 2) The presumed lower metabolism of the nerve fibre layer in relation to average retinal tissue. Point 1) will decrease and point 2) will increase the percentage of retinal oxygen coming from the pecten.

All these calculations have been based on the assumption that the fluid in the vitreous body is stationary. If fluid escapes from the pecten and spreads in the bulb, the transport of oxygen will be more efficient.

Although these estimates of the role of the pecten in retinal oxygen supply are very approximate and may be reliable only within a power of ten, they are sufficient to show that the oxygen flow from the pecten is of such an order of size that it may be functionally significant for the inner retinal layers. This is in agreement with the theory that the interruption of the oxygen flow from the pecten caused the degeneration of the retina after the operations. On the other hand, these values are hardly good enough to be regarded as positive proof.

The Oxygen Tension in the Bulb after Coagulation of the Pecten Vessels

The results reported up to now show that the pecten is necessary for the maintainance of a normal retina and have supported the theory that this dependence is a question of oxygen supply. It was shown that oxygen is given off from the pecten to the retina in amounts large enough to have a functional significance. However, it has not been conclusively proved that the degeneration of the retina after pecten operations depends on the interruption of this oxygen supply. It was, therefore,

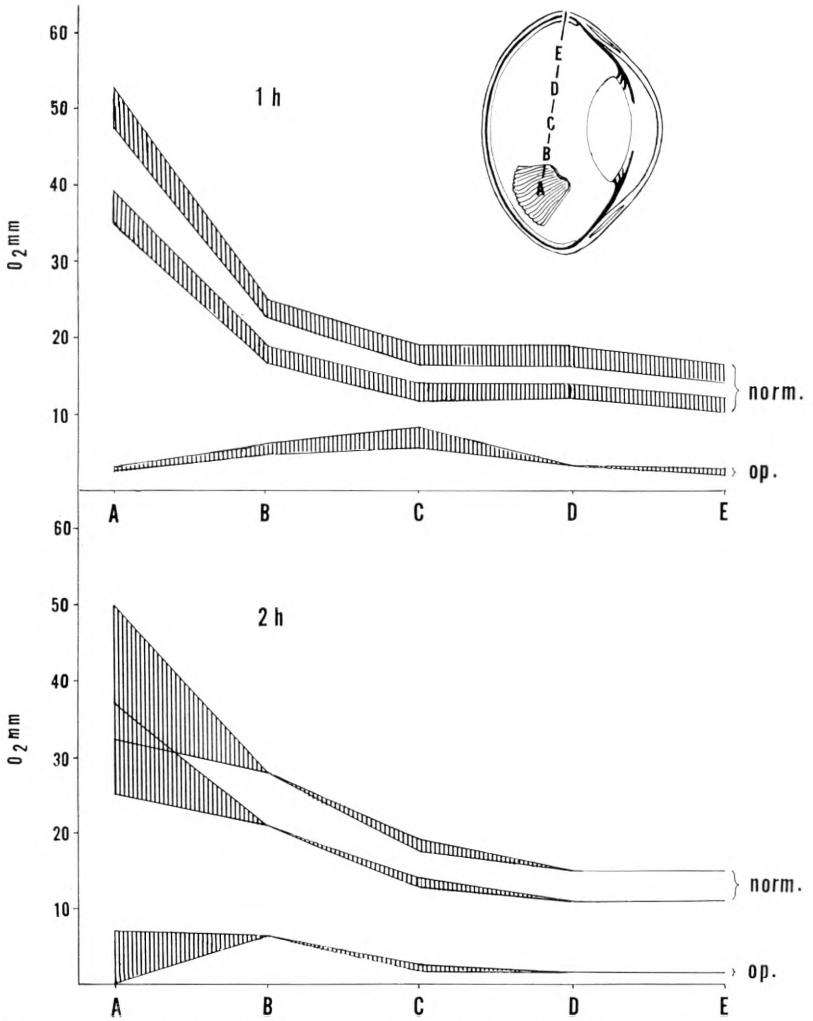


Fig. 16. Simultaneous recordings of oxygen pressure in the normal ("norm.") and operated ("op.") eye of a pigeon, one and two hours after the pecten vessels of the right eye had been blocked. Oxygen pressure in mm. Hg on the vertical axis, letters on the horizontal axis show sites of the electrode tips. All recorded values fall within the shaded areas.
As the electrode in the operated eye remained constant while the one in the normal eye changed, two graphs were obtained, corresponding to the calibration before and after (upper graph) the experiment. The values from the normal eye are low, probably because of long (5–6 hrs) and deep anaesthesia, but the highest values are similar to those obtained from other normal eyes under deep anaesthesia.

decided to record the oxygen pressure in the bulb after the pecten vessels had been blocked. According to the theory, the oxygen pressure would then be fatally low throughout the corpus vitreum.

Because the absolute values of the oxygen pressure are dependent on the depth of the anaesthesia, simultaneous recordings from the right, unoperated eye were

necessary for comparison with the values from the operated eye. The necessity of having reliable calibrations of two electrodes before and after each recording made these experiments rather lengthy, and in the end most of them had to be discarded because the operation, the anaesthesia, or one of the electrodes had failed. However, the few successful experiments are illuminating in several respects.

The first attempts were made with 7 pigeons which had been operated upon 7–27 *days* earlier, and which showed distinct ophthalmoscopic symptoms of beginning degeneration of the retina. The oxygen pressure was found to be very uniform throughout the corpus vitreum. In three cases somewhat higher values were found near the pecten, indicating beginning revascularization of the organ. In the other cases no distinct increase in the values could be observed when the pecten was approached. The highest values were recorded when the electrode tip was close to or inside the retina, and distinct rhythmic pulsations of the oxygen pressure were seen when the electrode tip reached sufficiently deep into the wall. This showed that the blood supply to the choriocapillaris was functioning normally. All this had been expected, but the absolute values of the oxygen pressure were astonishingly high in all pigeons a week or more after the operation. The values from two cases, when the calibration of the electrodes was satisfactory, indicate about 20–30 mm Hg throughout the bulb. This must mean that the retina was not normal in these eyes and that oxygen from the choriocapillaris could pass through and fill the eye interior without being consumed.

It was, therefore, obvious that irreversible changes, which strike the ganglion cells after the pecten operation, must be complete within a week. Retrograde changes in the layer of bipolars and sensory cells probably occur in the same period, causing the inactivity of the entire retina. As shown by the histological examination, this may lead to extensive changes in all layers in some cases, whereas only the inner layers break down in other eyes. The variations from one specimen to another may perhaps depend on differences in the time required for pecten revascularization and also on variations in the size of the regenerated vascular net.

If this interpretation is correct, low and fatal oxygen values in the vitreous body would be expected during the first few days after blockage of the pecten vessels. Consequently, the authors started a series of recordings in the bulb immediately after the operations.

Critical oxygen values were obtained from one newly operated pigeon only, but in this case good recordings were obtained both *1 hour and 2 hours* after the pecten vessels were blocked. The electrode on the normal side changed its calibration a little during the experiment, but this is accounted for in the diagram in Fig. 16. One hour after the operation the oxygen pressure had fallen to below 10 mm Hg throughout the vitreous body of the side operated upon. The highest values were recorded in the centre of the eye, where some oxygen still remained. In the dorsal part of the bulb, and near the bridge of the pecten, 2–3 mm only were recorded. These latter values are so close to zero that the difference is hardly significant.

2 *hours* after the operation some values as high as 7 mm were obtained near the base of the pecten, where oxygen may leak out from the choriocapillaris, and 6 mm was recorded near the lower margin of the iris, where influence from the corpus ciliare is probable. All other values were below 3 mm. This can only mean that the oxygen pressure in the inner retinal layers in contact with the vitreus was between

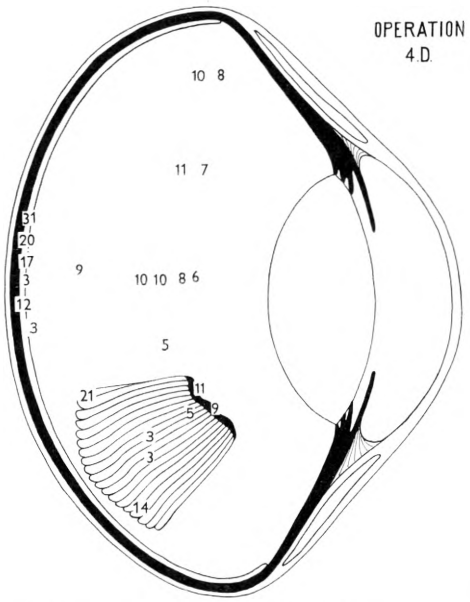


Fig. 17. Oxygen pressure in mm Hg, recorded in the left bulb of an anaesthetized pigeon, 4 days after the pecten vessels of the eye had been blocked by operation. Note the high values recorded when the recording tip was pushed into the retina of the fundus.

zero and 3 mm, and irreversible changes followed by degeneration would be expected in the ganglion cells, if these behave like ordinary neurons.

Measurements in another pigeon *4 days* after the operation showed that the oxygen pressure was still very low in the vitreous body (Fig. 17). Recordings near the surface of the pecten and the retina gave only 3 mm, whereas somewhat higher values were obtained in the central parts of the vitreous body (5–11 mm), probably because of diffusion from the ciliary body. Values higher than 11 mm were obtained only when the electrode tip was pushed into the retina or into the papilla of the optic nerve, so that the recording space came into the diffusion field of the choriocapillaris. When this happened, values as high as 31 mm were recorded, showing that the choriocapillaris supply was intact.

Although few, these experiments show that the operations were efficient in blocking the pecten vessels, and that this results in a drastic decrease of oxygen pressure in the vitreous body within an hour. It is also shown that the choriocapillaris remains intact after the operations. The degeneration of the retina which follows, does, there-

fore, not depend on interference with the choriocapillaris. This had been predicted on the basis of the morphology of the vessels (p. 26).

The values in the peripheral parts of the vitreous body one and two hours after an operation were below 3 mm Hg, and many of them were, in fact, not significantly different from zero. The oxygen pressure in the inner layers of the retina must have been equally low or probably lower, as these layers consume oxygen. Such low oxygen pressure would be expected to cause irreversible changes and degeneration in the retinal ganglion cells, if these behave as ordinary neurons. Thus, the results support the hypothesis that oxygen supply from the pecten is essential for the inner retinal layers, and that these layers degenerate because of oxygen deficiency after operations. The only point which prevents a definite conclusion is that the minimum oxygen pressure tolerated by the retinal ganglion cells is unknown. It is presumed that the minimum requirements of these cells are similar to those of other ganglion cells, and as this appears to be a realistic postulate, the arguments appear to be rather strong.

Discussion on the Function of the Pecten

The discussion set out step by step in the preceding chapter ended with the conclusion that the pecten is necessary for the maintainance of a normal retina in the pigeon, and that this is so because the pecten supplies the inner layers of the retina with oxygen. The first point is shown by the degeneration of the retina, after the pecten vessels had been surgically blocked (p. 41). No such symptoms were seen in the retina after operations which were performed in the same way, but leaving one or more pecten arteries intact. The conclusion that the pecten is necessary for the maintainance of a normal retina is, therefore, well supported by experimental facts.

The second part of the conclusion, viz., that the oxygen supply from the pecten stands for part of this dependence, is supported by the following points:

1) Measurements of the oxygen pressure in the vitreous body revealed an oxygen gradient, showing that oxygen does diffuse through the vitreous body from the pecten to the retina (p. 47).

2) Numerical calculations on the basis of the recorded oxygen values show that the amount of oxygen transferred from the pecten to 1 cm^2 of retina per hour is about $2.5 \cdot 10^{-4}$ to $9.9 \cdot 10^{-4}$ ml (p. 48). Comparison with the oxygen consumption of the mammalian retina indicates that the said amounts are large enough to be functionally significant in the inner retinal layers (p. 50).

3) After the pecten vessels are surgically blocked, the oxygen pressure in the peripheral parts of the vitreous body falls to values below 3 mm Hg. This is enough to explain why the inner layers of the retina degenerate, if it is presumed that the retinal ganglion cells have the same oxygen requirements as other neurons (p. 54).

The results are thus in agreement with the old idea that the pecten is a nutritive organ, supplying the inner layers of the retina and compensating for the absence of

intra-retinal vessels (H. Müller 1872, Beauregard 1876, Rochon-Duvigneaud 1920, 1943, 1950, Mann 1924 a, b, Walls 1942, Leiner 1951, and others). The reader is referred to Walls' (1942) convincing discussion, where he interprets the pecten of birds, the cone of reptiles, and the intra-retinal and hyaloid vessels of other vertebrates as being different solutions to the same functional problem: the supply of the inner layers of the retina. When no such supplying structures are found, the retina is either very thin or is presumed to use less oxygen because it contains fewer cones.

In some teleosts and in Amia, a particularly interesting solution to the problem of retinal supply is found. In these fish, the choriocapillaris is fed by a choroid rete mirabile ("the choroid gland"), which appears to function as a counter-current multiplier for oxygen. This explains why values as high as 250–800 mm Hg were recorded with an oxygen cathode in the vitreous body of fishes with a large rete (J. B. and B. A. Wittenberg 1962), whereas only 10–20 mm were recorded in fishes without a rete. As the arterial oxygen pressure of fish must be below 160 mm (atmospheric tension), it follows that oxygen is actively secreted into the bulb by the rete-choriocapillaris system. In the pigeon, the vessels of the pecten are not arranged in a way likely to satisfy the requirements of an efficient counter-current system, and the oxygen pressure in the bulb does not exceed that of arterial blood. There is, therefore, no reason to assume that the pecten acts as an oxygen multiplier.

A comparison with the supply system of the human retina is of some interest in the present discussion. According to Michaelson (1951) the outer 130 μ of the human retina are supplied from the choriocapillaris, as this layer is avascular, and because all parts of the retina lying more than 130 μ from the choroid are supplied by the intra-retinal capillaries belonging to the centralis retinae system. Michaelson's view is supported by the fact that the last-mentioned inner layers are the first to degenerate after obstruction of the central retinal vessels. In man, the capillary bed of the a. centralis supplies the nerve fibre layer, the ganglion cell layer, the inner plexiform layer, and the inner nuclear layer. In the pigeon, the supply from the inner side appears to be restricted to the nerve fibre layer and the ganglion cell layer, as these layers may be the only ones which show pathological changes after interruption of supply from the pecten. This seems to indicate that the zone supplied by the choriocapillaris is considerably thicker in the pigeon than in man. In the pigeon, this zone, including all layers from the pigment epithelium to the inner plexiform layer, is about 200 μ thick in the fundus and 110–180 μ thick in the peripheral parts of the retina. When this is compared with the 130 μ supplied from the choriocapillaris in man, it provides some indirect support to the functional interpretation of the pecten: If only 130 μ of retina can be supplied from the human choriocapillaris, it is improbable that the whole retina in the pigeon could be supplied from this source, for its thickness may exceed 250 μ in the fundus part. The suggestion that the inner parts of the retina are supplied from the pecten offers a solution to this problem.

Franz (1909) did not believe that the pecten is a nutritive organ because the walls of the capillaries are so thick; he admits, however, that their impermeability remains

to be proved. GRIFFIN (1953) found it unlikely that significant amounts of oxygen can be transferred by diffusion over the fairly large distance from the pecten to the retina. Both objections to the theory of oxygen supply from the pecten are invalidated by the results of the present investigation. Oxygen passes out of the pecten and diffuses to the retina in amounts large enough to be functionally significant (p. 50).

In this paper attention has been exclusively focused on the oxygen supply from the pecten, but it is possible and even probable that removal of carbon dioxide from the inner bulb is an equally important function of the organ. This was suggested by LEINER (1951) and KAUTH and SOMMER (1953), who maintained that the high content of carbonic anhydrase in the pecten facilitates this function. It is certainly probable that oxygen supply and removal of carbon dioxide are combined in the pecten, as in other organs, and diffusion of carbon dioxide in the vitreous body is probably almost as rapid as that of oxygen. However, until quantitative data have been presented, all estimates of the diffusion of carbon dioxide will be little more than guesses, as the absolute concentrations and the hydration to carbonic acid will influence the issue.

Whether other blood-borne substances such as glucose, amino acids, and fatty acids can be transported to the retina from the pecten is still more uncertain. These substances diffuse very slowly, and it appears doubtful whether they could reach the retina in significant amounts without the aid of special transport mechanisms.

Although some problems remain to be solved, they do not interfere with the main result of the present investigation, viz.:

that the pecten is a nutritive organ, necessary for the maintainance of the inner layers of the retina. This must be considered the principal function of the pecten, as structures necessary for vision are seriously damaged when this function fails.

The possibility that the pecten can have other, "subsidiary" functions cannot be excluded, but none of the other potential activities has ever been shown to be so important that its break-down could cause significant deterioration of the eyesight. In the search for subsidiary functions of the pecten, attention is drawn to the numerous theories listed on pp. 8–10. The following activities appear possible or even probable, although their significance in relation to eyesight is unknown:

1. The pecten can take part in the formation of the vitreous body during the embryonic development, as suggested e.g. by v. HUSEN (1913). However, the vitreous body in other animals is formed, whether a pecten homologue is present or not. The root-like fibres of the vitreous body, which penetrate into the bridge of the adult pecten, could indicate formation of vitreous from the bridge in adult birds. However, it appears equally probable that these fibres serve to support the pecten mechanically.

2. As suggested by several authors (pp. 9, 10), the pecten may secrete intra-ocular fluid. It would hardly be realistic to suggest that the organ is impermeable to water and other low-molecular substances when it is easily permeable to fluorescein (ABELSDORFF and WESSLEY 1909). Absolute proof regarding an active secretion of water from the pecten, and for a significant role in the regulation of intra-ocular

pressure, is still wanting, however (pp. 12–13). In the present experiments, pressure on the bulb during operations caused some loss of fluid, with the result that the cornea was soft and uneven when the hooks were removed. An apparently normal, smooth and firm cornea was always reestablished within 5 minutes, probably in part because of hyperaemia of the choroidal vessels. Throughout the post-operative period the cornea remained firm and smooth, and no differences could be felt when control eyes and eyes with degenerated pectens were compared. Therefore, the ciliary body alone must be capable of maintaining a normal or nearly normal pressure in the bulb. According to SEAMAN and collaborators (1963), the pressure-regulating mechanisms of the pecten should come into play when the system is over-loaded, but this appears to be very difficult to prove critically.

3. It is possible that diffusion from the pecten plays some role in the supply of the posterior parts of the lens and the vitreous body. As the vitreous body has a negligible metabolism, and as the ciliary body would appear to be in a better position to cover the comparatively small needs of the lens, it seems improbable that this particular function of the pecten should be decisive. In mammalian eyes the said structures are supplied without the aid of a pecten. The lens and the vitreous body did not show significant changes after the pecten vessels had been blocked.

4. It is probable that the pigmented pecten absorbs some diffuse light in the bulb, as suggested by TREVIRANUS (1828), THOMSON (1929), and VERRIER (1936), but it is an open question whether this can significantly contribute to clearer vision.

5. It appears logical to assume that some heat is given off to the eye from the blood in the pecten (KAJIKAWA 1923), and it is also possible that some heat can be carried off with the blood when the pecten is strongly illuminated (GRIFFIN 1953). Since these problems are solved without a pecten in other vertebrate eyes, it appears less probable that these activities should be a condition for the normal functioning of the avian eye.

A series of other functional theories should be abandoned in view of the fact that they are highly improbable or in direct contradiction to established facts. Some of these theories require no comment, but a few of them will be discussed here:

The theories based on the presence of pecten shadows on the retina cannot be upheld, as these particular kinds of shadow cannot be cast by the pecten in the pigeon's eye (pp. 9–10). The ophthalmoscopic observations supporting this conclusion are found on pp. 10–12 and 14–15.

The theory that the pecten is a dark mirror, reflecting on the dorsal retina images of birds of prey in the sky (p. 10), is unacceptable, as no reflecting surfaces have been found.

All theories that the pecten is a sensory organ meet with the difficulty that nerve fibres have not been found, and, if present, must be very few (p. 19).

All ideas according to which the pecten plays an active role in accomodation appear untenable after it has been shown that the pecten remains unchanged during accommodation (ANDRÉ and BEAUREGARD 1874, ABELSDORFF 1910).

It appears probable that the pecten vessels are partly emptied when intraocular pressure suddenly increases through muscular action or violence, and that the pressure change is somewhat counteracted in this way. However, all vessels tend to empty when exposed to pressure, and it has not been shown that the emptying of pecten vessels under the presumed conditions has any specific significance in the visual organ. The supposition that emptying occurs in connection with accommodation is hardly feasible in view of the experiments referred to above (André and Beauregard 1874, Abelsdorff 1910).

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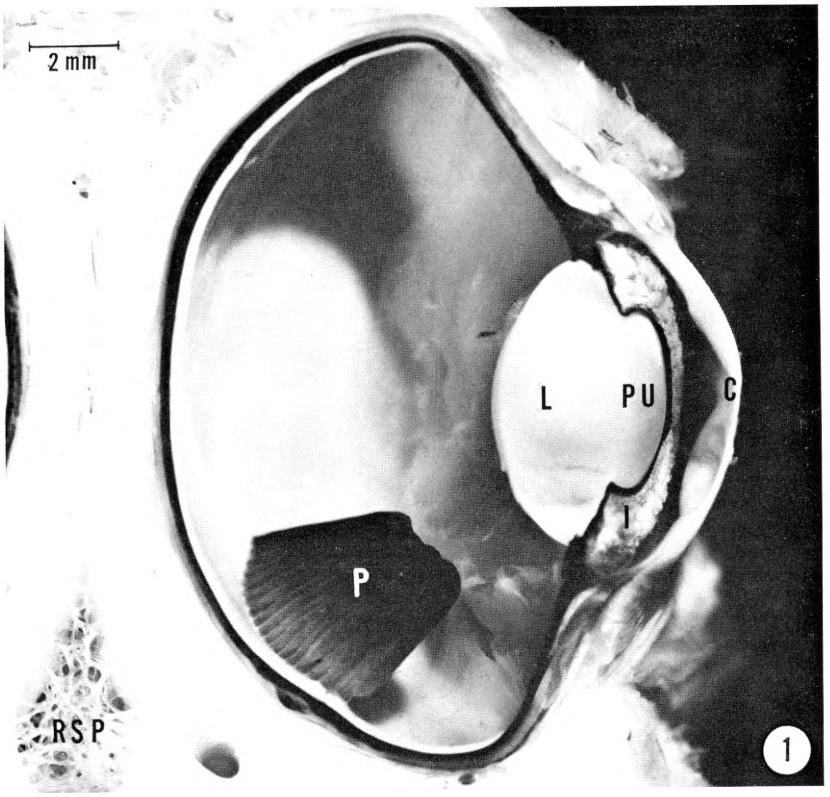
PLATES

Plate I

1. The eye of a pigeon with the pecten (P), cut open by a transverse section through the head. The head was fixed by perfusion with Bouin's fluid and decalcified before being cut. — C = cornea, I = iris, L = lens, P = pecten, PU = pupilla, RSP = rostrum sphenoidale.

2. The pecten, seen from the side. Fundus end to the left. — B = the thickened bridge which covers the folded part.


2 mm
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PU
C
I
P
RSP
1

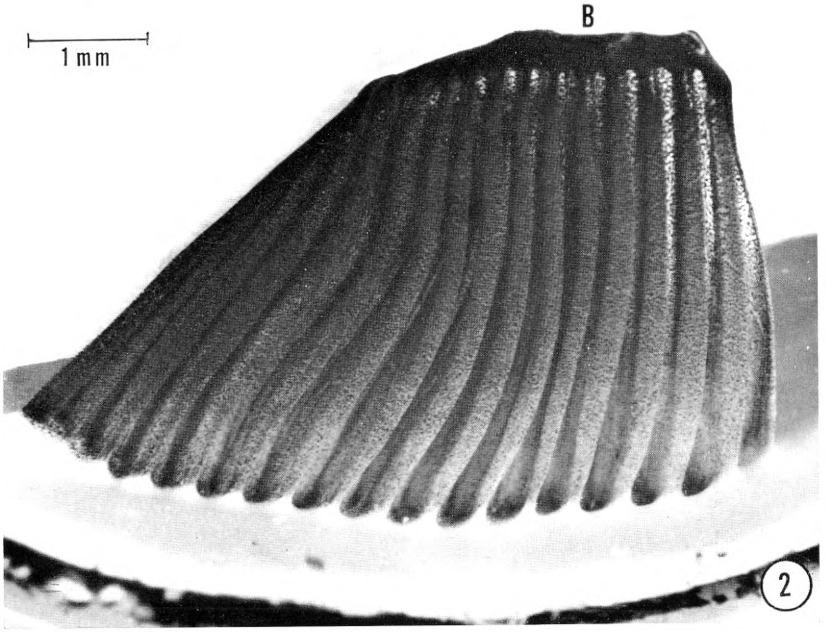

1 mm
B
2

PLATE II

Horizontal section through a pigeon's head, showing the pecten attached to the papilla of the optic nerve. Fixed in alcohol-formalin-acetic acid, 75 μ celloidin section, Mallory's phosphotungstic acid hematoxylin (WINGSTRAND 1951). — CH = chiasma, HG = Harderian gland, LG = lacrymal gland, OI = m. obliquus inferior, OP = v. ophthalmica, OT = a. and v. ophthalmo-temporalis, P = pecten, PY = m. pyriformis, RA = m. rectus anterior, RP = m. rectus posterior, SC = scleral cartilage, SO = a. and v. supraorbitalis, SR = ossicular ring, TMN = tendon of the membrana nictitans. V_1 = ramus profundus trigemini.

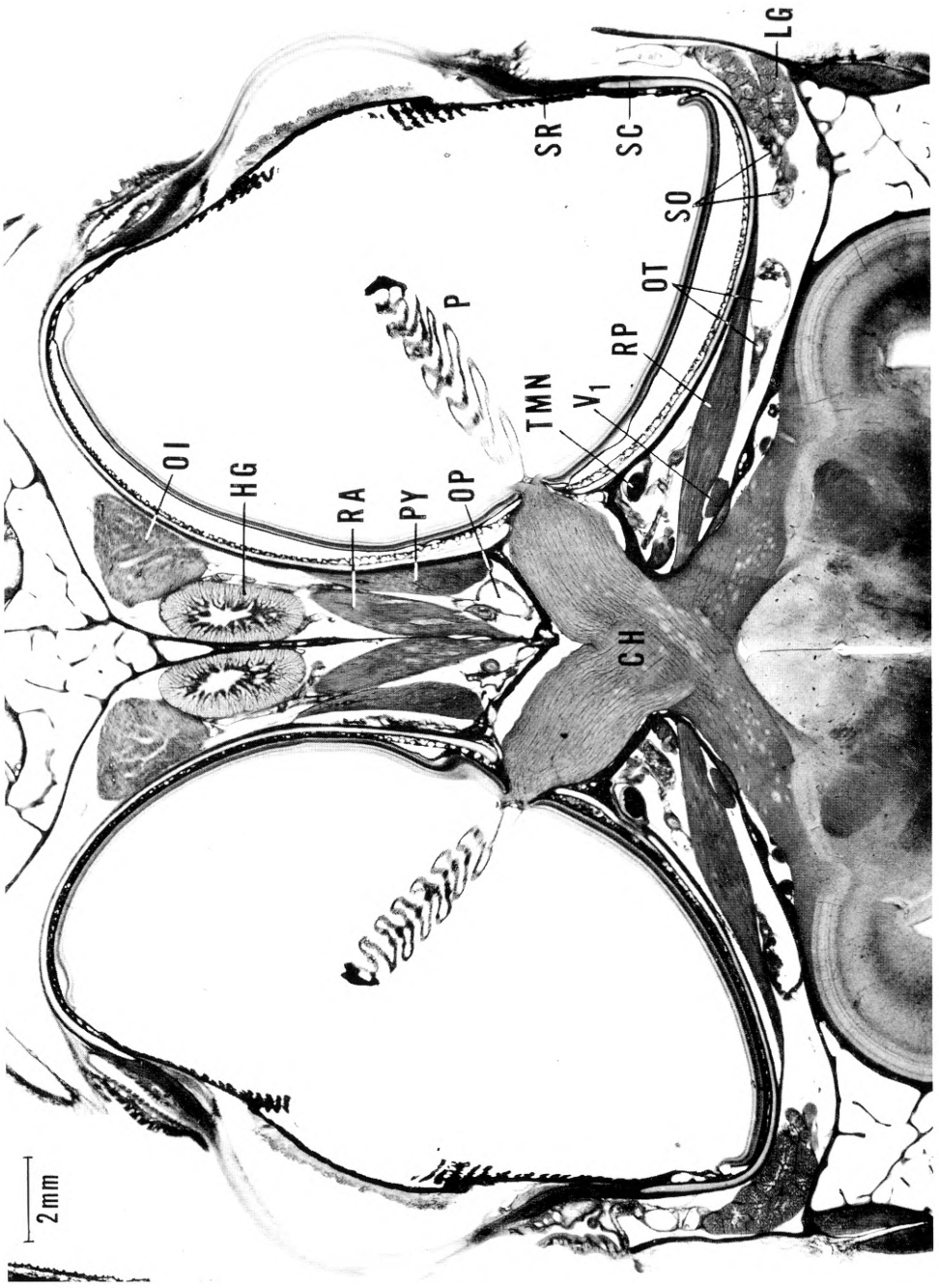
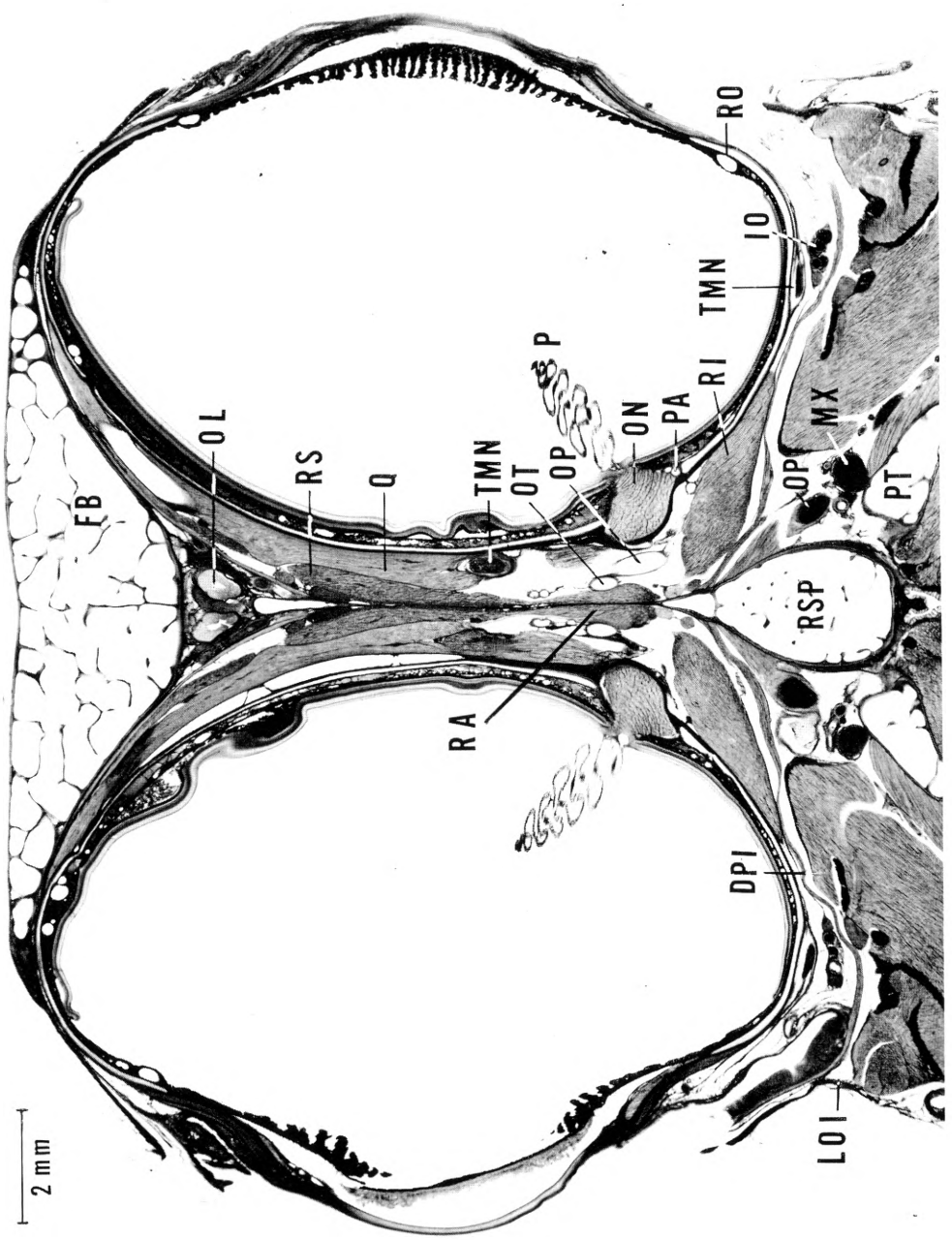

OI
HG
RA
PY
OP
P
TMN
V1
RP
OT
SO
SC
SR
LG
CH
2 mm

Plate III

Transverse section of a pigeons head through the papilla of the optic nerve. Technique as Plate II:1. DPI = m. depressor palpebrae inferioris, FB = os frontale with pneumatic cavities, IO = a. and v. infra-orbitalis, LOI = ligamentum orbitale inferius, MX = v. maxillaris, OL = n. olfactorius, ON = n. opticus, OP = vena ophthalmica (cut twice), OT = a. ophthalmo-temporalis, P = pecten, PA = pecten artery, PT = pterygoid bone, Q = m. quadratus, RA = m. rectus anterius, RO = venous ring sinus of the ora serrata, RI = m. rectus inferius, RS = m. rectus superius, RSP = rostrum sphenoidale, TMN = tendon of the membrana nictitans.


FB
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2 mm

PLATE IV

Electron micrograph of cross section through the folded wall of the pecten — Perfusion with glutaraldehyde, postfixation in OsO_4, methacrylate, staining with UAc. — ICS = intercellular spaces, MUS = superficial mucopolysaccharid membrane, STR = stroma cells with numerous processes (the one in the middle with damaged pigment granules). X = places where the extension of the intercellular space between the capillary wall and the superficial mucopolysaccharid membrane can be seen.

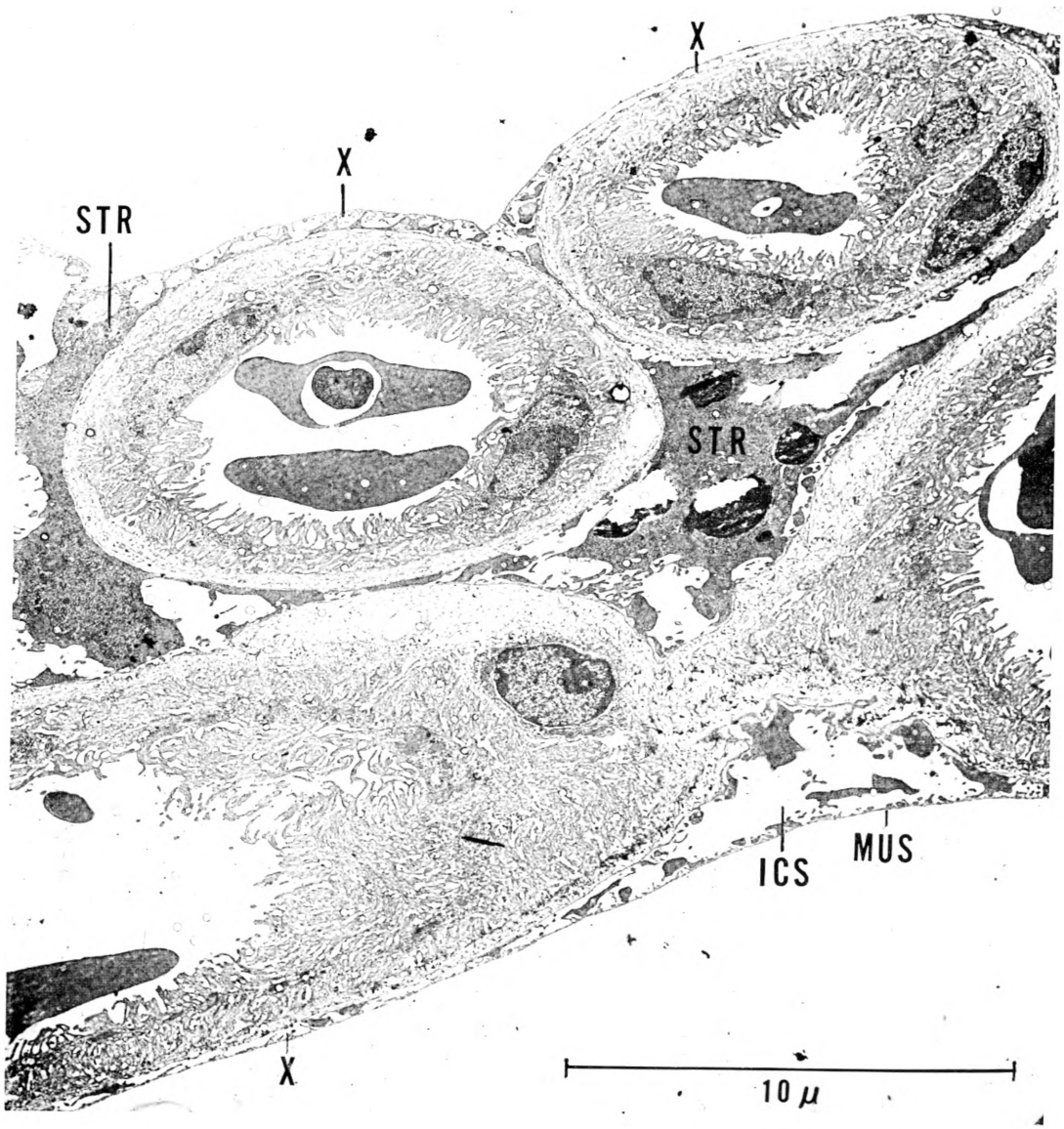
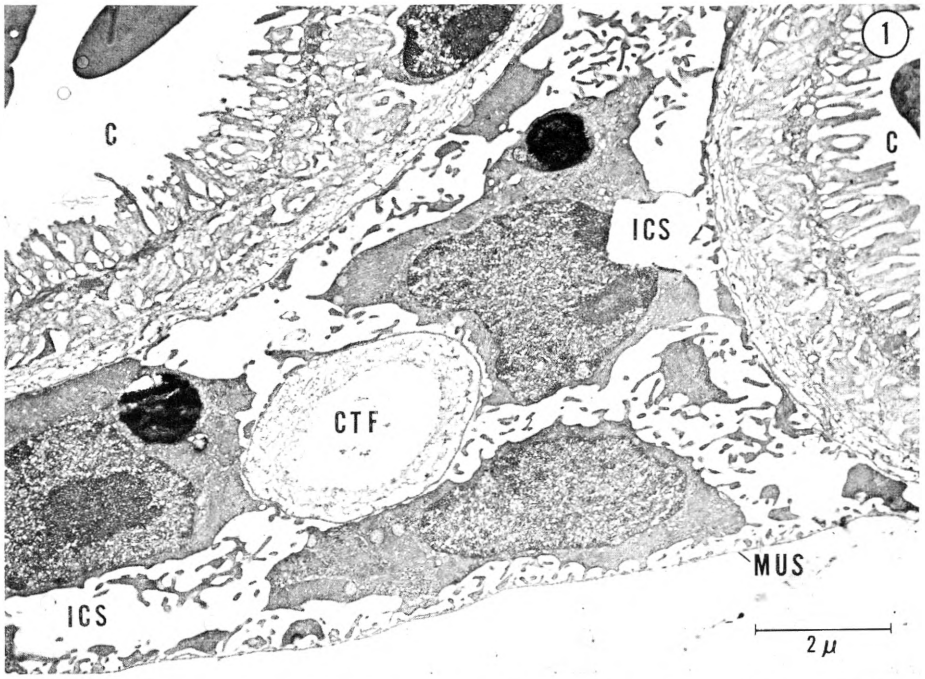

X
X
STR
STR
ICS
MUS
X
10 μ

Plate V

1. Electron micrograph from the folded part of the pecten, showing three stroma cells, two of which contain pigment granules, and their numerous ramified processes in the intercellular space (ICS). Some of these processes end under the superficial mucopolysaccharid membrane (MUS), some on the outer wall of capillaries (C), and some on the connective tissue string (CTF). Technique as Plate IV:1.

2. Plastic cast of the arteries of the pecten. The camera was focused on the fundus from a lateral direction, after the choriocapillaris, the anterior eye segment, and most veins had been removed. The figure shows the a. ophthalmo-temporalis (OT), which makes a loop below the entrance of the optic nerve (ON). The arteries to the pecten (P) and the long ciliary artery (LC) are emitted from the loop.


1
C
C
ICS
CTF
MUS
ICS
2 μ

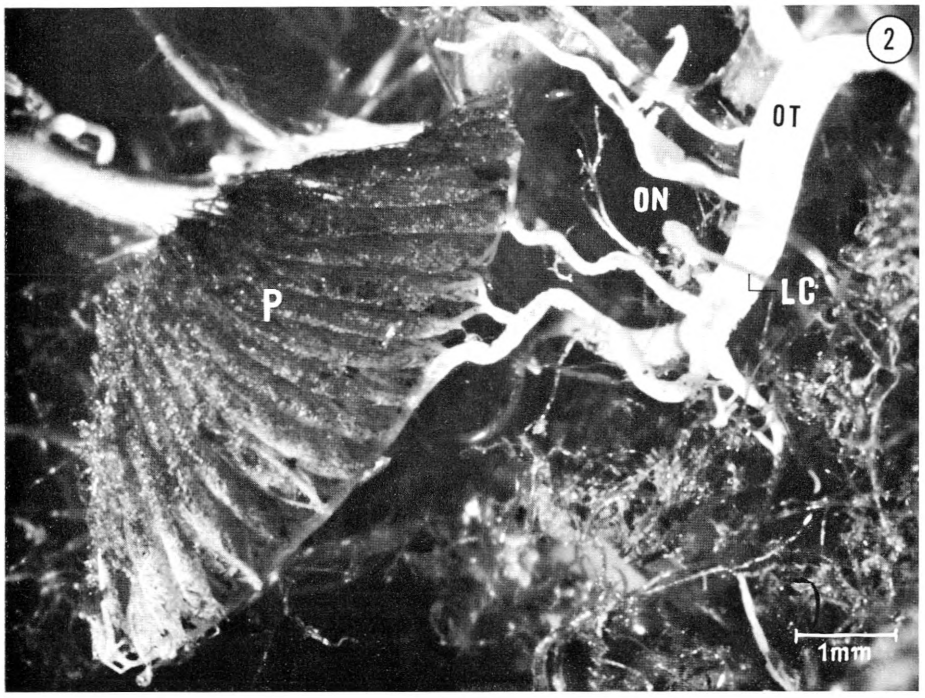

2
OT
ON
LC
P
1mm

PLATE VI

Electron micrograph of a capillary wall in the folded part of the pecten. Mitochondria (M) and some ergastoplasm is seen in the cytoplasm of the endothelial cell (E), which sends inner villi (IV) towards the lumen of the capillary (C) and outer villi (OV) towards the perivascular membrane (PM), in which connective tissue fibrils are visible. The stroma cell (STR) sends dark processes into the intercellular space (ICS) and is attached to the outer mucopolysaccharid membrane of the capillary. — Perfusion with glaturaldehyde, post-fixation in OsO_4, Epon, staining in lead hydroxyde.

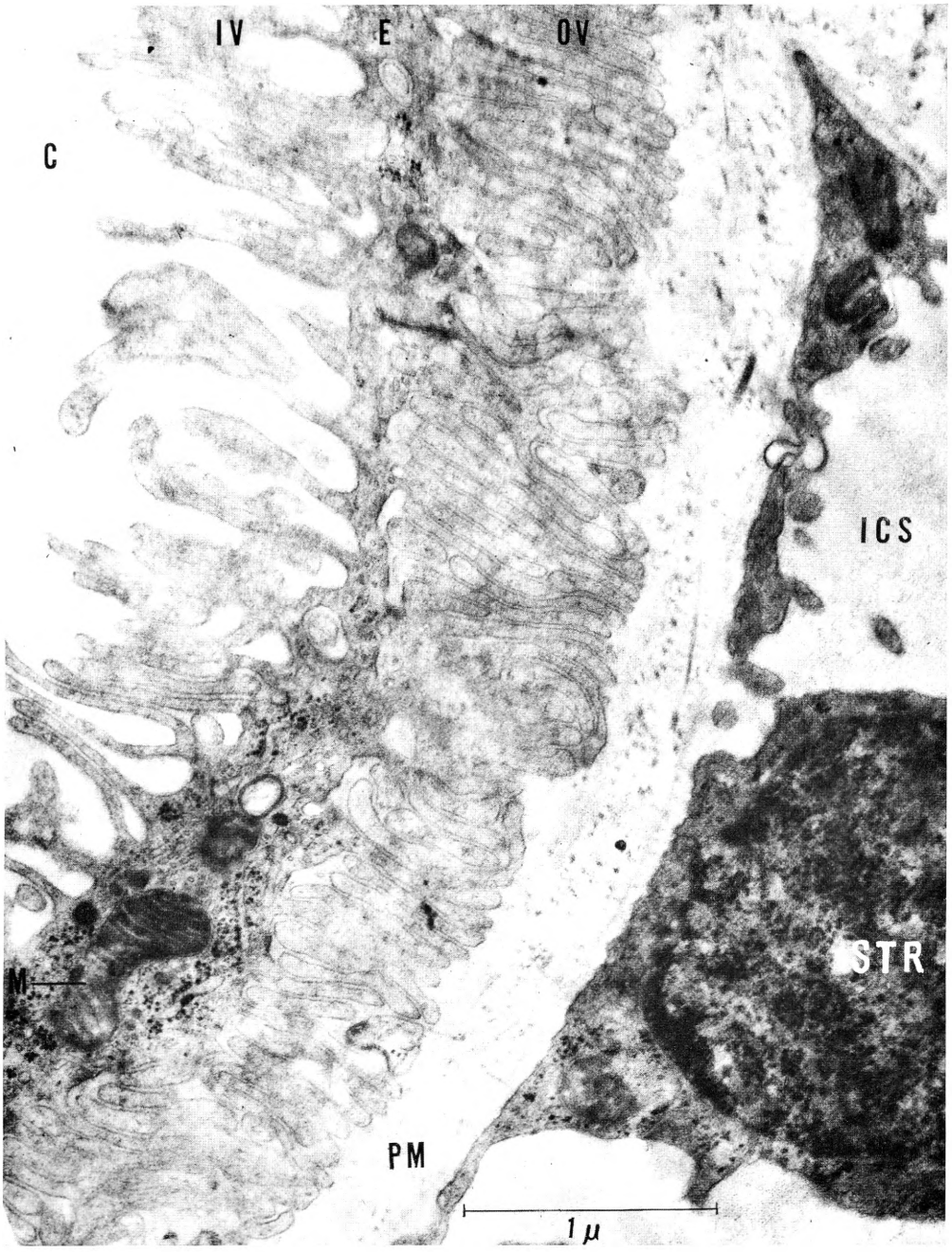
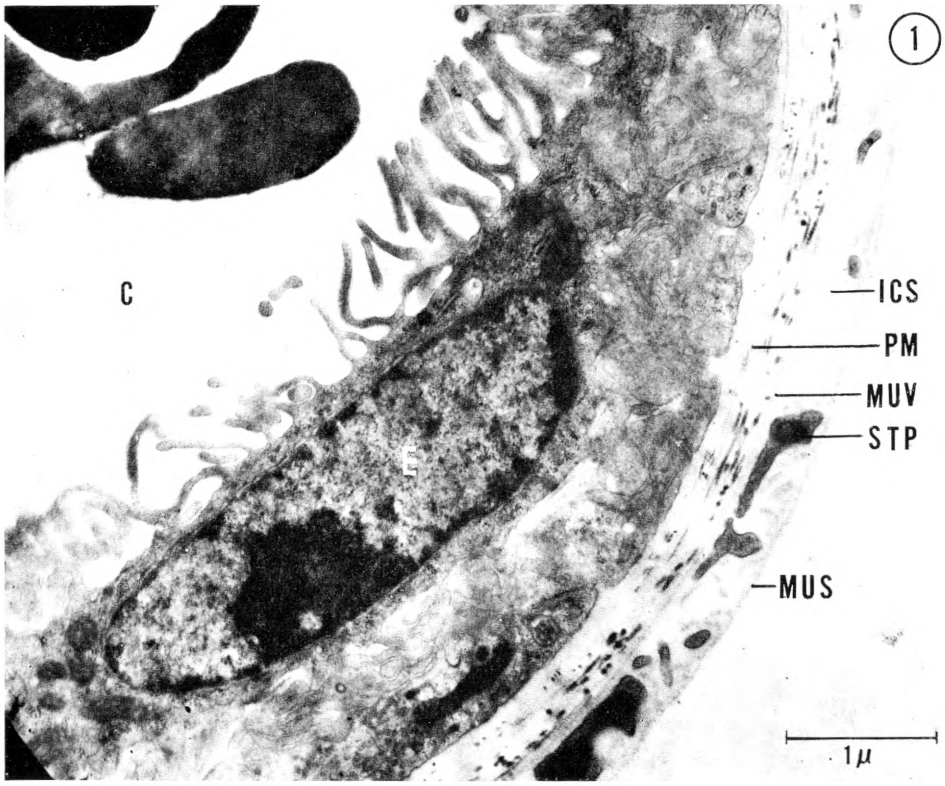

IV
E
OV
C
ICS
STR
M
PM
1 μ

Plate VII

1. Electron micrograph of the folded part of the pecten, showing the wall of a capillary (C), an endothelium cell with its nucleus (E), the perivascular membrane (PM) with collagen fibrils and the mucopolysaccharid membrane of the vessel (MUV). The intercellular space (ICS), separates the wall of the vessel from the superficial mucopolysaccharid membrane (MUS). Stroma cell processes (STP) are seen in the intercellular space. The outer villi of the endothelial cell are not distinct because they are parallel with the plane of sectioning. — Perfusion with glutaraldehyde, post-fixation in OsO_4, Epon, staining in lead hydroxyde.

2. Electron micrograph from the bridge of the pecten of the pigeon, showing numerous stroma cell processes, some with pigment granules (PIG), separated by fairly narrow intercellular spaces (ICS). "X" marks two processes, in which numerous small vesicles are visible. — Fixation in OsO_4, Epon, staining in lead hydroxyde.


1
C
ICS
PM
MUV
STP
MUS
1μ

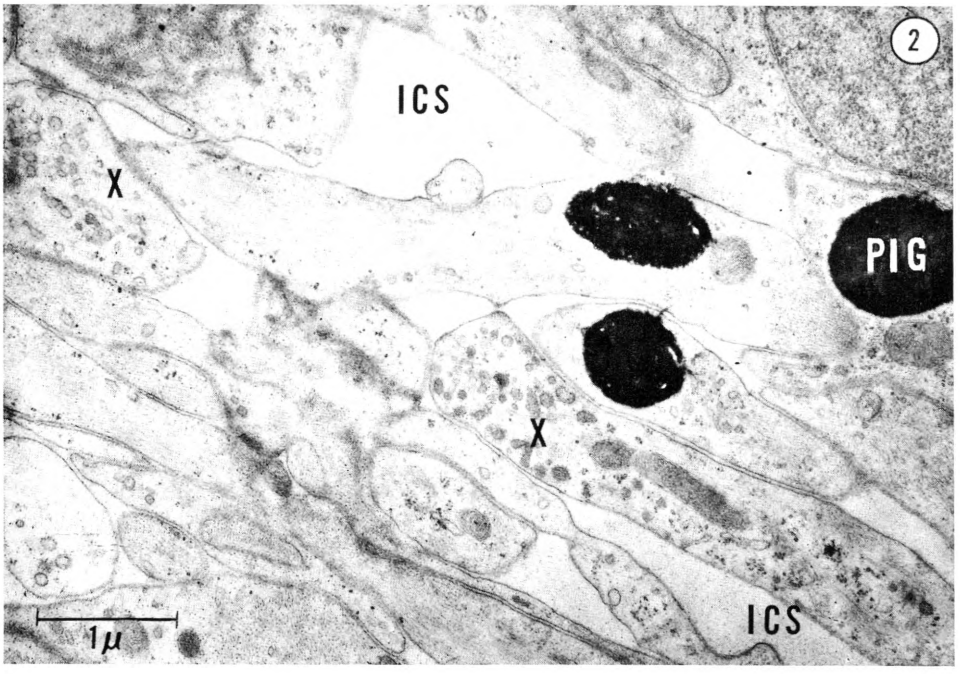

2
ICS
X
PIG
X
1μ
ICS

Plate VIII

Electron micrograph of the surface of the bridge of the pecten in a pigeon. Several stroma cell processes pass out to the surface, where a mucopolysaccharide membrane (MUS) delimits the collagen of the corpus vitreum (CVT). One stroma cell nucleus (N), pigment granules (PIG), a large mitochondrion (M), and some ergastoplasm (ER) can be seen. A fairly large intercellular space (ICS) does not reach the surface. All stroma cell processes contain filaments of the glial type, e. g. at "F".

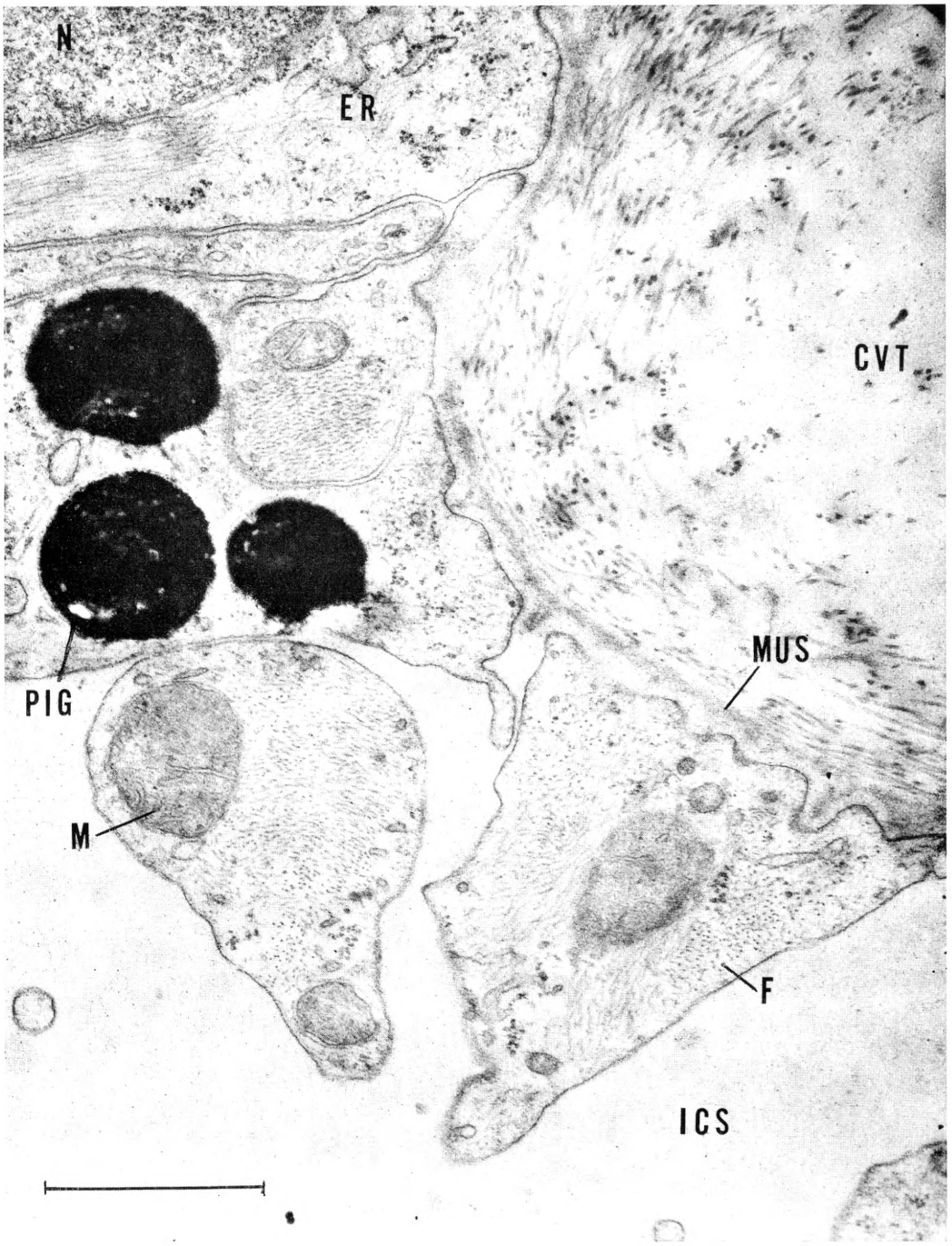

N
ER
CVT
MUS
PIG
M
F
ICS

Plate IX

The operational procedure used when the pecten arteries were approached, demonstrated on a dead pigeon, injected with starch-vermilion in the arteries and with starch-cobalt blue in the veins. For the purpose of illustration, the wound is made much larger than in actual operations.

1. The pigeons head fixed with plaster tape. Note the piece of glass tubing in the bill.

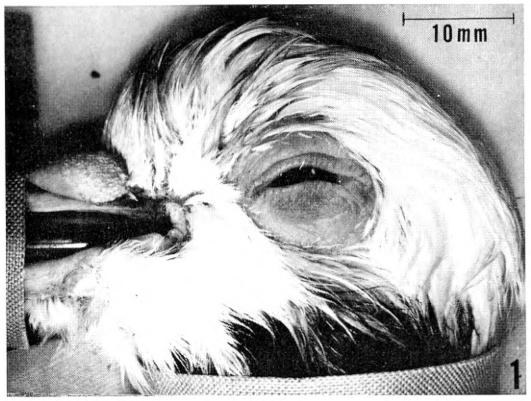
2. A piece of the supraorbital crest of the frontal (FB) has been detached through skin incision above the eye. The stippled line indicates the location of the skin incision below the eye.

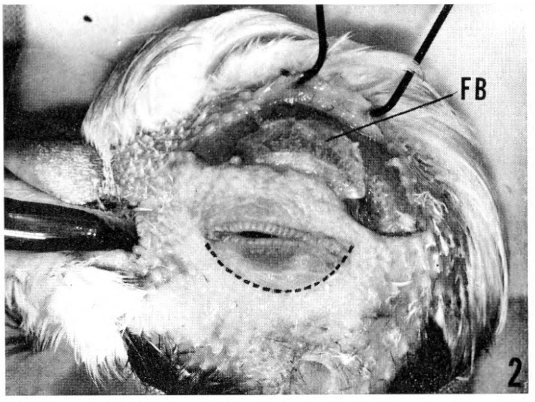
3. Skin incision below the eye, exposing the ligamentum orbitale inferius (LI, whitish). The stippled line indicates where the ligament is cut along the lower margin of the orbit.

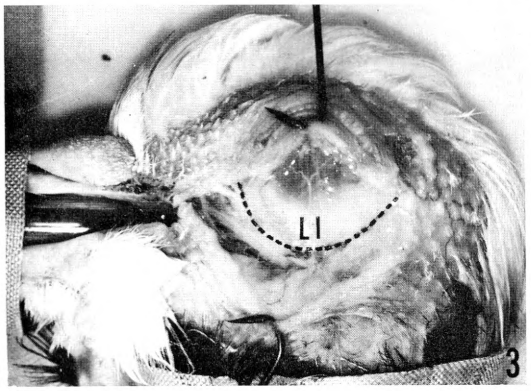
4. The ligamentum orbitale inferius is cut through, exposing the infraorbital vessels (IO) and the m. depressor palpebrae inferioris (DPI). J = jugal arch. The stippled line indicates where the depressor muscle is split.

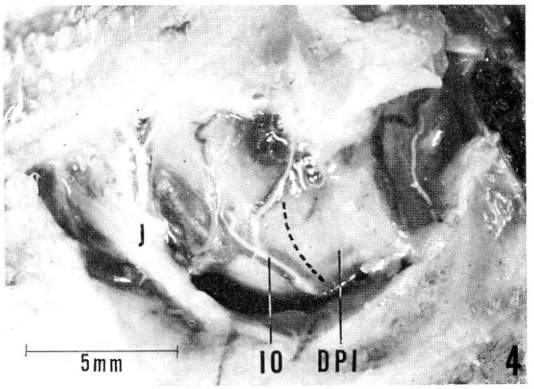
5. The m. depressor palpebrae inf. is split, and the broad hook (H) is applied in the opening, pulling the bulb dorsally. The pecten arteries are embedded in veins and fat in the angle between the m. rectus posterior (RP) and m. r. inferior (RI, difficult to discern).

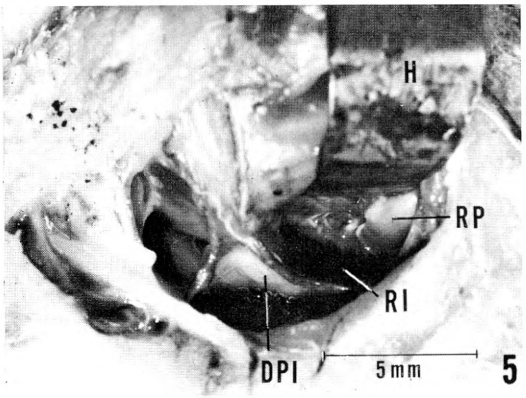
6. Veins and fat removed, the a. ophthalmotemporalis (OT) with the pecten arteries (P) exposed. LC = a. and n. ciliaris long., ON = optic nerve extension, RI = m. rectus inferior, RP = m. rectus posterior.


10mm
1


FB
2


LI
3


J
5mm
IO
DPI
4


H
RP
RI
DPI
5mm
5

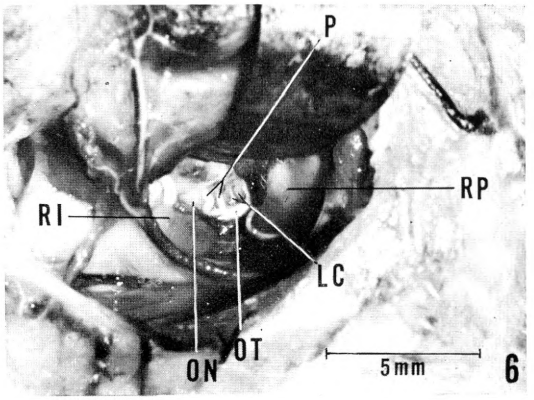

P
RP
RI
LC
ON
OT
5mm
6

PLATE X

1 and 2: Sections through the folded part of the pecten of the operated, left eye (1) and the normal, right eye (2) of a pigeon, 15 days after the operation. — 1: Azan staining, 2: hematoxylin-eosin. Magnification same in both figures. N. A. 0.20.

3 and 4: Details of the pectens shown in 1 and 2, resp. — 3: Azan staining, 4: PAS-hematoxylin. N. A. 1.0.

5. The pecten of the operated eye 165 days after the blocking of the pecten vessels. Scattered vessels have regenerated. — Azan staining, N. A. 0.20.

6. The pecten of a pigeon's eye 21 days after the vessels had been blocked. Heavy degeneration and invasion of retinal pigment cells, filling the spaces between the folds. — Azan staining, N. A. 0.20.

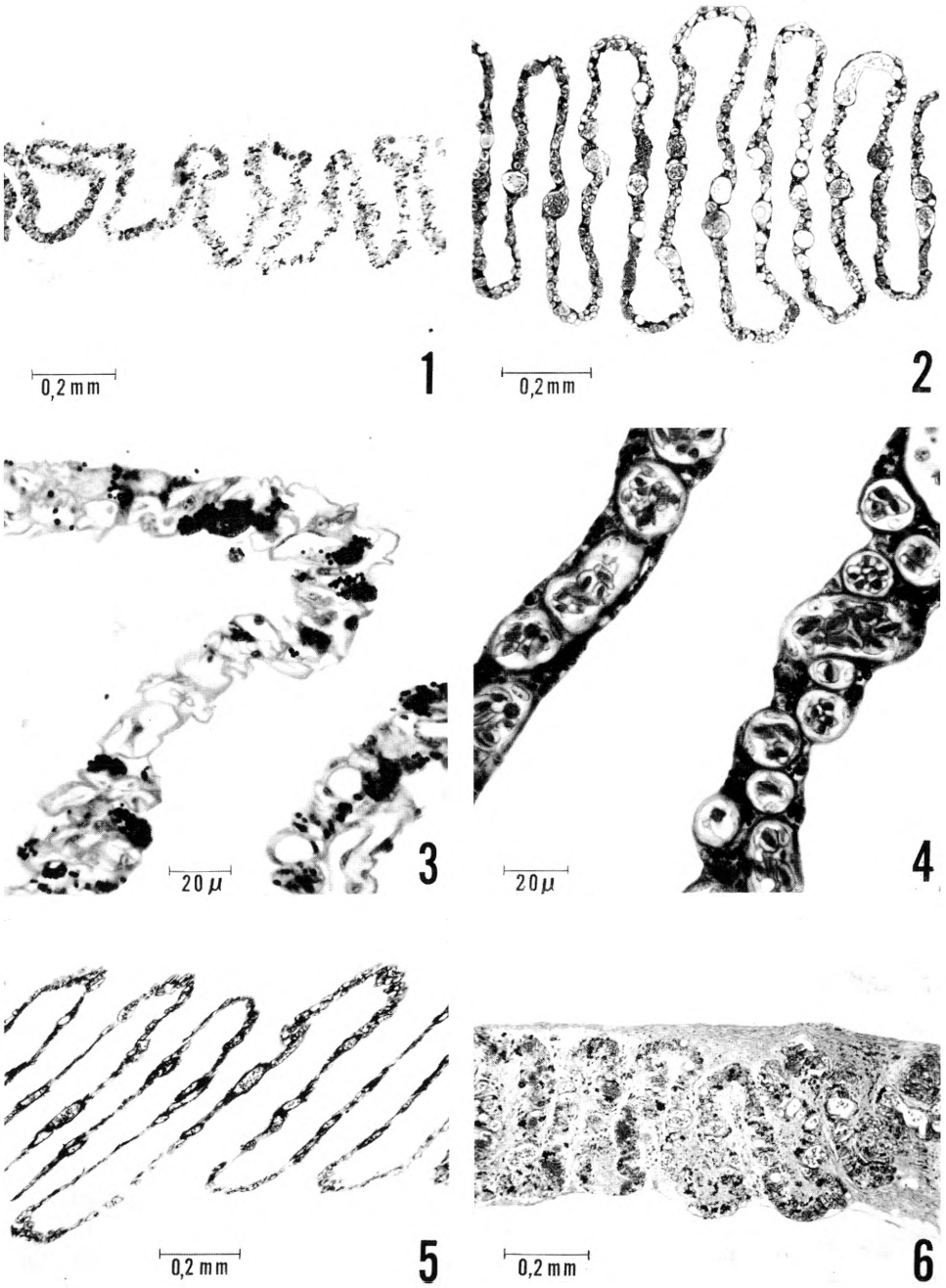
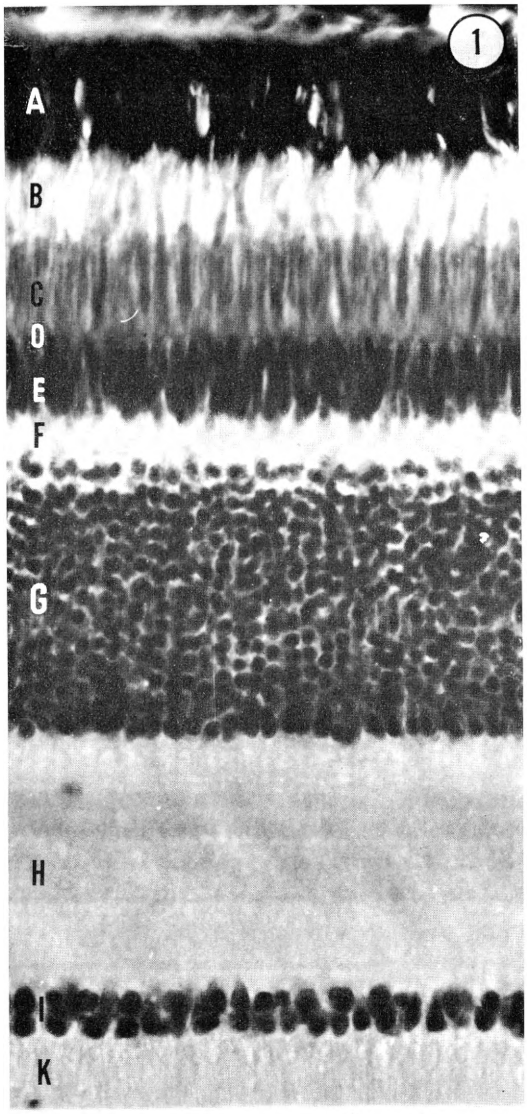

0,2 mm
1
0,2 mm
2
20 μ
3
20 μ
4
0,2 mm
5
0,2 mm
6

Plate XI

1. Normal retina of the right eye of a pigeon. A = pigment layer, B = zone of outer segments, C = zone of inner segments, D = membr. limitans ext., E = outer nuclear layer, F = outer plexiform layer, G = inner nuclear layer, H = inner plexiform layer, I = layer of ganglion cells, K = layer of nerve fibres. — Hematoxylin-eosin, N. A. 0.60.

2. Retina of the left, operated eye of the same pigeon, 15 days after the pecten vessels were blocked. Marked reduction of all layers, particularly of ganglion cells and optic fibres. Numerous macrophages, particularly in inner layers. — Hematoxylin-eosin, N. A. 1.0. Same magnification as 1.


1
A
B
C
O
E
F
G
H
I
K
20 μ

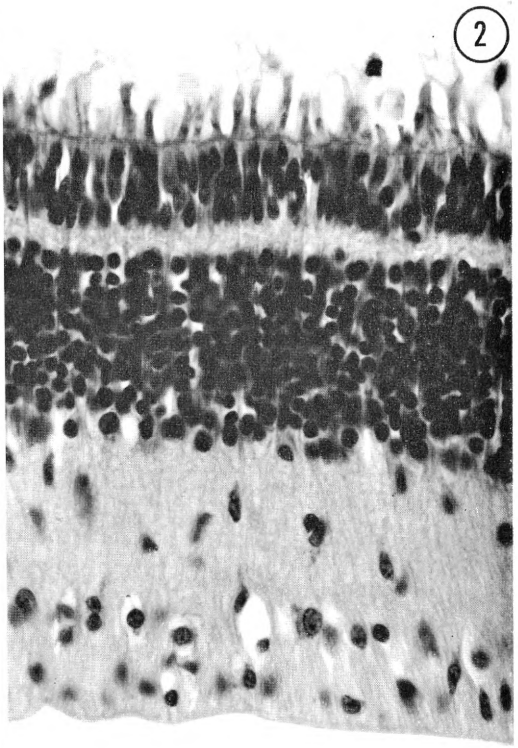

2

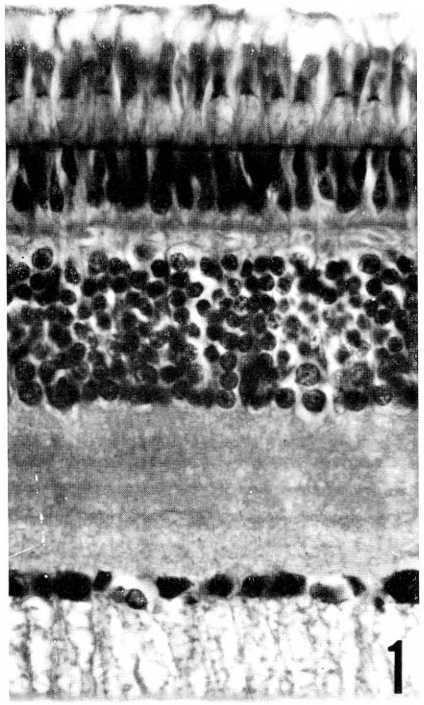
PLATE XII

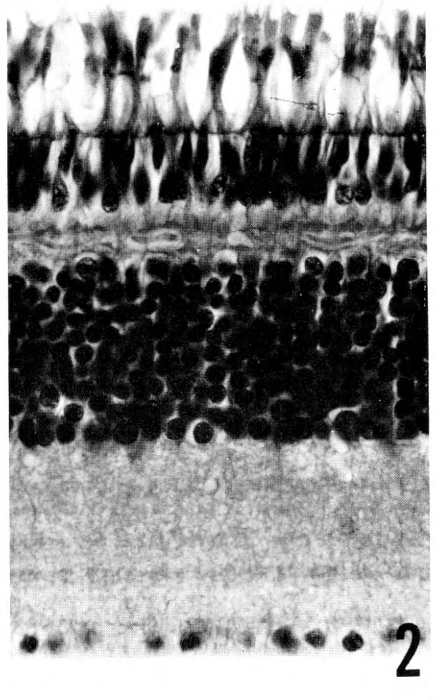
1 and 2: The retina of the right, normal (1) and of the left, operated (2) eye of a pigeon, 165 days after the pecten vessels were blocked in the left eye. Note the total absence of optic nerve fibres and the degenerate ganglion cells.

3. Retina of the operated eye of a pigeon 7 days after the pecten vessels were blocked. Note presence of macrophage cells in the nerve fibre layer (arrows).

4. Retina of the operated eye 15 days after the pecten vessels were blocked.

All figures from the nasal retina near the equator, stained with hematoxylin-eosin. Same magnification in all figures. N. A. 1.0.


1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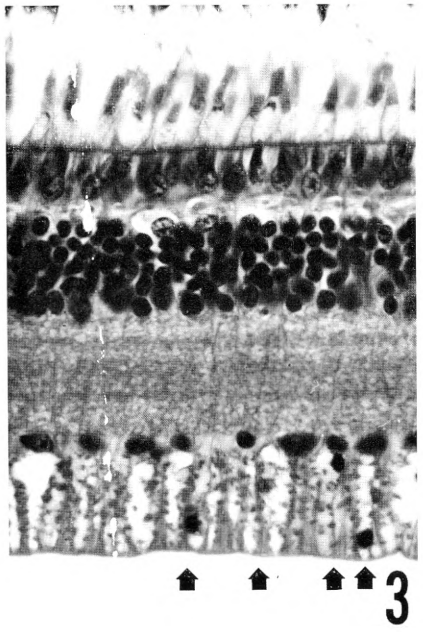
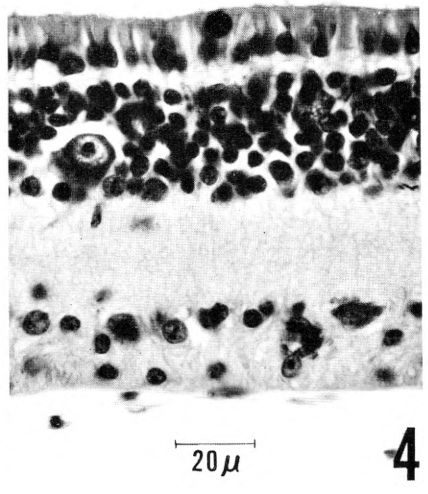

3


20μ
4

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