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A SCHEMATIC EYE FOR THE PIGEON

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INTRODUCTION

IN A previous paper (MARSHALL, MELLERIO and PALMER, 1972) we calculated the incident light on a pigeon retina and for this purpose required the *f*-number and the focal length. Therefore we measured several eyes, calculated the cardinal points and specified a schematic eye. Appreciating that the pigeon is commonly used in vision research, we are now publishing our findings in the form of tables and a diagram.

METHOD

Adult specimens of *Columba livia* of various sizes and both sexes were obtained from a laboratory animal breeder. To obtain the required information we adopted the following scheme.

(*a*) *Refraction*

Nine pigeons were fully refracted in lighted surroundings in both eyes to ¼D by an experienced refractionist. We assumed this was the relaxed condition because in the dark the birds accommodated by about 2D. Off-axis aberrations were very marked, and the measurements were made where these effects were minimal, that is, along the optic axis.

(*b*) *Dimensional determinations*

The refracted pigeons were killed with an interplural injection of nembutal, and the left eye was extracted and fixed in 2·5% glutaraldehyde buffered in 0·1 molar sodium cacodylate at pH 7·4. It was then hemisected in a suitably modified ocular hemisector through the vertical meridian between corneal pole and optic nerve exit. The blade always entered at the posterior of the globe and emerged from the cornea. This method minimized traumatic distortion of the globe as the blade cut through the sclerotic ossicles. One half was photographed (Fig. 1) together with a calibrated grid so that the ocular dimensions could be determined by projection and tracing.

From the tracings we first estimated the axis of symmetry, using a strip of glass in order to compare each surface with the reflection of the other half. Particular attention was paid to the cornea because it is the principal refracting surface, but the whole procedure was imprecise because the surfaces were obviously not well centred. Along the axis, we then measured the depth of the anterior chamber, the lens thickness and the distance from the posterior lens surface to the junction of the retina and choroid. Assuming the sphericity of the surfaces, we estimated their radii with a gauge of calibrated concentric arcs. The precision in all dimensions was better than 0·1 mm.

We were concerned that our fixation and sectioning should not unduly distort the tissues, so we compared four eyes before and after fixation to estimate possible changes in the overall shape and size of the globe and cornea. We also compared the fixed eyes before and after sectioning. No changes could be detected. Distortions in the lens could not be investigated, but optically these would be less important than proportionately similar deformations in the cornea and axial length.

(*c*) *Refractive index determinations*

The refractive indices of the aqueous and vitreous humours and the lens were measured in a few eyes with an adapted form of Pulfrich refractometer (Fig. 2). The specimen was applied to one face of a 45°, 90° glass prism, and illuminated with sodium light (589 nm). A single lens reflex camera served as a viewing telescope in which the images could be recorded photographically. This was mounted on a rotatable arm whose angular position could be read from a protractor. The image *I* of the specimen, as seen through the adjacent face of the prism, was set at the centre of rotation of the arm.

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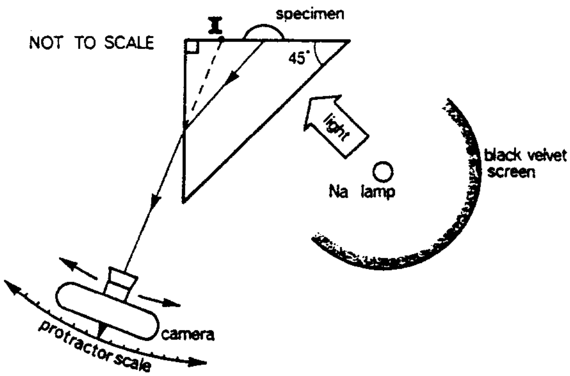

FIG. 2. Pulfrich refractometer adapted to photograph lens sections with sodium light. The camera arm is pivoted about the image I of the specimen.

The principle of the instrument is to find the critical angle at which light can just penetrate from the medium into the prism. There are two possible illuminating conditions, either from the rear of the specimen, with grazing incidence as in the conventional Pulfrich refractometer (DAISH, 1968), or through the hypotenuse of the prism. The present media, being biological, were all slightly cloudy, and for both types of illumination the small inclusions scattered enough light for photography. By using a small lamp with a black screen behind it, very good contrast was obtained as the specimen flashed up.

A hemisected lens could be photographed at different angles of viewing to show the contours of refractive index (Fig. 3). For this purpose, the lens surfaces had to be dried carefully on filter paper before cutting, to avoid contaminating the cut surface with aqueous or vitreous.

(d) Computation of the schematic eye

From the measured refractive indices, the radii of the refracting surfaces and their separations, we computed by standard ray-tracing the positions of the anterior and posterior foci, and the principal planes and nodal points (CONRADY, 1957).

We averaged the linear dimensions and the refractive indices of aqueous and vitreous. We disregarded the variation of index within the lens, and instead calculated that bulk value for the averaged eye which would make the calculated refractive power agree with the averaged power determined by retinoscopy.

RESULTS

Figure 1 shows a photograph of a hemisected eye and Table 1 gives the averaged dimensions for nine eyes, with the standard deviations about the mean results, which are due mainly to variations between the pigeons. Also shown in this table is the averaged pupillary diameter for eight pigeons from the previous study (MARSHALL, MELLERIO and PALMER, 1972), when completely surrounded by screens uniformly illuminated with white light at 2000 cd. m^{-2}.

Table 2 gives the averaged refractive indices of aqueous, vitreous and lens of a few pigeons from which material was available from the other unsectioned eye. As only small quantities of material were used these quickly assumed the temperature of the room (25°C). However, correcting the indices of aqueous and vitreous to eye temperature (presumably slightly less than the body temperature of 38°C) has a negligible effect on the calculations for the schematic eye, if the temperature coefficients are similar to that of water (KAYE and LABY, 1959).

Figure 3 shows a hemisected lens photographed at various critical angles so as to demonstrate the contours of refractive index. There is a slight variation of critical angle across the field for a given index, which can easily be allowed for. We have made little use of such

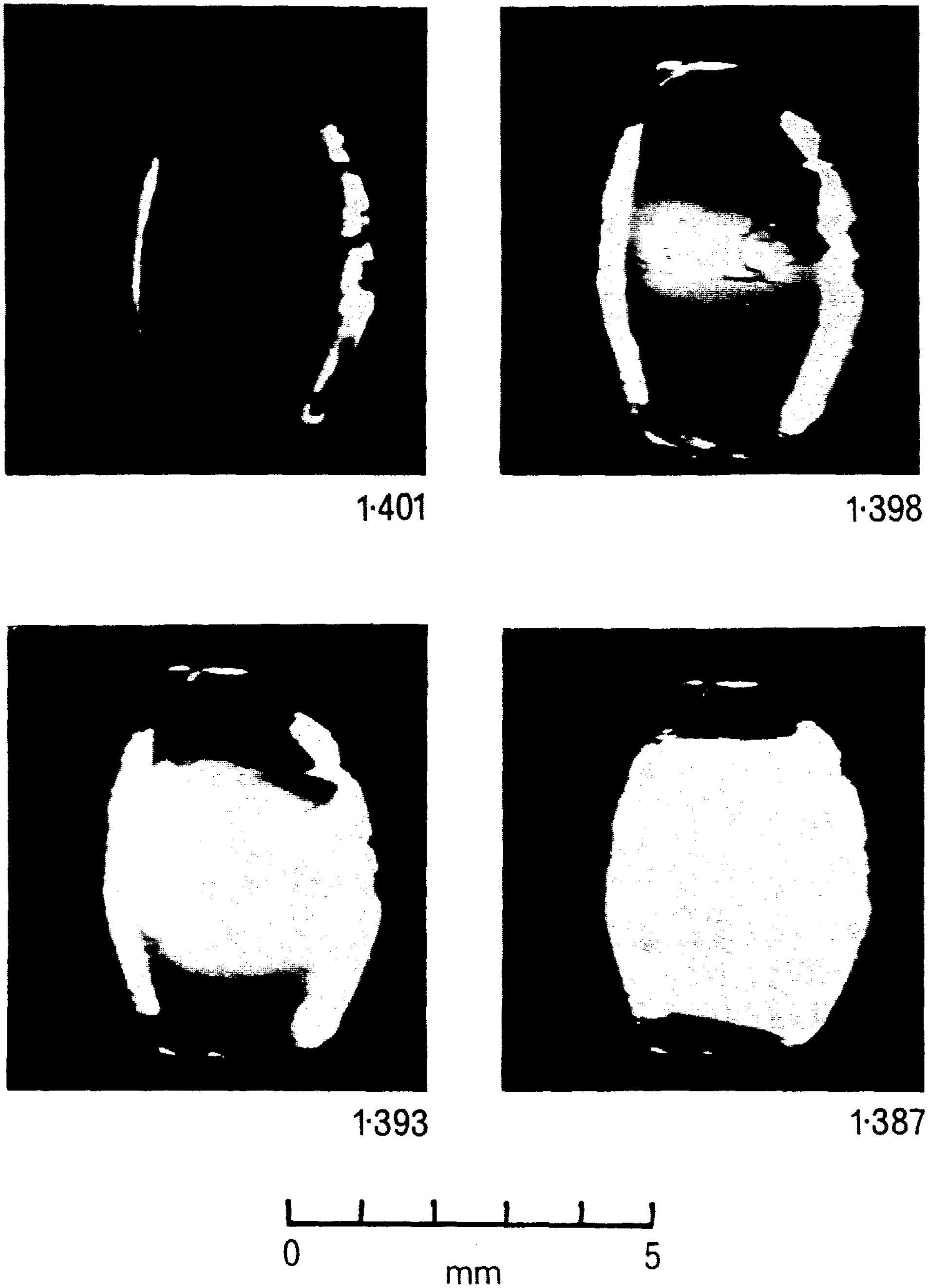

FIG. 3. Photographs of sagittal sections of a pigeon lens in the refractometer to show contours of constant refractive index at critical angles corresponding to indices of 1·401, 1·398, 1·393 and 1·387 for sodium light (589 nm). The anterior surface faces left, and the photograph has been printed anamorphically, to compensate for the prismatic distortion in the refractometer. The scale divisions represent 1 mm.

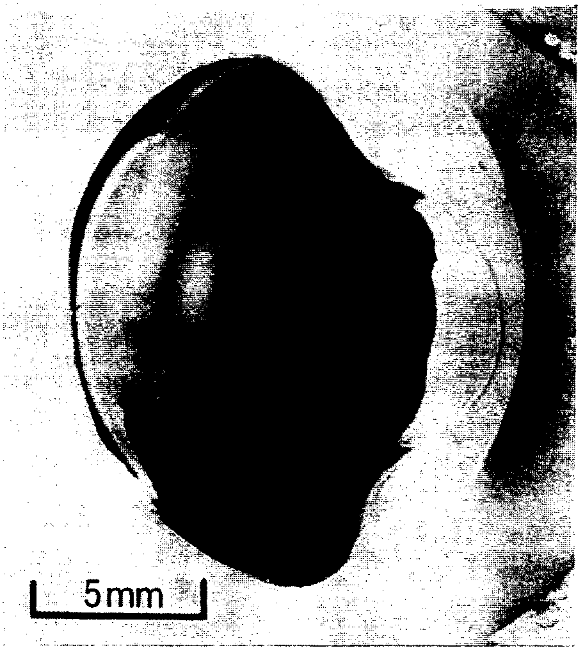

FIG. 1 A vertically hemisected pigeon eye showing the optic nerve exit in the lower half. The corneal profile and the lens outline are the refracting surfaces and are obviously not well centred.

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Table 1. The means and standard deviations of various dimensions of the pigeon eyes. The third decimal place, whilst generally not significant, was used in calculating the cardinal points of the schematic eye in Fig. 4, to avoid rounding-off errors

Parameter	Mean (mm)	Standard deviation (±)	Number of birds
Radius of cornea	3·443	0·217	9
Radius of lens anterior surface	4·174	1·113	9
Radius of lens posterior surface	3·080	0·305	9
Depth of anterior chamber	1·771	0·159	9
Thickness of lens	2·924	0·169	9
Distance from lens posterior surface to retina	6·576	0·321	9
Pupillary diameter at 2000 cd m^{-2}	2·0	0·2	8
Refractive error by retinoscopy	+2·4D	0·2D	9

Table 2. Mean refractive indices and standard deviations of the ocular media. The absolute accuracy of the refractometer is about ±0·001. The standard deviations in this table are therefore mainly due to differences between specimens

Medium	Mean refractive index at 25°C for light of wavelength 589 nm	Standard deviation (±)	Number of specimens
Aqueous humour	1·334	0·002	4
Vitreous humour	1·341	0·004	3
Lens cortex	1·383	0·009	8
Lens nucleus	1·409	0·010	8
Assumed bulk lens	1·408	—	—

detailed information in setting up the schematic eye, and have included this plate mainly to show what information can be obtained. The lens margin is revealed, presumably because of local drying which has increased the refractive index. There was no evidence of other changes due to evaporation for at least 0·5 hr, and measurements were usually complete within 15 min of extraction from the animal. This statement also applies to the aqueous and vitreous determinations.

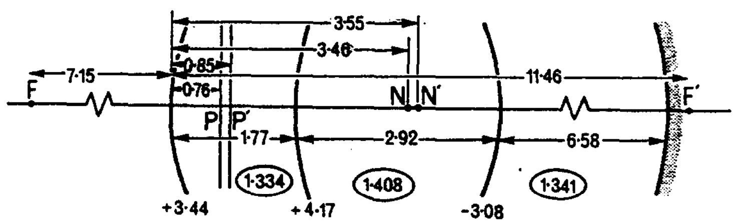

Fig. 4. The schematic eye of the pigeon derived from measurements of nine eyes. The pole of the cornea is taken as the origin of the distances in millimeters of the cardinal points along the axis. P and P′ are the anterior and posterior principal planes, N and N′ the nodal points and F and F′ the foci. The radii of curvature of the refracting surfaces are given in millimeters (in the cartesian sign convention) at the bottom of the diagram. The refractive indices of the ocular media are ringed. The total optical power of the schematic eye is 126 dioptres.

The schematic eye appears diagrammatically in Fig. 4. The effective *f*-number, which is essential for the estimation of retinal illuminance, is given by the distance from the posterior nodal point to the retina divided by the pupillary diameter. The pupil diameter quoted in Table 1 for a luminance of 2000 cd.m^{-2}, which corresponds to that of an overcast sky, gives an *f*-number of about 4. The variation in the avian pupil with illuminance is small, but we suggest that interested investigators should measure pupil size under their own experimental conditions.

DISCUSSION

All nine pigeons were slightly hyperopic according to retinoscopy, and this is reflected in the schematic eye. However, ray-tracing in the individual eyes using the assumed bulk refractive index for the lens of 1·408 indicated a large range of refractions, from 10D of myopia to 17D hyperopia. This spread is considerably more than the total range of only 4D found in the retinoscopy of the same pigeons. The differences between ray-tracing and retinoscopy ranged from −14D to +13D, and in order to explain such discrepancies, we looked for distortions of the eye induced by fixation and sectioning as no reasonable value for the assumed bulk index of the lens could account for these figures. Four eyes were examined and showed no distortion, but this does not exclude the possibility in the other eyes. We did not investigate possible changes due to excision, for example from the relaxation of Crampton's muscle, which might increase apparent hyperopia (WALLS, 1963).

Differences between retinoscopy and ray-tracing could also arise from the techniques adopted. The refractionist made no allowance for the origin of the retinal reflex; any error is hardly likely to exceed 4D which corresponds to the retinal thickness (350μm).

The refractive index measurements were very precise and propagated the smallest errors. The vitreous index of 1·341 (Table 2) is higher than that of distilled water (1·333, KAYE and LABY, 1959) and that of the human vitreous (1·334, EMSLEY, 1952). The measurements of the lens material were not crucial to the schematic eye because of our method of adjusting the bulk index, so that ray-tracing through the eye of averaged dimensions agreed with the averaged refraction found by retinoscopy.

The results are for light of wavelength 589 nm. We did not use other wavelengths, but it is reasonable to assume from experiments with other species, e.g. man (EMSLEY, 1952), that the dispersion will vary with wavelength like that of water. For the human eye, EMSLEY (1952) quotes a difference of refraction of 0·47D between 589 nm and 461 nm. The corresponding difference in the pigeon eye will be greater in the ratio of the respective optical powers, i.e. 126/60, or about 1·0D. Thus given 2·4D of hyperopia at 589 nm (in Table 1) there will be about 1·4D hyperopia at 461 nm.[2]

In the photographs of the hemisected eyes, the retinae were not usually normal to the apparent optical axis (Fig. 1). This tilt combined with the imprecision of locating the axis could result in a precision of about 2D in the calculated refraction. The precision of 0·1 mm in the linear measurements produces a further uncertainty of about 3D. If these figures are combined according to the usual r.m.s. formula, the overall precision in calculated refraction is about 4D. As already mentioned, some calculated refractions differ from the corresponding retinoscopy measurements more widely than this.

We are confident that we have not introduced large systematic errors into the averaged eye, although we cannot explain all the discrepancies. The extremes quoted almost cancelled

[2] The difference in refraction between the sodium light assumed for ray tracing and the "yellow" tungsten light used in retinoscopy was estimated as less than ¼ D.

out in the averaging, and any residual effect would be eliminated by our technique of adjusting the bulk index of the lens. It is reassuring that this assumed value lies plausibly within the measured range (Table 1). To keep the discussion in perspective, it should be noted that the worst discrepancy in an individual pigeon is only 11 per cent of the total power of 126D.

A schematic eye is a paraxial optical system and may not be used for rays more than 10° off-axis. We did not investigate off-axis imaging except to note by retinoscopy the very rapid increase in aberration away from the axis. The tilt of the retinae was always consistent with Millodot and Blough's findings that pigeons are more myopic in the upper retinal quadrant (MILLODOT and BLOUGH, 1970).

There remains, however, the interesting fact that although our schematic eye is hyperopic on axis, the red spot (a specialized area of high cone density) lies above the axis in the myopic region of the retina. The pigeon retina also has a fovea, which is probably visually important, but we cannot comment on the refraction there, because it was not in the plane of our section.

We must stress, therefore, that our schematic eye refers properly only to the paraxial optics, and does not completely describe the eye from a behavioural standpoint.

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Abstract—The dimensions of several pigeon eyes have been measured, together with the refractive indices of the ocular media. From these data a schematic eye has been constructed.

Résumé—On mesure les dimensions des yeux de plusieurs pigeons ainsi que les indices de réfraction des milieux oculaires. On construit un oeil schématique à partir de ces données.

Zusammenfassung—Die Abmessungen von mehreren Taubenaugen und die Brechungsindices ihrer Medien wurden gemessen. Von diesen Daten ausgehend wurde ein schematisches Auge konstruiert.

Резюме—Определены размеры нескольких глаз голубя, совместно с коэффициентами преломления оптических сред. На основании этих данных был построен схематический глаз.