ON THE VISUAL SYSTEM OF *NAUTILUS POMPILIUS*

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SUMMARY

The anatomy of the eye of *Nautilus pompilius* Linnaeus was studied, using light and electron microscopy. The outer and inner surfaces of the iris were found to be lined with columnar epithelium bearing microvilli, except for the groove running ventrally from the pupil over the outer surface of the iris, where the epithelial cells bear cilia. Many mucus cells are also present.

The epithelium of the inner surface of the iris merges smoothly with the retina. There is no significant variation in receptor packing or rhabdome length between different parts of the retina. Screening pigment is present, but shows no photomechanical movements in response to light. Immediately beneath the retina the nerves are collected into well-organized bundles, which run in a direction suggesting that they may form an optic chiasma analogous to that found in other cephalopods.

Visual acuity was also determined, using the optomotor response. The minimum separable angle was found to lie between 11·25 and 5·5°. This agrees well with the value expected on the basis of the gross dimensions of the eye and pupil, and also with expectation based on photographing a visual test chart with a scale model of the eye. It is, however, considerably worse than would be expected from the dimensions of the receptor mosaic.

INTRODUCTION

The various species of *Nautilus* alive today are the only known representatives of a once highly successful group of cephalopods, the Nautiloidea, that originated in the Cambrian and radiated and multiplied over the next four hundred million years or so before being replaced by the ancestors of the present day coleoid cephalopods (Teichert & Moore, 1964). As far as can be judged, *Nautilus* has remained unchanged in many respects since Jurassic times, and its study is thus of special interest in attempts to reconstruct how the organization of the modern cephalopods has developed to its present state. The visual system is among many features that may be primitive in *Nautilus*. Thus, firstly, the eye has no lens, but operates on the principle of a pin-hole camera, and secondly, the nerves leaving the retina appear to pass directly to the optic lobes, whereas in all other cephalopods so far studied, with the one further exception of a cirroteuthid (Young, 1977), there is a chiasma such that the nerves from the top of the retina go to the bottom of the optic lobe and *vice versa*.

Previous studies on the visual system of *Nautilus* have covered various aspects of

gross anatomy, image formation, histology and central nervous connections (e.g. Owen, 1832; Hensen, 1865; Griffen, 1900; Mugglin, 1937; Young, 1965; Barber & Wright, 1969). The present paper presents further information on these topics.

MATERIALS AND METHODS

Material

Nautilus were trapped off the main reef at Suva, at depths between 165 and 600 m, and kept in glass aquaria in a cold room at temperatures between 7 and 13 °C. The water was changed regularly, and the animals fed occasionally on fish. Under these conditions they remained alive for 2 weeks or more, though reliable optomotor responses (see below) could only be obtained during the first 4 or 5 days, indicating that their condition was deteriorating.

Histology and gross anatomy

For light microscopy the animals were anaesthetized in 4 % urethane solution, killed, and specimens of various tissues dissected out and preserved in 10 % formol in sea water. The specimens were then embedded in Emix resin, sections cut at 2 μm and stained with Toluidine blue. For electron microscopy specimens were fixed in 3 % gluteraldehyde in phosphate buffer at pH 7·4 for 3 h, then transferred to buffer alone. After post-fixation with osmium tetroxide for 1 h sections were cut at 90 nm. Sections were cut in various planes (Fig. 1). Assuming that the eye approximates a sphere, with the back half formed by the retina and the front half by the iris, and with its axis orientated vertically, some sections were cut in a plane that passes through the centre of the sphere (i.e. perpendicular to the retina or iris) and through a line of longitude. Such sections will be referred to as meridional sections. Other sections were cut in a plane that passes through the centre of the sphere and through two points of equal latitude. Although the term is not strictly accurate, such sections will be referred to as parallel sections. By tangential sections are meant those cut parallel to the surface of the retina or iris.

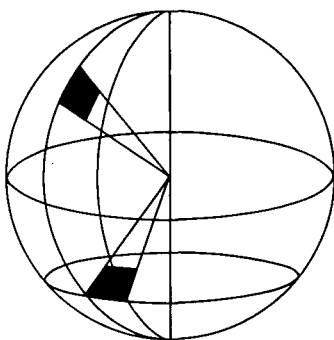The gross dimensions of the eye were obtained from photographs of intact eyes that

Fig. 1. Planes in which sections were cut. The upper black rectangle shows the plane of a meridional section, the lower black rectangle the plane of a parallel section.

▮▮d been bisected in various planes. Both fresh material and formol-fixed material were used: comparison of measurements before and after fixing showed that this fixative caused little shrinkage.

The optomotor response

The optomotor response was tested using the apparatus shown in Fig. 2. The animal was placed in the glass vessel in the centre, which was filled with water to such a depth that the bottom of the shell just rested on the bottom of the vessel. In this way the animal could be positioned so that the eyes were near the centre of the apparatus, which is necessary in order to reduce as much as possible distortions caused by the curved sides of the glass vessel. The animals did not remain in this position for long, but the initial response was usually a simple rotation, achieved using the funnel, which could be clearly seen before the animal left its central position. Only animals caught within the previous 3 or 4 days were used.

The outer drum was constructed from thin sheet metal, and the stripes were made on cylinders of thick paper, which could be inserted within it. The drum was rotated by hand at a speed such that one complete revolution took, very approximately, 14 s. The apparatus was illuminated by the general room lights (Sylvania F40 coolwhite fluorescent tubes), and the luminance of the white stripes, measured with a photographic exposure meter subsequently calibrated against a UDT 40X optometer, was $17\,\mathrm{cd\,m^{-2}}$.
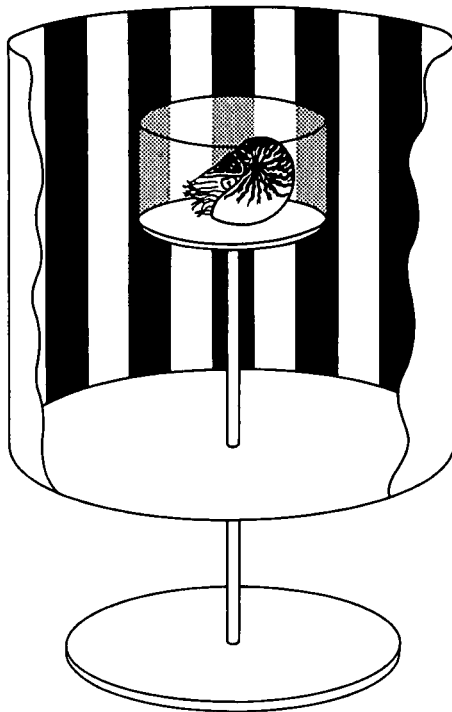

Fig. 2. Optomotor apparatus. The inner glass vessel containing the animal is 25 cm in diameter, which gives the scale.

Gross anatomy of the eye

The horizontal dimension of the eye was always greater than the vertical dimension. In four eyes for which accurate measurements were made the average horizontal dimension was 15·2 mm (range 13·5–16 mm), and the average vertical dimension 10·2 mm (range 9·1–10·3 mm). The average distance from the pupil to the centre of the retina was 8·7 mm (range 8·0–9·1 mm). Fig. 3 shows the appearance of vertical and horizontal sections through the centre of two eyes that were fixed in 10 % formol. Before fixing the vertical dimension of one of the eyes of this animal was 10 mm and the horizontal dimension 16 mm, so fixation caused little change in size. The shape of the fundus of another formol-fixed eye, after the front of the eye was removed, is also shown. The anterior part of the eye can be seen to be slightly smaller than the posterior part (Figs 3B, C). The pupil of this eye was an irregular oval, and measured 1·13 mm in the horizontal direction and 0·44 mm in the vertical direction: since, however, the pupil of *Nautilus* is contractile, its size is probably affected by fixation.

Structure of the retina

Fig. 5A shows a parallel section taken from near the centre of the retina. As described by Barber & Wright (1969), two sorts of cell can be seen in the retina, retinula cells (receptors) and supporting cells, the former recognizable by the presence of the myeloid body. Electron microscopy confirmed the appearance of the myeloid body described by Barber & Wright (1969). Measurements made on sections taken from a retina at the 12 positions shown in Fig. 4 gave a mean rhabdome length of 359 μm, and showed little variation with retinal locus, except at the very edge of the retina where their length decreases rapidly before they disappear entirely (Table 1). Measurements on sections from six loci on another retina gave a mean length of 375 μm,
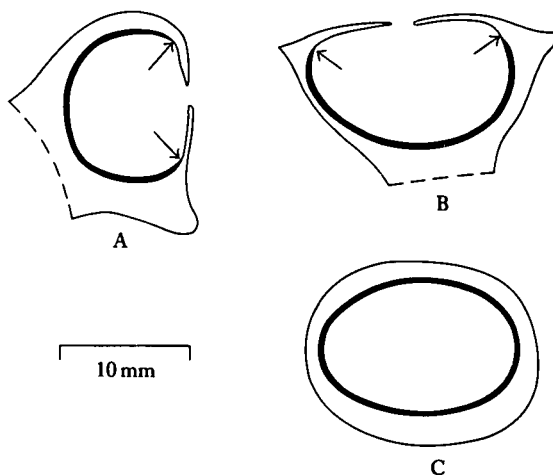

Fig. 3. Gross dimensions of the eye. (A) Vertical section, (B) horizontal section, (C) view of fundus. In (A) and (B) the arrows indicate the limits of the retina, which is shown black, and the dashed line shows where the optic stalk was cut.

Table 1. *Rhabdome lengths and retinal packing at different locations on the retina of* Nautilus pompilius

Location	1	2	3	4	5	6	7	8	9	10	11	12	Mean
Rhabdome length (μm)	315	415	410	270	415	290	450	270	290	390	340	450	359
Receptor density per mm^2	19600	18400	18400	18000	21600	21200	24800	17200	14400	22800	20800	20000	19767

The approximate positions on the retina from which sections were taken are shown in Fig. 4.
Rhabdome lengths are given to the nearest 5 μm.
Density counts were made over 50 × 50 μm squares in each case, and converted to give the number per mm^2.
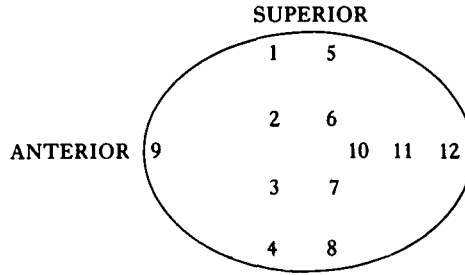
SUPERIOR

ANTERIOR

Fig. 4. Approximate positions on the retina at which the data given in Table 1 were obtained. The retina is shown as if flattened out.

and from 10 loci on a third retina a mean length of 345 μm. In these cases also there was little variation with retinal position. Pigment granules occur at the junction between the retinula cell perikarya and the rhabdomal portion of the cell. Specimens taken from light- and dark-adapted animals showed no sign of any migration of this screening pigment, such as occurs in some other cephalopods (Young, 1963).

Below the basal lamina the optic nerves collect together to form bundles, and as reported by Barber & Wright (1969) for *Nautilus*, and by Dilly, Gray & Young (1963) for *Octopus* and *Eledone*, many axons are enclosed by one glial cell (Fig. 5B). These bundles are very regularly organized, as can be seen from Fig. 5A and also Fig. 5D, which shows a tangential section taken at the level of the bundles. In many sections nerve fibres from the receptors can be clearly seen entering the bundles (Fig. 5E).

Meridional or parallel sections, and in many cases both, were taken from all the 28 specimens from three retinas that were used to measure rhabdome length (see above), in an effort to determine the direction in which these nerve bundles run. Such estimates of direction can only be approximate, as it is difficult to tell whether a section has been cut exactly across or along a nerve bundle. Nevertheless it is clear that over the whole of the retina, except the anterior and posterior poles, the bundles run more or less longitudinally. This is true at both the superior and inferior edges of the retina, and also centrally in front of the optic stalk. At the anterior and posterior poles bundles occur that run in the other direction.

Fig. 5C shows a slightly oblique tangential section taken through the rhabdomes, and through the layer of pigment granules. The appearance of such sections is similar to equivalent sections of *Octopus* retina, although the rectangular arrangement found in *Octopus* is lacking (Young, 1962). The retinal packing of *Nautilus* may be

Fig. 5. (A) Parallel section from near the centre of the retina, showing the general structure. *r*, rhabdomes; *s*, screening pigment; *n*, layer of nuclei of receptors and supporting cells, and myeloid bodies; *b*, basal lamina; *bn*, layer with bundles of nerve fibres. Toluidine blue. Scale bar, 50 μm. (B) Parallel section through a nerve bundle. Individual nerve fibres can be seen, surrounded by glial cells to form nerve bundles. Toluidine blue. Scale bar, 20 μm. (C) Slightly oblique tangential section through the rhabdomes. The pigmented zone between the perikarya and the rhabdomal part of the receptor cells is in the lower half of the figure; in the upper half the section goes through the rhabdomal part of the receptors. Toluidine blue. Scale bar, 50 μm. (D) Tangential section through the layer of nerve bundles. Toluidine blue. Scale bar, 100 μm. (E) Oblique tangential section, showing nerves from the receptors crossing the basal lamina (arrowed) and entering the nerve bundles. Nuclei of the receptors and supporting cells, and myeloid bodies, are seen above and to the left, nerve bundles lower right. Toluidine blue. Scale as Fig. 5C.
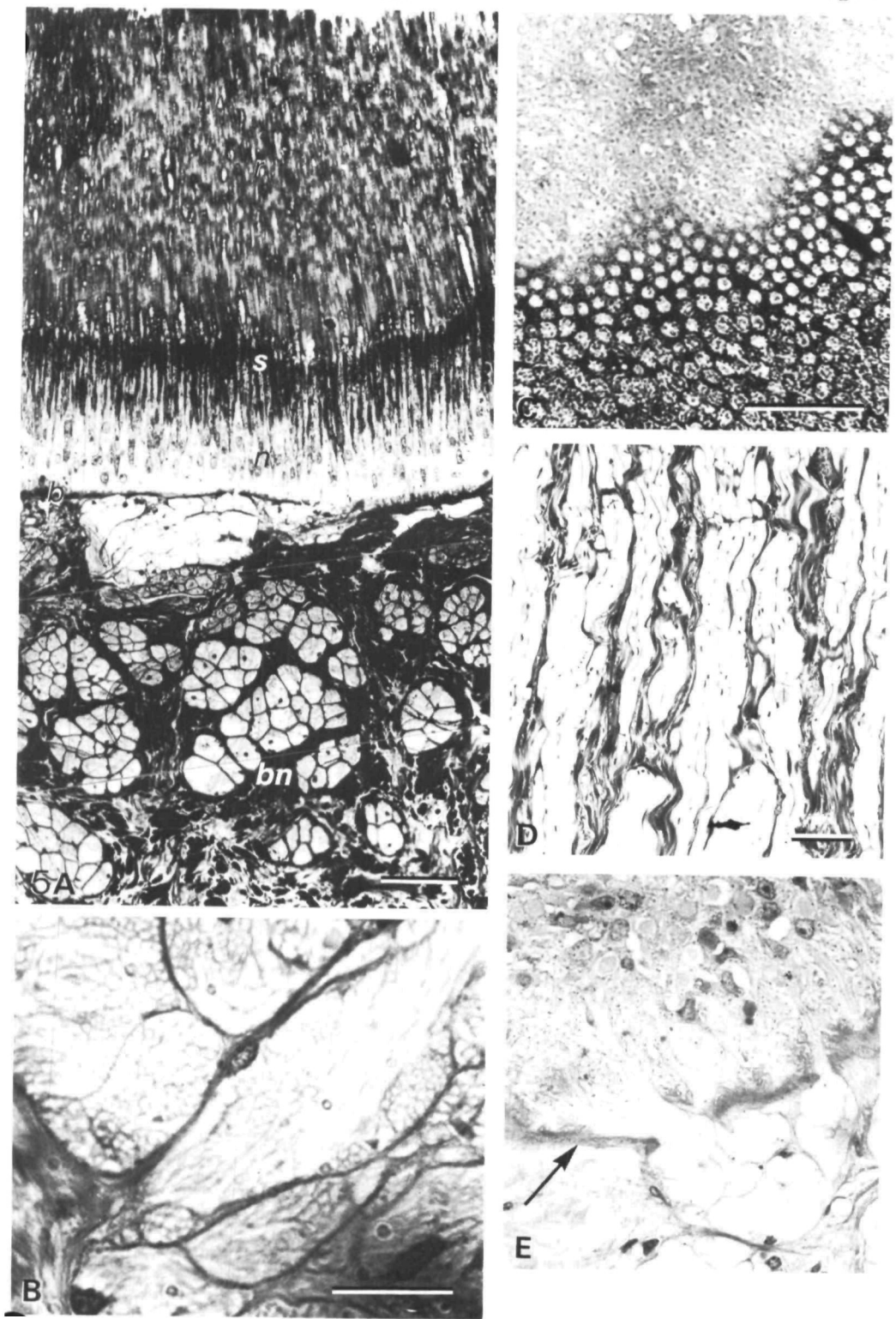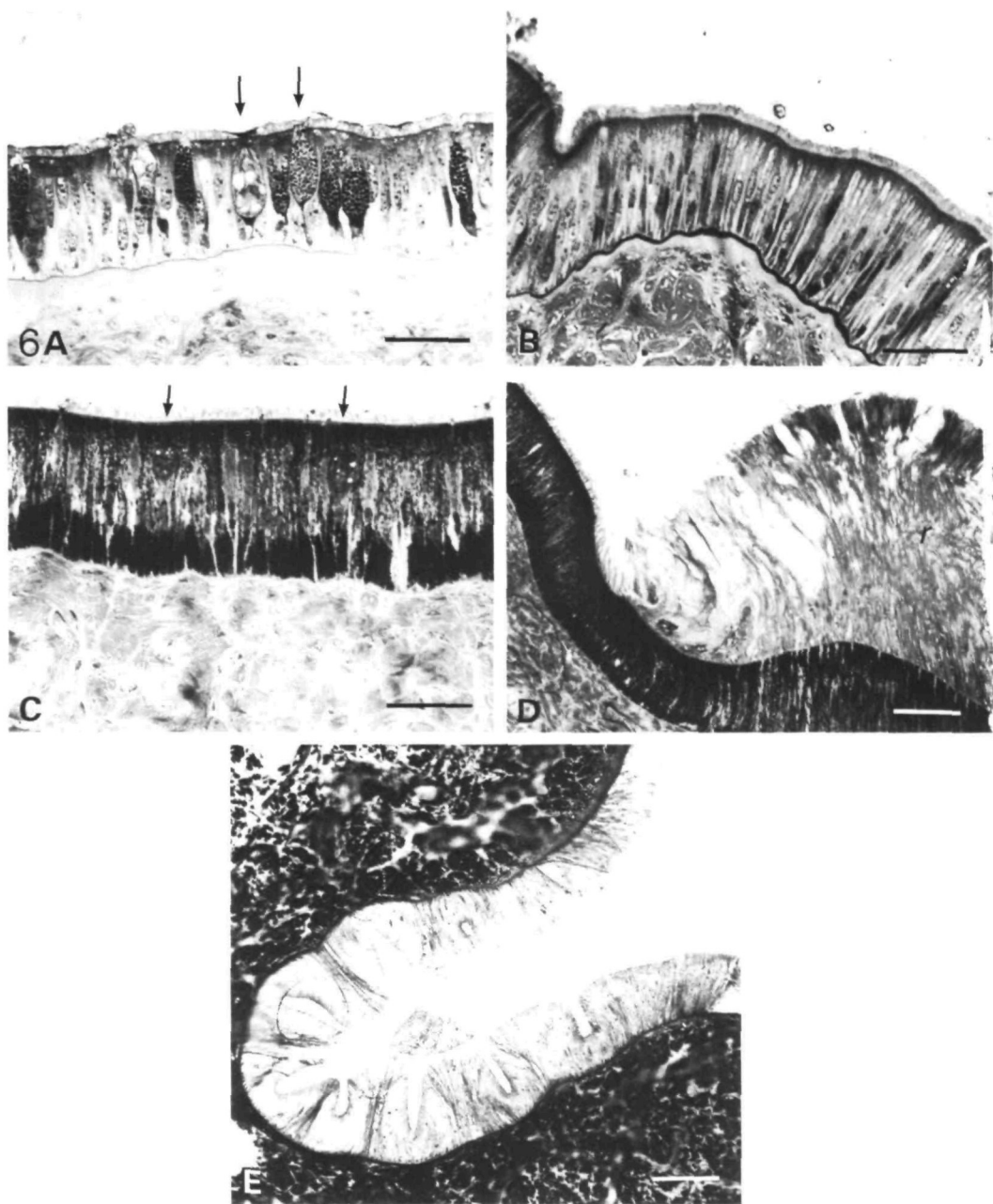
Fig. 6. (A) Epithelial lining of skin from the outside of the bulb of the eye. Two types of mucus cell can be seen (arrowed). Toluidine blue. Scale bar, $50 \mu m$. (B) Epithelial lining of outside of iris. Toluidine blue. Scale bar, $50 \mu m$. (C) Epithelial lining from inside of iris. Two mucus cells are shown arrowed. Toluidine blue. Scale bar, $50 \mu m$. (D) Transitional zone between the inside of the iris (left hand side of figure) and the retina (right hand side). r, rhabdomes. Toluidine blue. Scale bar, $100 \mu m$. (E) General appearance of the groove running ventrally from the pupil on the outside of the iris. Toluidine blue. Scale bar, $100 \mu m$.

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estimated from sections such as that shown in the bottom half of Fig. 5C, on the assumption that the pigment acts to isolate functional units. Such counts for various parts of the retina are given in Table 1. The mean is close to Young's (1962) estimate for the packing of the rhabdomes of *Octopus vulgaris*. There are no appreciable changes in retinal packing with location (Table 1).

Structure of the pupil and iris

The inside of the iris is lined with pigmented epithelium and mucus cells, the latter showing a typical purple metachromic response to toluidine blue. The skin on the outside of the iris, and on the outer surface of the bulb of the eye, also contains mucus cells which appear to be of two types (Fig. 6A, B, C). Fig. 6D shows how the epithelial cells of the inside of the iris merge with the retina itself. As Barber & Wright (1969) described, the epithelial cells on the inside of the iris possess microvilli: similar microvilli are also present on the outside of the iris (Fig. 7C, D). Muscle fibres are present, and are presumably responsible for the contractile properties of the pupil.

Running downwards from the pupil is a conspicuous groove, which is wide and shallow immediately beneath the pupil but deepens rapidly as it passes inferiorly. The groove is lined with ciliated epithelium that is thrown into folds (Figs 6E, 7A, B): in cross section these cilia show the typical arrangement of two central microtubules surrounded by nine further pairs of microtubules.

The optomotor response

Animals were tested with stripes subtending 22·5, 11·25, 5·5 and 2° at the centre of the apparatus: the above figures refer to a single stripe and therefore a complete black and white cycle will subtend double the angle in each case. Responses to the two larger sets of stripes were very clear in all animals. The basic movement was a rotation of the whole animal: there were no obvious movements of the eyes with respect to the body. At the slow speeds at which the stripes were moved the animals rotated at the same speed as the drum, so that the display remained stationary with respect to the retina. While simple rotation was the most common response, the animals on occasion swam after the stripes, following them round the edge of the glass dish.

The two smaller stripe sizes failed to elicit consistent responses. The animals remained active, but their movements did not correlate with the direction of the drum's rotation. On the basis of the optomotor response the minimum separable visual acuity of *Nautilus* is thus between 11·25 and 5·5°.

Properties of a model eye

A further estimate of the optical properties of the pin-hole camera eye of *Nautilus* was made by constructing three scale model eyes, as was done by Mugglin (1937), and using these to take photographs of a Lizars eyesight test chart. Such photographs can also give a qualitative impression of the image quality that may be expected.

The model eyes had a depth of 9 mm from the pupil to the photographic film, which for constructional reasons was flat, rather than slightly curved as the retina is in life. The three models had horizontal oval pupils measuring 2·8 × 1·7 mm, 2 × 1 mm, and 1 × 0·4 mm respectively, which covers the range found in life (Hurley, Lange & Hartline, 1978), and were painted matt black inside and outside.

The photographs were taken from a distance of 12·5 cm, and the results are shown in Fig. 8. At this range, resolving the top line of the chart represents a visual acuity of 4°, and the second line an acuity of 2·4°. At the smallest pupil size used, the 4° letter is barely resolvable, while at the larger pupil sizes the resolving power is clearly worse than 4°. It can also be seen that, as would be expected, the horizontal pupil degrades the vertical elements of the letters more than the horizontal elements.

DISCUSSION

The pin-hole camera eye of *Nautilus* must have many disadvantages compared to the lens-bearing eyes of other cephalopods: the resolution will be worse, the sensitivity considerably decreased, and the field of view narrowed. As far as visual resolution is concerned, it is known that the quality of the image formed by a pin-hole depends both on the size of the aperture and the distance between the aperture and the sensitive screen (Rayleigh, 1891). With an aperture the size of that found in *Nautilus*, the effects of diffraction will be negligible compared to the blur circle caused by the large size of the pupil. This blur circle may be calculated by geometrical optics, and for distant points, from which the light rays can be considered to be parallel, it is simply equal to the size of the pupil itself. Taking the depth of the eye as 8·7 mm, and assuming a pupil diameter of 1 mm, which appears fairly typical (Hurley *et al*. 1978), and further assuming that two objects cease to be discriminatable when the blur circles from them on the retina just touch, we can calculate that the minimum separable visual acuity of *Nautilus* should be about 6·5°. This compares well with the behavioural tests, which indicated a value between 11·25 and 5·5°, and with the results for the model eyes shown in Fig. 8.

Thus both calculation and experiment suggest that the ability of *Nautilus* to resolve objects is poor. The retina, however, appears much more finely organized than the optical quality of the image would warrant: the size and packing of the receptors in *Nautilus* is, for example, comparable to that of *Octopus* (Young, 1962), an animal with a minimum separable visual acuity of 17' or better (Sutherland, 1963). Various possible reasons exist for this apparent mismatch between the optics of the eye and the fineness of the retinal mosaic. It may be, for example, that the optomotor response is not a good test of the visual capabilities of *Nautilus*, and that at the depths at which *Nautilus* lives the eye is used mainly to detect bioluminescence. Bioluminescent animals seen at a distance are often effectively point sources of light, and in theory could be localized accurately, even in the absence of any lens or other optics, by the position of the shadow of an edge of the pupil on the retina. The fact that the pupil changes in size would, however, present difficulties for such a system of localization. It is perhaps more likely that the fineness of the retinal mosaic has no visual function. The eye of *Nautilus* is, at least superficially, similar to the first stage in the development of the eye of later cephalopods (Sacarrão, 1954), consisting of a simple invagination of

Fig. 7. (A) Low power electron micrograph of one of the folds in the iris groove. Scale bar, 10 μm. (B) Electron micrograph of cilia lining the iris groove. Scale bar, 1 μm. (C) Electron micrograph showing microvilli on epithelial cells from the outer surface of the iris. Scale bar, 1 μm. (D) Electron micrograph showing microvilli on pigmented epithelial cells from the inner surface of the iris. Part of a mucus cell can also be seen (*m*). Scale bar, 1 μm.
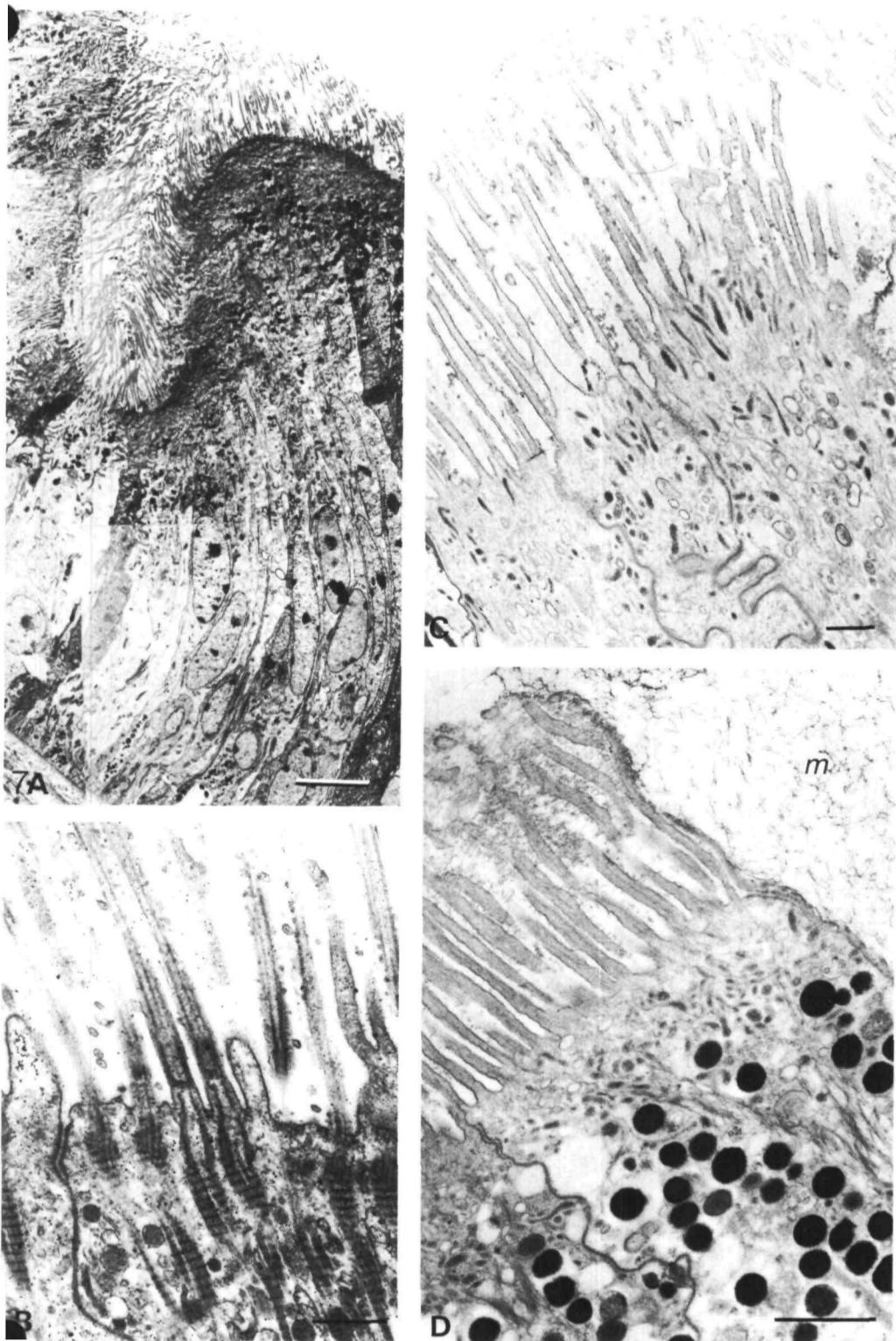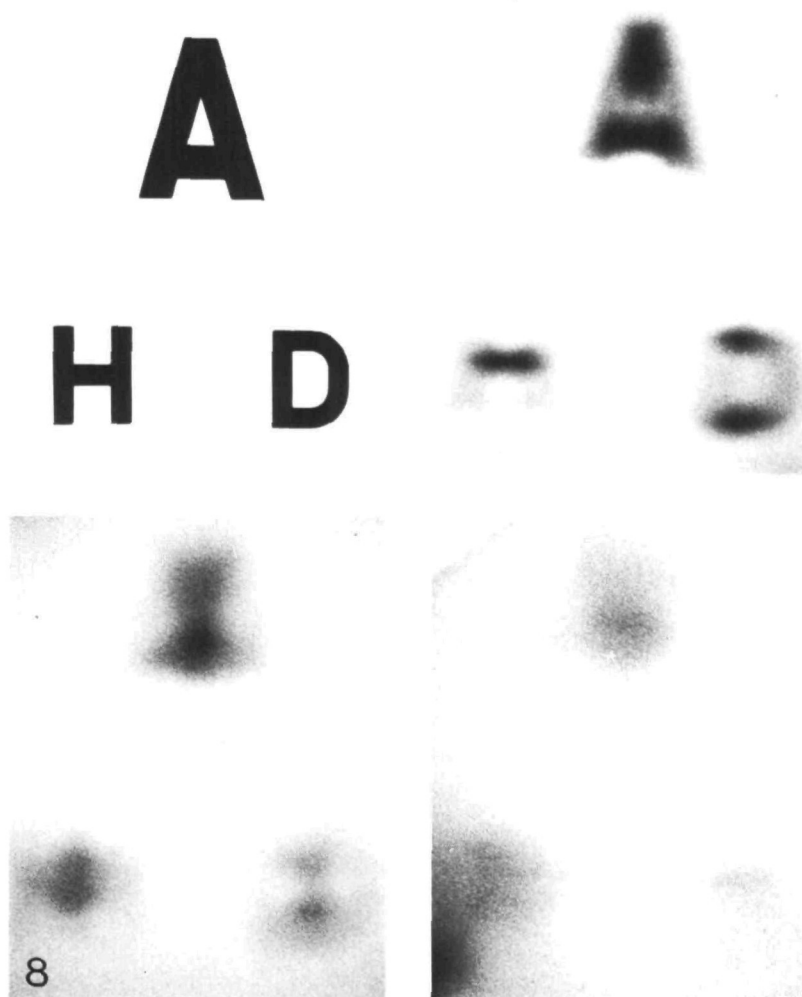
Fig. 8. Photographs taken through model eyes with horizontal oval pupils of different sizes. The top left-hand figure shows the appearance of the eye-test chart used. The other parts of the figure show the results when the pupils measured 1×0.4 mm (top right), 2×1 mm (bottom left) and 2.8×1.7 mm (bottom right) respectively. The distance from the pupil to the photographic film was 9 mm in all cases.

pidermis. The size of the retinal receptors might thus be determined by the same factors as determine the size of the epidermal cells from which they arose, and have no relationship to the quality of the retinal image. The epidermal cells of the inner surface of the iris and the retinal receptors themselves are similar in size, and form a continuum in their appearance (Fig. 6D).

The horizontal axis of the eye is longer than the vertical axis, which is a typical cephalopod feature. Packard (1969), for example, reports that in three groups of octopuses of different sizes the vertical dimension of the eye was on average 0·9 times the horizontal dimension. In *Nautilus* the elongation is greater than this, and may be associated with the fact that the horizontal dimension of the pupil is also usually greater than the vertical dimension (Hurley *et al.* 1978).

In general the ability to discriminate between objects will be improved by increasing the distance between the pupil and the retina, so the shape of the eye might improve vision in forward and backward directions. The horizontal enlarging of the pupil means that its effective aperture will also remain larger for extreme forward and backward lines of sight. The improvement in vision that would result from this would, however, be small, and why such lines of sight should be particularly important for *Nautilus* also remains obscure. With a pin-hole eye the field of view cannot exceed 180°, and since the eyes of *Nautilus* are parallel to each other and about 62 mm apart this will result in an area of this size all round the mid-plane where vision is impossible.

The sensitivity of the eye of *Nautilus* will also be considerably reduced because of the lack of a lens. Using the methods given in Moon (1961, p. 262), and the ocular dimensions assumed above, it can be calculated that the retinal illumination will be $3·3 \times 10^{-3}$ times the luminance of the scene being looked at, when these are in compatible units (e.g. lux and candelas per square metre). A similar calculation for a fish with an eye obeying Matthiesson's ratio, using the methods given in Le Grand (1957), shows that in this case the retinal illumination will be about half the scene's luminance. Thus in a given situation the brightness of the retinal image of *Nautilus* will be over two log units lower than that of a typical fish. It is not possible to calculate the absolute sensitivity of *Nautilus* in the absence of information on the sensitivity of its retina. However, the lack of a lens must certainly have an adverse effect on this, which appears especially deleterious when it is remembered that *Nautilus* occurs at depths up to 500 m, and is usually said to be nocturnal in its behaviour (Haven, 1972).

The above argument applies to extended sources, such as the daylight that penetrates from the surface. As with acuity, the problem of sensitivity might be less if *Nautilus* used its eyes mainly to detect bioluminescent point sources. In such cases the amount of light entering the eye is not affected by the presence of a lens, but depends only on the size of the pupil, and for a given pupil size neural summation can, in principle, achieve the same sensitivity as could be achieved by a lens. Since however the pupil of *Nautilus* is small in absolute terms compared to that of a typical fish, even with complete neural summation sensitivity would remain relatively low. For example, in a fish for which the eye obeys Matthiesson's ratio, and measures 8·7 mm from the retina to the centre of the lens, the pupil diameter will be about 7 mm, compared to a diameter of about 1 mm in *Nautilus*. This would give the fish a pupil area, and hence potential sensitivity, approximately 49 times greater than that of *Nautilus*. There is also no evidence that *Nautilus* responds particularly to bioluminescence.

Although bioluminescent crustacea are on occasion found in its stomach, these crustacea emit their bioluminescence as a luminous cloud when disturbed, and presumably use it as a method of distracting predators.

The presence of a well-differentiated retina, a mobile pupil, statocyst-mediated eye stabilization (Hartline, Hurley & Lange, 1979), and a well-developed optomotor response, all suggest that vision is important for *Nautilus*, and under the circumstances it is surprising that the optics of the eye are so simple. Owen (1832) and Hensen (1865) seriously considered the possibility that a lens is present in life but had disappeared for some reason from their preserved material. They concluded however that this was unlikely, and more recent work with fresh material has never revealed any sign of a lens, or of any structure to which a lens might have been attached. It is of course also possible that the lack of a lens is not a primitive feature at all, but an example of degeneration, but this seems unlikely since the rest of the visual system does not look degenerate and visual behaviour is well developed.

The visual system of *Nautilus* is also unusual in appearing to lack an optic chiasma. However the finding that in the centre of the eye the optic nerve bundles just behind the retina usually run longitudinally suggests the possibility that these bundles form a chiasma equivalent to the optic chiasma of other cephalopods. The directions in which the bundles run at the periphery of the retina would be expected whether a chiasma is present or not, since they have to run over the surface of the eye in order to reach the optic stalk. If, however, the bundles were to run to the central nervous system by the most direct route, without any crossing, we would not expect to find longitudinally orientated bundles at the centre of the eye opposite the optic stalk. The function of the optic chiasma of cephalopods is unclear, but it is presumably related to the way the image is formed on the retina (Young, 1964). The present results are also of course not conclusive evidence for an optic chiasma: it may be possible to obtain definite information on this point from serial sections when more material becomes available. If, however *Nautilus* does indeed have a functional chiasma this would be a further indication that the pin-hole eye forms an effective and functional image.

The function of the groove that runs from the pupil to the inferior margin of the iris is unclear. Hensen (1865) describes the epithelium lining the outer surfaces of the eye and iris, and the groove, as all being ciliated, and he suggests the groove may direct a stream of water across the eye, preventing the entry of foreign bodies. The present results show that the epithelia of the eye and iris have microvilli, not cilia. The presence of cilia within the groove is, however, confirmed, and it is possible that the groove does indeed generate a current of water, directed either towards or away from the pupil.

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