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A PRONOUNCED FOVEA IN THE EYE OF A WATER FLEA, REVEALED BY STEREOGRAPHIC MAPPING OF OMMATIDIAL AXES

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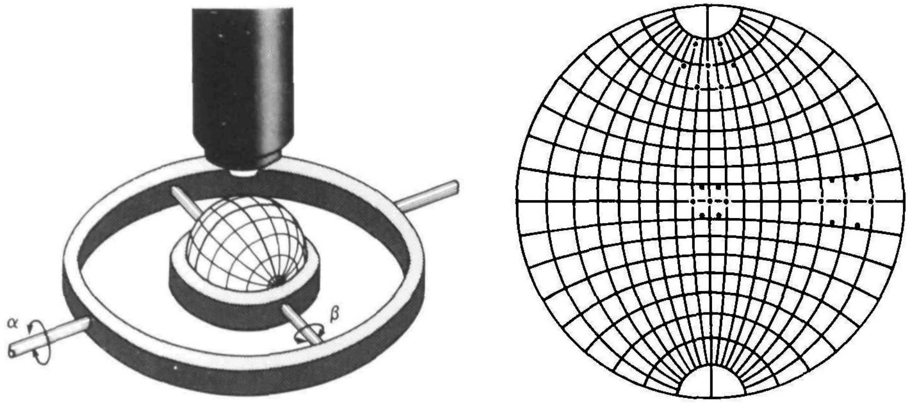
The small compound eyes of water fleas are usually regarded as unsophisticated, with low visual acuity. Indeed this is true for the most common water flea, *Daphnia* (Young & Downing, 1976). However, another species, *Polyphemus pediculus*, is a visually guided predator (Ischtereyt, 1933). The cyclopic eye of *Polyphemus* is not larger than that of *Daphnia* but it certainly appears more elaborated. Looking at the pseudopupil, it is obvious that the interommatidial angles are different in different regions of the eye. To reveal the extent of these regional differences, the interommatidial angles were recorded. This was done by mounting an animal in a goniometer and observing the position of the pseudopupil while the goniometer was turned (Horridge, 1977*a*) (Fig. 1A). The recorded co-ordinates can be characterized as points on a spherical surface. Transforming this spherical surface to a flat map inevitably introduces distortions in the angular pattern. Different chartographic projections imply different types of distortions (see Deetz & Adams, 1945; Raisz, 1948; Strahler, 1969). After a thorough consideration, a stereographic projection, named *Wulff's network* (Kleber, 1970), was chosen. This projection is conformal (true shape) which entails that the packing geometry of visual axes is not altered (Fig. 1B). Moreover, this projection covers a hemispheric field, which is large enough for mapping an entire eye.

The eye map of *Polyphemus* reveals a zone of high acuity (fovea) in the central upper part of the visual field. Here, the interommatidial angles are as small as 2° (Fig. 2), which must be considered exceptional for an eye not more than 0·2 mm in diameter. The fovea comprises about 20 ommatidia and the rest of the 130 ommatidia are spread out on the map with increasing interommatidial angles towards the periphery.

The interommatidial angles were correlated to the acceptance angles in the fovea and in the periphery of the eye. Acceptance angles were estimated by measuring the angular span in which an ommatidium remains in the pseudopupil. The pseudopupil covers a small number of ommatidia, with the central ones black and the peripheral ones brown. Only the black area was taken as the true pseudopupil, because the brown colour probably originates from screening pigment. When plotting the acceptance angle on the map, care must be taken as to the scale magnification in the periphery of the stereographic projection. To do this, the diameter of each circle was



A B

Fig. 1. (A) Goniometer recording and (B) Wulff's network. In (A) the eye (not drawn in the figure) that is mounted in the centre of the goniometer is viewed by a microscope objective. A presumed sphere with an angular grid is drawn to show the correlation between recording and plotting. The eye itself need not be spherical if it is much smaller than the distance to the observing objective, as it is the eye's visual axes and not its surface that is recorded. The α-axis is turned along meridians and the β-axis along parallels. (B) Wulff's network with parallels and meridians drawn for each 10°. A symmetric and equally spaced hexagonal pattern is plotted at three locations.

multiplied by a factor corresponding to the scale magnification at the actual distance from the centre of the map. Projection geometry (see Kleber, 1970) proves that the linear distance from the centre of the map can be expressed as a function of the angular distance from the centre, by the equation

$$d_s = \tan \tfrac{1}{2}\gamma, \tag{1}$$

where d_s is the linear distance from the centre, expressed as a factor of the map radius, and γ is the angular distance from the centre. The magnification (change in scale) is then revealed by the derivative equation (1):

$$F = \frac{2}{1+\cos \gamma} \tag{2}$$

where F is the scale magnification at the angular distance γ.

Using equation (2) it is possible to calculate the proper diameter of each circle irrespective of its localization on the map, by multiplying the diameter it should have at the centre of the map by the factor F. The scale at the centre can be determined by equation (1) once the size of the complete map hemisphere has been decided.

Acceptance angles from two places in the eye were introduced in the map, according to the above principles. It is revealed that the acceptance angles correlate nicely with the interommatidial angles, and the visual overlap is approximately the same in the fovea and the periphery.

A detailed study of the optics and anatomy of the *Polyphemus* eye will be given (D-E. Nilsson & R. Odselius, in preparation). Beside the present findings on the *Polyphemus* eye, stereographic mapping has proved to be a suitable method for large field representation of visual axes in compound eyes.

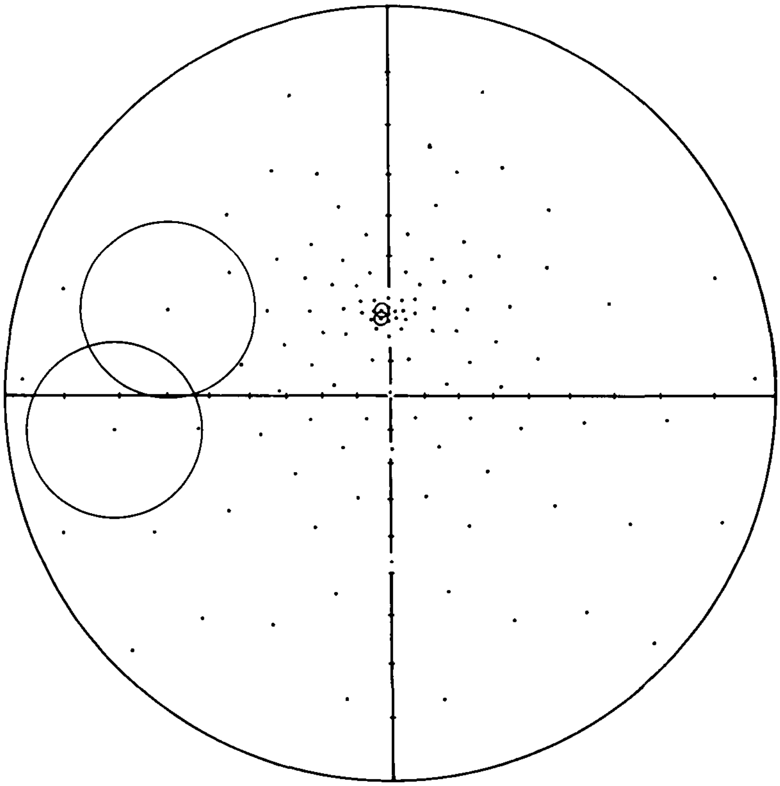


Fig. 2. Hemispherical mapping on Wulff's network of the cyclopic eye of *Polyphemus pediculus*. The parallels and meridians in Wulff's network can easily give an illusion that the projection is different for different directions. To avoid this, the net is removed leaving only the vertical and horizontal axes which are given the angular scales. The map is centred around the front of the animal. As it is a freshwater animal, it was immersed in water during the measurement. The dark pseudopupil of the eye was used to detect the optical axes. Each dot represents the optical axis of one ommatidium. The map reveals an extreme fovea with relatively high acuity and a rapidly decreasing acuity towards the periphery of the visual field. The acceptance angles are plotted for two foveal and two peripheral ommatidia.

An angular map of ommatidial visual axes reveals the nature of an acute zone as well as quantifying the spatial resolution in any part of the visual field. Angular maps can also be used for plotting Airy discs (Snyder, 1977; Horridge, 1978), acceptance angles (Young & Downing, 1976; Mimura, 1981), neurone receptive fields (Swihart & Schümperli, 1974) and visual fields of entire eyes (Hughes, 1979; Kuster & Evans, 1980).

The following points summarize the advantages of Wulff's network. (1) It retains the shape of the receptor optical packing pattern (for compound eyes; packing pattern of ommatidial axes). (2) It enables accurate plotting of circles such as Airy disc circles on the map. (3) It gives full control over the distortion (scale magnification) as it is uniform in all directions from the centre. This property is essential to assure that the map distortions are not interpreted as regional differences in the eye. Further, all the above properties are valid for the entire hemisphere.

If a single receptive field is to be plotted on a map, the small angular span makes chartographic projection unnecessary. For maps not larger than ±20° on both axes an ordinary cartesian co-ordinate net will suffice. The principle described in this work was developed to cope with the special problems that arise with large field mappings.

If the measurements are restricted to one dimension (following a straight line) (Rossel, 1979), and if the recording is made along a great circle (i.e. a meridian or the equator), the mapping is completely free of distortions. Therefore, it is essential not to do line-mappings by turning the inner (β) axis of a tilt–tilt goniometer when the outer (α) axis is not in zero position (see Fig. 1).

In a number of publications (Horridge, 1977*a*, *b*, 1978, 1980) a two-dimensional map is constructed by plotting more than one line-map onto a cartesian co-ordinate system. The resulting map is accurate along the lines (if recorded according to the criteria above), but the rest of the map is undefined.

Clarkson (1966, 1969) demonstrated the visual sampling of fossil trilobites on an angular grid, called the Lambert equal-area net. This projection is circular and covers a hemisphere. It resembles Wulff's network, but differs by being equivalent (true area) instead of conformal (true shape). The Lambert equal-area net cannot therefore correctly represent the packing geometry of visual axes. Furthermore, circular fields of centre in this projection are represented as ellipses, making the mapping procedure inconvenient.

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REFERENCES

CLARKSON, E. N. K. (1966). Schizochroal eyes and vision of some silurian acastid trilobites. *Paleontology* **9**, 1–29.

Clarkson, E. N. K. (1969). On the schizochroal eyes of three species of *Reedops* (Trilobita: Phacopidae) from the lower devonian of bohemia. *Trans. R. Soc. Edinb.* **68**, 184–205.

DEETZ, C. H. & ADAMS, O. S. (1945). *Elements of Map Projection.* Special Publ. 68, U.S. Department of Commerce. Washington, D.C.: U.S. Government Printing Office.

HORRIDGE, G. A. (1977*a*). Looking at insect eyes. *Sci. Am.* **237**, 108–120.

HORRIDGE, G. A. (1977*b*). Insects which turn and look. *Endeavour* **1**, 7–17.

HORRIDGE, G. A. (1978). The separation of visual axes in apposition compound eyes. *Phil. Trans. R. Soc. Lond.* B **285**, 1–59.

HORRIDGE, G. A. (1980). Apposition eyes of large diurnal insects as organs adapted to seeing. *Proc. R. Soc. Lond.* B **207**, 287–309.

HUGHES, A. (1979). A schematic eye for the rat. *Vision Res.* **19**, 569–588.

ISCHTEREYT, G. (1933). Über *Polyphemus pediculus* L. *Arch. Hydrobiol.* (*Biologischer Teil*), **25**, 261–290.

KLEBER, W. (1970). *An Introduction to Crystallography.* Berlin: VEB Verlag Technik.

KUSTER, J. E. & EVANS, W. G. (1980). Visual fields of the compound eyes of four species of cicindelidae (Coleoptera). *Can. J. Zool.* **58**, 326–336.

MIMURA, K. (1981). Receptive field patterns in photoreceptors of the fly. *J. comp. Physiol.* **141**, 349–362.

RAISZ, E. (1948). *General Cartography.* New York: McGraw-Hill.

ROSSEL, S. (1979). Regional differences in photoreceptor performance in the eye of the praying mantis. *J. comp. Physiol.* **131**, 95–112.

SNYDER, A. W. (1977). Acuity of compound eyes: Physical limitations and design. *J. comp. Physiol.* **116**, 161–182.

STRAHLER, A. N. (1969). *Physical Geography*, 3rd ed. New York: John Wiley.

SWIHART, S. & SCHÜMPERLI, R. (1974). Visual fields of butterfly interneurons. *J. Insect. Physiol.* **20**, 1529–1536.

YOUNG, S. & DOWNING, A. C. (1976). The receptive fields of *Daphnia* ommatidia. *J. exp. Biol.* **64**, 185–202.