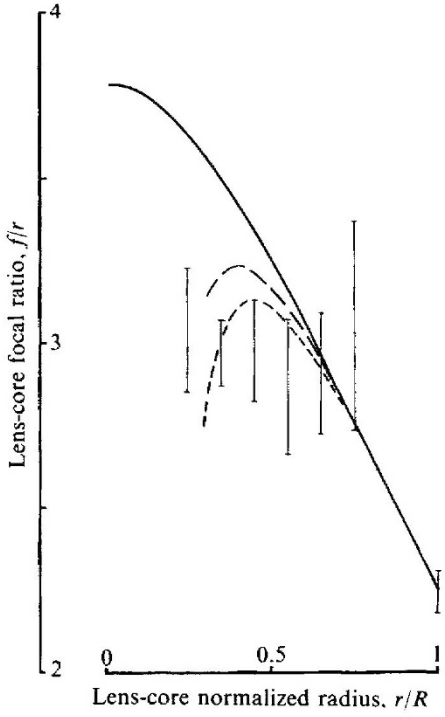

Fig. 2 The focal ratio f/r of the gradient lens model; curves as for Fig. 1.

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MELANIE C. W. CAMPBELL*
Department of Applied Mathematics, R. S. Phys. S. and Department of Physiology, JCSMR, Australian National University, Canberra, ACT, Australia

P. J. SANDS
Division of Computing Research, CSIRO, Canberra, ACT, Australia

* To whom correspondence should be addressed. Present address: School of Optometry, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada.

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FERNALD AND WRIGHT REPLY — Brewster[1], Maxwell[2] and Matthiessen[3] independently investigated fish eye lenses and each concluded that such a spherically symmetrical lens which produces a reasonably focused image must have a gradient of refractive index from the centre to the edge. More than a century later, Luneburg[4] formulated an integral equation describing the refractive index profile of a spherical lens which produces a perfect image and solved it for one case in which an exact analytical solution was possible. Since then, such lenses have become known as 'Luneburg lenses' and the solution extended[5–8] so that the refractive index gradient which depends on the focal length of the lens (Fig. 2 of ref. 8) can generally be given in analytical form. Such lenses must produce a perfect image and have a continuous refractive index gradient from the centre to the edge of the lens.

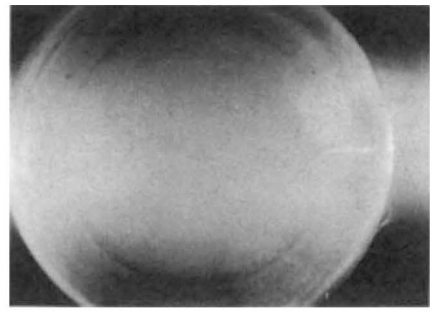

Fig. 3 Lens of the teleost, *H. burtoni*, imaging a laser beam (494 nm) placed about 1 focal length behind it. Note the concentric discontinuities in the lens substance in the cortex of the lens. The innermost discontinuity corresponds to the juncture between the core and cortex of the lens.

We analysed the teleost fish lens[9] and hypothesized that the distribution of refractive index diverged from that of the Luneburg lens based on physical measurements of the refractive properties of the intact lens as compared with the lens as it was surgically reduced in size. We suggested that the lens had a core of approximately uniform refractive index, surrounded by a shell with an appropriate refractive index gradient.

Based on ray tracing, Campbell and Sands suggest that our hypothesis is incorrect, offering two possible sources for this difference. First, that the equivalent refractive index we calculate at the core of the lens is higher than Matthiessen[3] found, and second, that in measuring the paraxial focal length, our laser beam may not have been reduced in proportion to the size of the lens being measured.

Regarding the first suggestion, measurements more recent than Matthiessen's of the magnitude of the refractive index of the fish lens near the centre, including our own, place the value near 1.56, and for some crystalline proteins, refractive indices of approximately 1.6 have been measured[10]. Thus, our computed value of the equivalent refractive index of 1.606, while high, is not unreasonable given the variance in our measurements (Fig. 3 of ref. 9). Regarding the second suggestion, we did reduce the size of our measuring beam in proportion to the core size being measured to the limiting aperture available. So, for larger lenses, we met this condition, whereas for very small lenses we did not. Nonetheless, there are not significant, consistent differences between these measurements as predicted by Campbell and Sands.

We propose that there may be another way to account for the discrepancy between the physical measurements and the theoretical ray tracing. As noted above, there are two requirements for 'Luneburg' type of refractive index gradient profile to apply: first, the lens must be perfect (without spherical aberration), and second, the refractive index must vary continuously (without discontinuities) throughout its extent. It is not known how deviation from these two conditions would be reflected in deviations from an otherwise obligatory 'Luneburg' refractive index profile.

The fish lens, although not optically perfect, is clearly of high quality (see cover photograph of ref. 9) and our measurements show that the resolution of the lens approaches the diffraction limited value (R.D.F. and S.E.W., in preparation). Thus, the first condition is approximately met. It is not clear, however, that the refractive index is without discontinuity. Figure 3 shows a lens from the African cichlid fish, *Haplochromis burtoni*, which is transilluminated. Distinct concentric discontinuities are evident, particularly in the cortex, as have been reported previously for teleost lenses (see Plate I of ref. 11). Indeed, in many fish, particularly larger ones, a discontinuity in the lens is visible during retinoscopic inspection. The existence of different zones within the fish lens has been demonstrated as optical anisotropy (birefringence)[1,12] and related to differences in supramolecular organization[13]. This is consistent with the fact that the lens crystallins are differentially synthesized during lens development and therefore not distributed uniformly through the lens[13,14]. Thus, there may be one or more discontinuities in the refractive index which must be ascertained before ray tracing can adequately be carried out. Since our original technique was not sensitive enough to detect such discontinuities, we intend to measure the refractive index profile more directly either using the backscattered ray method[15] or protein concentration distribution[16], to test directly our hypothesized profile of refractive index within the teleost lens.

RUSSELL D. FERNALD
STEPHEN E. WRIGHT
Institute of Neuroscience, University of Oregon, Eugene, Oregon 97403, USA

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