tic, it should polymerize all along the particle range. The measured length of the tracks was 20 ± 1.5 μm, which corresponds to the average expected range of fission fragments. Furthermore, the density of the tracks varied directly with the irradiation time. However, at the present state of development, we have a recording efficiency of about 50 percent for etched tracks in CTA. (Track efficiency is the percentage of tracks relative to the total number of bombarding particles.) Since oxygen inhibits polymerization, we performed an experiment in an oxygen-free environment. The results indicate that it should be possible to detect fission fragments with 100 percent efficiency.

The tracks are not etched by acrylic acid, nor does the dye fix onto them in ungrafted samples. Before being dyed, irradiated samples treated with acrylic acid do not show any tracks when the grafted samples are viewed under the microscope. Therefore, it is concluded that acrylic acid does not etch. Furthermore, irradiated samples were processed in 15 percent acrylic acid solution at 55°C for 24, 48, 72, and 96 hours, and then dyed. In the last sample, the background was too intense for any tracks to be seen, but in the other samples the diameter (1.5 to 2 μm) and the length of the tracks remained approximately the same. If the tracks were due to acrylic acid etching we would expect them to increase in diameter. We tried to obtain tracks by processing ungrafted samples for more than 6 hours in the boiling dye solution and then for 48 hours in the same solution at room temperature, which increased the opportunity for the dye to fix if this could possibly happen: no tracks were formed. Therefore, we conclude that the tracks observed after the whole graft-and-dye process are not due to preferential fixation of the dye along the particle's path.

The question can be raised whether we have really formed graft copolymer. Although the low density of fission fragments precludes the measurement of any increase in weight, we demonstrated in several ways that acrylic acid was grafted along the tracks. One indication of grafting is that the dye was preferentially fixed on the tracks. Tracks were still visible in a sample extracted for 48 hours at room temperature and then for 16 hours in a Soxhlet apparatus before dyeing. This apparatus keeps fresh pure solvent (water) around the sample, and increases the efficiency of the extraction process. Since we extracted much longer than the time necessary to remove the water-soluble monomer, the dye must have been fixed onto copolymer. A compelling indication of the formation of copolymer is that the efficiency of track recording decreased when polymerization inhibitors were added to the acrylic solution. When the grafting solution was made with 0.004 percent *p*-ethoxyphenol added as an inhibitor, the track recording efficiency decreased to about 5 percent. If a small amount of copper ions was also added, we rarely found a track.

We believe that polymer grafting can be developed into a valuable method for detecting ionizing particles. Our progress in grafting acrylic acid onto CTA indicates that we will be able to obtain tracks as distinct as those obtained by etching. An advantage of polymer grafting over particle track etching is that it does not remove the track core. Also, plastics that are difficult or impossible to etch, such as Teflon and the polyolefins, have been graft copolymerized in bulk (*2*, *7*). The development of tracks by graft polymerization in these materials would be especially interesting.

This new technique may find useful applications in many problems. The track etching technique implies a continuous trail of damage, the intersection of this trail with the surface detector, and a detection threshold. In principle, these three limitations should be suppressed in the graft polymerization technique of particle detection. This means that it might be possible to record tracks of relativistic heavy ions or particles with low linear energy transfer. It would also be possible to visualize an event originating in the detecting medium, such as fission induced by neutrons or pions. In addition, if we can fix a heavy element compound instead of rhodamine and use the electron microprobe associated with a Stereoscan electron microscope, we should be able to record and count the tracks automatically. The graft polymerization technique is not restricted to acrylic acid copolymerization but can be extended to several other convenient monomers. It would be possible to choose the monomer according to the detection sensitivity needed without degrading the detectors, which occurs with the track etching technique. But much more has to be done before this new detection technique for ionizing particles is developed into a valuable method.

MICHEL M. MONNIN
GEORGE E. BLANFORD, JR.
Laboratoire de Physique Corpusculaire, Université de Clermont, 63170 Aubière, France

References and Notes

1. M. Monnin and G. Blanford, *C. R. Acad. Sci. Paris Ser. B* **276**, 398 (1973).
2. A. Chapiro, *Radiation Chemistry of Polymeric Systems* (Interscience, New York, 1962), pp. 596–691.
3. J. Faïn, M. Monnin, M. Montret, paper presented at the eighth International Conference on Nuclear Photography, Bucharest, Rumania, July 1972.
4. R. L. Fleischer, P. B. Price, R. M. Walker, *Science* **149**, 383 (1965); D. Isabelle and M. Monnin, Eds., *Proceedings of the International Conference on Solid State Track Detectors* (Université de Clermont, Clermont-Ferrand, France, P. B. Price and R. L. Fleischer, *Annu. Rev. Nucl. Sci.* **21**, 295 (1971).
5. J. C. Bonnefis, thesis, University of Paris (1969).
6. A. Davenas, thesis, University of Paris (1971).
7. A. Chapiro, G. Derai, A. M. Jendrychowska-Bonamour, *Eur. Polym. J.* **7**, 1595 (1971).
8. We thank J. Gelas for his valuable assistance and J. Marchand for useful discussions about graft copolymerization.

23 February 1973; revised 21 May 1973

Late Glacial and Postglacial Productivity Changes in a New England Pond

Abstract. *During the late glacial and postglacial the productivity of Berry Pond in Berkshire County, Massachusetts, underwent a number of significant oscillations. This is suggested by data on sedimentary chlorophyll degradation products, diatoms, and Cladocera. The productivity changes were apparently controlled by changes in weathering, terrestrial vegetation in the watershed, litter production, and runoff. There are associated changes in cladoceran community structure.*

Berry Pond is a small glacial lake (surface area, 3.9 ha; water depth, 2.8 m) located on a ridge crest (elevation, 600 m) in the Pittsfield State Forest, Berkshire County, Massachusetts. The pond has one outlet, a small stream which flows over a rocky ledge on the western shore, and is surrounded by a forested watershed of about 28 ha. The forests are northern hardwoods.

The ridge is underlain by metamorphic rocks (Berkshire schist) (*1*).

Evidence suggests that Berry Pond has undergone significant trophic changes during its history. In the late glacial and early postglacial, productivity increased to a maximum (13,000 to 8800 years ago) and then declined (7000 to 5000 years ago). During the middle postglacial, productivity increased once again (to an even higher level) and then declined (5000 to 3800 years ago). There is some evidence of additional cycles of eutrophication in the upper half of the profile.

The initial period of increasing productivity coincided with the development of coniferous forests (first spruce, then pine) in the region, the decline with the establishment of northern hardwood forests. The second cycle of eutrophication coincided with a sharp decline of hemlock; increases of birch, oak, beech, and other hardwoods; and a significant acceleration in the rate of delivery of leaf cuticle fragments to the pond.

We suggest that the initial productivity oscillation was controlled in part by the leaching of nutrients from till and in part by differential nutrient retention by the watershed ecosystem. The mid-postglacial oscillation may have been caused by the release of nutrients from the leaves (or leaf fragments), which were delivered to the sediments at a greater rate during this time interval. The change in the rate of leaf delivery was probably caused by (i) the replacement of hemlock by hardwoods, and (ii) changes in spring and summer runoff. The uppermost productivity oscillation may represent cultural eutrophication or an increased growth of *Isoetes* on the lake bottom, or both.

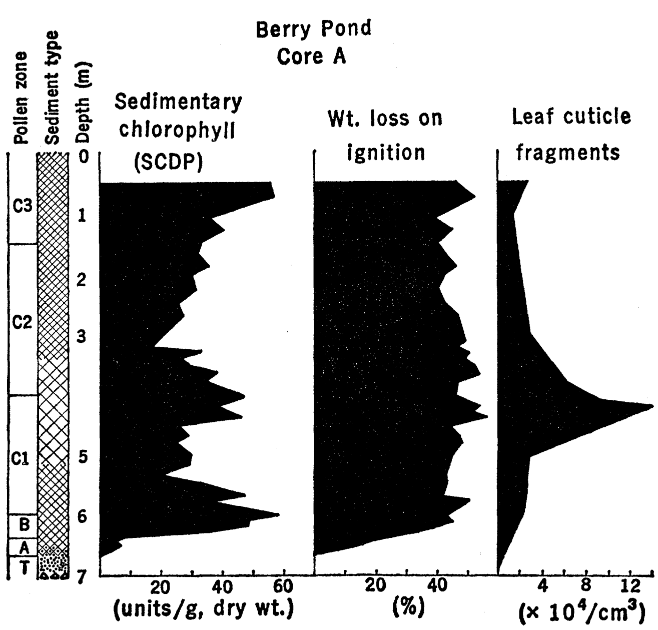
An analysis of sedimentary chlorophyll degradation products (SCDP) (*2*) and the organic content of the sediment (Fig. 1) from a core from the deepest portion of Berry Pond indicated that the early history of the pond was not unusual. A sigmoidal pattern of eutrophication during the late glacial with the establishment of a trophic equilibrium from 8800 to 7000 years ago is suggested (*3*). After this the pond's history diverges from the "normal" pattern. The SCDP values are low between 7000 and 5000 years ago, increase to another maximum between 5000 and 3800 years ago, and then decline once again. The chlorophyll content of the sediment increases once again in the top meter of the core.

Analysis of a second core (Fig. 2) taken about 10 m south of the first demonstrates the same changes in SCDP and weight loss on ignition. Pollen data from the two cores indicate that the changes were synchronous. It appears that there were significant trophic changes during the late glacial and postglacial (*4*).

This generalization is supported by the available microfossil data. Analysis of diatoms from the second core (Fig. 2) indicates that the absolute diatom frequency parallels the SCDP oscillation. Preliminary data on Cladocera show a similar pattern. There are distinct maxima for both *Bosmina* and chydorids in the early postglacial and even more striking contemporaneous maxima in the middle postglacial (Fig. 2). Although data for Cladocera in the upper half of the profile are incomplete, there are indications of additional changes.

There are analogous changes in abundance of *Pediastrum* species, although the peaks are slightly out of phase with SCDP, diatoms, and Cladocera. The *Pediastrum* maxima seem to occur shortly before and shortly after the productivity peaks. *Pediastrum boryanum*, the dominant species in the Berry Pond profile, is considered to be an indicator of mesotrophic conditions (*5*).

There is a significant maximum of dinoflagellates (mostly *Peridinium* sp.) associated with the mid-postglacial productivity peak. In addition there is a distinct maximum of microscopic leaf cuticle fragments (Fig. 1) (the sedimentation rate for leaf cuticle fragments changed from 3700 cm^{-2} $year^{-1}$ 6000 years ago to over 13,000 cm^{-2} $year^{-1}$ 4500 years ago; subsequently it declined to the previous rate). The leaves were derived from



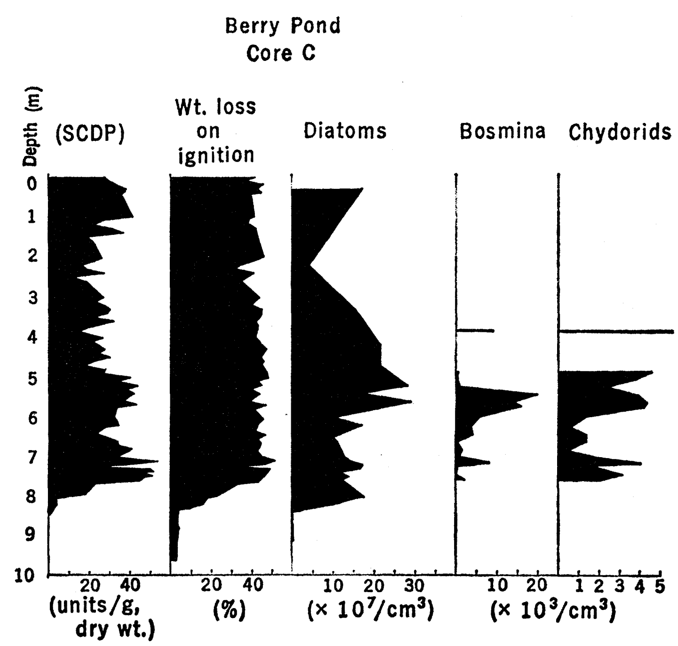


Fig. 1 (left). Data on sedimentary chlorophyll, weight loss on ignition, and leaf cuticle fragments from core A. Pollen zones are described in (*14*). The sediment symbols are: (fine crosshatch) gyttja; (coarse crosshatch) fibrous gyttja; (stippling) clay; (triangles) till. Fig. 2 (right). Data on SCDP, loss on ignition, diatoms, and Cladocera from core C.

the terrestrial vegetation of the watershed.

Palynological data indicate that the initial period of increasing productivity occurred while the forests of the region were changing from park-tundra to boreal in character (dominated first by spruce and then by pine). Productivity was stabilized during the "pine period" and declined as hardwood species (and hemlock) replaced pine (approximately 9000 years ago). The second productivity oscillation (5000 to 3800 years ago) corresponds to the transition between pollen zones C1 and C2 (Fig. 1). At this point there is a sharp decline for hemlock and increases for birch, oak, beech, and, eventually, pine. The uppermost productivity increase is initiated just below the rise of *Ambrosia* (indicative of European land clearance) and coincides with a sharp increase in frequency of *Isoetes* microspores.

It is interesting to speculate why Berry Pond departs from the once traditional model (*6*) of lake development. We think that the initial phase of eutrophication was a function of both weathering of till and vegetational changes within the watershed. This cycle of increasing productivity occurred during the late glacial and early postglacial, a time interval during which there was rapid amelioration of the climate (*7*), which presumably resulted in an accelerated rate of leaching of the freshly exposed glacial soils. The reversion in productivity probably reflects the steady depletion of readily leachable components of the till.

The correlation of production changes with vegetational changes suggests that other controls may be exercised as well. The work of Bormann and Likens (*8*) demonstrated the extent to which a complex northern hardwood forest may influence both the discharge and the quantity of nutrients flushed from the system by groundwater flow (*9*). Thus, we suggest that an additional factor influencing the reversion of production in Berry Pond was a change in the ability of the terrestrial ecosystem to hold nutrients due to the shift from boreal to northern hardwood forests. Boreal coniferous forests are lower in productivity and biomass than temperate deciduous forests (*10*). Rates of litter decomposition are lower as well (*11*). Furthermore, this lower capacity of boreal forests to retain nutrients would be accentuated by the acid litter characteristic of such forests. This would result in increased leaching and flushing of nutrient cations from soil particulates into groundwater (*12*). There is also some evidence that nitrification proceeds rapidly in coniferous forests, but is suppressed within deciduous forests (*13*). Accordingly, the rate of nitrate delivery to the groundwater (and hence to the pond) would be greatest during the late glacial and early postglacial and would drop sharply as the northern hardwood complex became dominant. As loss of a variety of cations seems to be controlled indirectly by nitrification (*8, 9*), a similar temporal pattern would be evident for the rate of cation delivery to the pond.

This suggested correlation is apparently not unique to Berry Pond. Preliminary work on SCDP from the Pownal Bog in southwestern Vermont (*14*) shows a similar correspondence between late glacial and postglacial pollen zones and an SCDP oscillation. The same correspondence is evident for Bethany Bog and Linsley Pond in Connecticut (*15*), Pretty Lake in Indiana (*16*), and Kirchner Marsh in Minnesota (*17*). This lends support to the contention that changes in the composition of a terrestrial ecosystem may influence processes in adjacent aquatic systems. However, the relationship is not simple, as has been pointed out in studies of Linsley Pond (*18*), where the availability of phosphorus has been controlled by a number of factors.

The mid-postglacial production change is more difficult to comprehend. It is tempting to suggest that the oscillation is a function of the sharp increase and subsequent decline in the rate of leaf (or leaf fragment) input to the basin. The decomposition of leaves would release nutrients which would, in turn, generate a change in production. The change in leaf input could be a function of both vegetational changes and alterations in spring and summer runoff. At this point in the profile (approximately 5000 years ago) there is a sharp decline in hemlock (the influx rate for hemlock grains drops from 6300 to 1800 cm^{-2} $year^{-1}$ within 260 years) (*19*) and increases for birch, beech, and oak. A portion of the increased leaf delivery might thus reflect the increased availability of leaves of deciduous trees in the litter. In addition, the elimination of hemlock and replacement by deciduous taxa could have caused a marked change in spring runoff. In coniferous forests the spring snow melt is spread over a relatively long time interval, while in deciduous forests it is often compressed into a very short span characterized by runoff sufficiently intense to remove much of the accumulated litter (*13*). It is also conceivable that there might have been periods of more intense summer runoff due to thunderstorm activity during the middle postglacial.

The uppermost SCDP peak could reflect cultural eutrophication, but the pollen data suggest that the increase was initiated shortly before European land clearance. There is no apparent increase in diatoms, sedimentation, or leaf input associated with this maximum, but there is an interesting correspondence with a sharp peak for *Isoetes* microspores. The inception of the peak might reflect the time at which the lake became sufficiently shallow (about 4 m at that time) to permit sufficient light penetration for *Isoetes* growth (*20*).

The changes in primary production suggest that it should be possible to approach questions relating to community structure (*21*). Our preliminary work on the structure of cladoceran communities suggests that there are significant changes associated with the mid-postglacial productivity oscillation. Diversity is high before the peak ($H \sim 3.0$), decreases during the peak ($H \sim 1.4$), and increases once again as productivity declines (*22*).

Many questions remain concerning the changes in production and community structure, but detailed work on diatoms, Cladocera, and sediment chemistry should provide further insight.

DONALD R. WHITEHEAD
HAYDON ROCHESTER, JR.
STEVEN W. RISSING
CLAUDIA B. DOUGLASS
MARK C. SHEEHAN
Division of Biological Sciences, Indiana University, Bloomington 47401

References and Notes

1. B. K. Emerson, *U.S. Geol. Surv. Bull.* **597** (1917).
2. J. R. Vallentyne, *Can. J. Bot.* **33**, 304 (1955); J. E. Sanger and E. Gorham, *Limnol. Oceanogr.* **15**, 59 (1970).
3. The dates cited in this report are based on 16 radiocarbon dates from the pollen core.
4. We have made the assumption that changes in primary production will be accompanied by comparable changes in the rate of delivery of SCDP, diatoms, other algae, and Cladocera to the bottom sediments.
5. D. S. Rawson, *Limnol. Oceanogr.* **1**, 18 (1956).

6. A. Thienemann, *Verh. Deut. Zool. Ges.* **31**, 29 (1926); G. E. Hutchinson and A. Wollack, *Amer. J. Sci.* **238**, 493 (1940); R. L. Lindeman, *Ecology* **23**, 399 (1942); C. N. Sawyer, *J. Water Pollut. Contr. Fed.* **38**, 737 (1966).
7. E. J. Cushing, in *The Quaternary of the United States*, H. E. Wright, Jr., and D. G. Frey, Eds. (Princeton Univ. Press, Princeton, N.J., 1965), p. 403; M. B. Davis, in *ibid.*, p. 377; in *Quaternary Paleoecology*, E. J. Cushing and H. E. Wright, Jr., Eds. (Yale Univ. Press, New Haven, Conn., 1967), p. 11; E. J. Cushing, in *ibid.*, p. 59; J. G. Ogden, III, in *ibid.*, p. 117.
8. F. H. Bormann and G. E. Likens, *Science* **155**, 424 (1967).
9. G. E. Likens, F. H. Bormann, N. M. Johnson, R. S. Pierce, *Ecology* **48**, 772 (1967); F. H. Bormann, G. E. Likens, D. W. Fisher, R. S. Pierce, *Science* **159**, 882 (1968).
10. L. E. Rodin and N. I. Bazilevich, *Production and Mineral Cycling in Terrestrial Vegetation* (Oliver & Boyd, London, 1967); H. W. Art and P. L. Marks, in *Forest Biomass Studies*, H. E. Young, Ed. (Univ. of Florida Press, Gainesville, 1971), p. 3.
11. C. F. Jordan, *Amer. Sci.* **59**, 425 (1971).
12. B. Nihlgard, *Oikos* **22**, 302 (1971).
13. W. D. Reiners, personal communication.
14. D. R. Whitehead and D. R. Bentley, *Pollen Spores* **5**, 115 (1963).
15. E. S. Deevey, Jr., *Amer. J. Sci.* **241**, 257 (1943); J. R. Vallentyne, *Limnol. Oceanogr.* **1**, 252 (1956).
16. R. G. Wetzel, *Limnol. Oceanogr.* **15**, 491 (1970); A. S. Williams, thesis, Indiana University (1971).
17. J. E. Sanger and E. Gorham, *Limnol. Oceanogr.* **17**, 840 (1972).
18. D. A. Livingstone, *Amer. J. Sci.* **255**, 364 (1957); ——— and J. C. Boykin, *Limnol. Oceanogr.* **7**, 57 (1962).
19. The decline of hemlock is evident in many diagrams from New England and the Midwest. It is particularly striking in a profile from Mirror Lake, N.H., and it has been suggested that it might be due to a pathogen (M. B. Davis, personal communication; paper presented at the annual meeting of the American Institute of Biological Scientists, Minneapolis, 1972).
20. W. C. L. Muenscher, *Aquatic Plants of the United States* (Comstock, Ithaca, N.Y., 1944).
21. R. Margalef, *Advan. Front. Plant Sci.* **2**, 137 (1963); *Perspectives in Ecological Theory* (Univ. of Chicago Press, Chicago, 1968); E. P. Odum, *Science* **164**, 262 (1969); H. L. Sanders, *Brookhaven Symp. Biol. No. 22* (1969), p. 71; C. E. Goulden, *ibid.*, p. 96; M. Tsukada, *Quaternary Res.* **6**, 101 (1967).
22. Information theoretical measures of diversity (both H and H') have been calculated according to the procedures outlined → M. Lloyd, J. H. Zar, and J. R. Karr [*Amer. Midl. Natur.* **79**, 257 (1968)].
23. Work on this project has been supported by NSF grant 12672. We thank J. P. Bradbury, W. D. Reiners, and W. A. Watts for invaluable discussion and D. G. Frey for a critical reading of the manuscript. S.W.R. was supported by NSF undergraduate research participation grant GY9750.

2 March 1973; revised 5 June 1973

Unusual Retinal Cells in the Dolphin Eye

Abstract. *By comparison to the cellular constituents of the retinas of certain other diving mammals, the elements of the dolphin retina include an unusually large number of specialized cells. Both cone and rod receptors may be identified. An unusual amacrine cell may be seen which produces a process that spans the cells between the inner plexiform and outer plexiform layers. Most unusual is a layer of giant ganglion cells which appears to serve most of the central retina. The giant ganglion cells support giant dendrites and optic nerve fibers which range up to 8 micrometers in diameter.*

Specialization of the auditory system of the bottlenose dolphin (*Tursiops truncatus*) has been established by research of the last two decades (*1*). But the visual system is not well described. Opinions on generalized cetacean visual capabilities are diverse. Rochon-Duvigneaud surveyed the eye anatomy of several species and concluded that function must be very limited (*2*). In contradiction, Mann has reported cone receptors (indicative of color vision and high resolution) in the whale (*Balaenoptera*) and proposed a mechanism that would correct for the optical problems which confront eyes used in both air and water (*3*). A recent evaluation of visual acuity of the Pacific dolphin (*Lagenorhynchus*) which showed thresholds of about 6 minutes of arc does not necessarily confirm the presence of a duplex (rod and cone) retina (*4*).

Similar acuity thresholds have been reported in the California sea lion (*5*), in whose retina we were able to find only rod receptors (*6*). Recently we have examined a limited supply of well-preserved eyes from Atlantic bottlenose dolphins, where retinas are structurally similar to those of terrestrial mammals such as dogs and cats (*7*), except that cones were found to be more plentiful and highly specialized. Amacrine and ganglion cells were numerous.

Eight eyes were quickly removed from dolphins killed for humane reasons by intracardial injection of pentobarbital. The eyes were opened, fixed in 4 percent buffered glutaraldehyde, and stained by the method of Golgi (*8*), hematoxylin and eosin, or silver techniques. Figure 1 shows a section of dolphin retina stained by Golgi technique. In the upper center is a typical cone outer segment, ellipsoid and cell body. Lateral to the cone outer segment are unstained, long filamentous structures that are probably rod outer segments, which we have seen stain occasionally by Golgi process. On the extreme right, in the receptor layer, are other bulbous structures which may be unstained cone outer segments. To the left is a large matrix of Müller cell fibers which have been stained heavily and obscure parts of several other receptors. In Fig. 2 are cells in the inner plexiform layer with characteristic lateral processes of amacrine cells. However, these cells also have processes that penetrate through the bipolar cell layer and terminate in the outer plexiform layer. In some thick sections, we have been able to follow these apical processes for 60 to 100 μm in the outer plexiform layer. Most frequently, the apical process terminates (as in Fig. 2) in a densely stained area. Therefore it is not possible to state that all such cells in the dolphin retina have extensive ramifications in the outer plexiform layer. Considering the general infrequency of staining of specific cell types by the Golgi technique, it is probable that this cell is common in the dolphin's eye since several such cells have been seen in each eye we processed.

In Fig. 3 is a transverse section of retina, pigment epithelium, and scleral tissue photographed through the interference contrast microscope (*8*). Although the tissue is unstained, all layers of the retina may be identified. This low magnification photograph shows several of the giant cells in the ganglion cell layer. The size and frequency of giant ganglion cells is the major difference between this and retinas of other mammals. The giant cell bodies range up to 150 μm in diameter and appear to predominate in the central 40° of retina. Most giant ganglion cells give rise to large dendritic processes and large optic nerve fibers. Both dendrites and axons may be seen in Fig. 3. The giant axon diameters range up to 8 μm and form a very thick nerve fiber layer. Even in thick sections, interference microscopy allows visualization of the cell body details including the nucleus and the nucleolus, which is seen as a central depression in the cells in Fig. 3. Less spectacular ganglion cells range down to cell body diameters in the 6 to 12 μm range. Occasionally, these cells stain by the Golgi technique. However, we have never seen a "giant cell" which had been silver stained. The smaller ganglion cells appear infrequently, interspersed below the giant cells which lie one against another forming a tightly packed pad of cells which is seen as the focal plane of the interference microscope varied throughout the 75 μm sections. Unusually large cells were seen occasionally in the inner plexiform layer. Their diameters were around 20 μm.