THE TAXONOMIC VALUE OF RETINAL STRUCTURE IN ETHEOSTOMATINE FISHES (PERCIDAE)

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PREFACE

Many of the difficulties and complexities that developed during the course of this investigation were not anticipated during its formulation in 1956. I then believed, erroneously, that satisfactory retinal diagnoses for comparative purposes could be obtained from median vertical plus dorsal and ventral tangential sections. Consequently, the description and comparison of retinal structures in the 28 Oklahoma darter species were considered feasible with only a few adult specimens of each species.

A preliminary survey of the literature on fish eyes revealed a dearth of information on darters, and there were no clues to the types of differences that might be expected between species. Most descriptions deal with cone types and mosaics, and other distinctive features such as tapeta, and these aspects were given first consideration. The techniques for bleaching and staining retinae employed by other workers gave poor results with darter retinae. Numerous hours and specimens were used as various techniques were tried with only moderate success. When a relatively simple but highly effective technique for showing photoreceptor structure was finally discovered, it was applied forthwith to the species still available.

Only then, when success seemed so near, was it full realized that a thorough evaluation of the variation in photoreceptor proportions within the species would be necessary before different species could be compared. This realization was based on the high degree of apparent intraretinal variation, and was supported as reports of recent studies on the changes

in the size and density of retinal structures that occur during growth became available. The evaluation of photoreceptor variation would have necessitated the collection of numerous specimens of different sizes and the preparation of many additional slides. In the interest of time, it seemed advisable to examine some other approach to the problem using the materials already available.

Consequently, the idea of using various cell-density ratios as a means of comparing species was developed. Since this approach was without precedent, neither the most diagnostic ratios nor the possible success of the method could be predicted. It was therefore necessary to calculate several ratios for as many species as possible. Because the slides were stained to emphasize the photoreceptors, many were unsuitable for cell counts and all species could not be included.

The method of using a combination of ratios to compare retinae of different species seems to be satisfactory. Because the method is new, and may be useful to other investigators, it is presented at this time even though it was not thoroughly tested or applied to all of the darter species in Oklahoma. The results of this investigation indicate that retinal diagnoses of some taxa not found in Oklahoma would reveal more taxonomic relationships than study of the remaining Oklahoma forms.

Assistance in this endeavor has come from several sources. I am deeply indebted to my major advisor, Dr. George A. Moore, for his invaluable advice, encouragement and assistance throughout this study, and for criticizing the manuscript. Drs. R. W. Jones, B. P. Glass, A. M. Stebler and W. S. Newcomer have served on my advisory committee and evaluated the manuscript.

Of the numerous individuals who have helped me obtain specimens, I wish to thank particularly Dr. K. Strawn, University of Arkansas, for supplying sand darters from Texas and assisting, along with Dr. B. A. Branson, with the seining of several species.

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INTRODUCTION

The readily accessible characters used to distinguish the species of darters show considerable variation and some overlap between groups of species. Consequently, Bailey (1951; in Bailey, Winn and Smith, 1954; in Bailey and Gosline, 1955) was obliged to lump all the darters into three genera and to designate 22 subgenera, many of which had been previously recognized as genera. Since this action was not supported by adequate published data, it was not readily accepted by some workers who continued to use the older generic names. With the idea that a more cryptic character might help to clarify the taxonomic relationships of darters, an investigation of the possible use of retinal structures in taxonomy was undertaken.

Secondary objectives included the description of several darter retinae and the correlation of retinal structure with the habits and habitat, if possible.

Except for a diagram of the cone pattern of Etheostoma coeruleum by Eigenmann and Shafer (1900), the retinae of darters have not been described. Darters are known to be sight-feeders and as expected, have retinae well-developed for acute vision.

Darters constitute the tribe Etheostomatini in the family Percidae and are currently divided into the three genera Percina, Ammocrypta and Etheostoma. They are endemic to the fresh waters of North America, and occupy a wide variety of habitat types ranging from swamps to rapid streams. The three genera and 13 subgenera are represented in Oklahoma

by 28 species. For convenience, and to limit arbitrarily the scope of this study, only readily obtainable Oklahoma species were studied. All 28 species were collected, but some were represented by only one or two specimens and some preparations proved unsatisfactory. Although 26 species are discussed, the information for some is incomplete.

The eyes of fishes have been studied by numerous investigators with various objectives. Most of the earlier works were primarily descriptive, with the emphasis on retinal structure. The photoreceptor cells received particular attention, probably because of their variability in size and kind. They were described in great detail for many species, whereas the other retinal structures received more casual treatment. Physiological studies were inspired by the Duplicity Theory, but the emphasis remained on the photoreceptors. With some knowledge of function, correlations of structural modifications with various aspects of ecology and behavior were frequently possible with knowledge of the retina based on sagittal sections only (see, e.g. Wunder, 1925, 1926a). Incompleteness and inconsistent methods among authors in describing retinal structures resulted in considerable confusion when comparisons of previously described species were attempted (Engström, 1960).

It has long been recognized that considerable variation in structure exists in different regions of fish retinae, and that the density of cones changes with growth (Shafer, 1900). However, these factors received little attention until Müller (1952) investigated the changes that occur with growth in different regions of the retina in the guppy, Lebistes reticulatus. He showed that retinal growth is allometric in relation to body length and emphasized regional differences, and thus initiated a new approach to the study of fish retinae. Allometric retinal growth was found in Salmo trutta,

and it probably occurs in all teleosts (Lyall, 1957a).

To obtain a valid comparison of retinae between species it is necessary to consider the entire retina and equate the eye size. By considering tangential sections from 16 regions and using the lens as an index of eye size, O'Connell (1963) apparently satisfied these conditions in comparing retinae of six marine teleosts. Cone types and regional variations in cone patterns of numerous species have been compared by Engström (1960, 1961, 1963b) and Engström and Ahlbert (1963), presumably on the assumption that the cone pattern is not influenced significantly by growth. Since most of their conclusions concern the cone arrangement within a family, growth changes may not have influenced their findings.

Although the retinae of numerous fishes have been compared, no attempts have been made to use the retina in taxonomy. Engström (1960, 1963b) concluded that the cone mosaic of the family is phylogenetically determined and species differences are ecologically determined. Otherwise, retinal structures have not been considered with respect to phylogeny.

It was necessary to ascertain the structure of the darter retinae before considering the other objectives. Microscope slides of sections from six planes of the retinae were prepared and used in describing the retina of each species. A basic similarity of structure was found between all species, the main differences being the densities of cells in various regions of the retinae. Cell counts from different parts of the retinae of a few specimens of various sizes showed that the density of retinal cells changes with growth and that absolute numbers are of little value in making comparisons. It was found that cell-density ratios could be utilized to minimize discrepancies related to growth. This method proved satisfactory within the scope of this study and some unexpected taxonomic

applications have resulted. Some possible phylogenetic relationships, based on retinal modifications, are suggested. Though limited by the number of taxa considered herein, relationships based on retinal structure closely resemble those based on other characters. Thus, the use of retinal structure as a taxonomic tool and as an aid in determining phylogeny of the darters is considered feasible.

A few observations of habits and habitat were made while collecting the specimens and some species were retained in aquaria for further observation, but it was necessary to rely largely on the literature for such information. Unfortunately very little detailed information is available, and it has been possible to correlate retinal structure with known habits in only a few species. No correlation of the general habitat with retinal structure was found, possibly because of the methods employed.

MATERIALS AND METHODS

Specimens from the localities listed below were captured with seines and retained alive for dark or light adaptation prior to fixation. Light adaptation was accomplished by placing the fish in a white container in bright light for an hour. Dark adaptation involved putting light-adapted fish in total darkness for an hour. The specimens were retained under appropriate lighting conditions for another hour in the fixative. The formula and procedure for using Kolmer's fluid suggested by Walls (1938) was used for all species. Perenyi's (1882) fluid was also used but proved unsatisfactory.

While in 80 per cent ethanol the head was split sagittally and trimmed until only enough tissue remained around the eye to facilitate orientation. The corneae of large specimens were slit to enhance infiltration of celloidin. Walls' (1932) hot celloidin technique was used for some specimens but the longer, room-temperature method seemed to be more satisfactory. The celloidin was hardened in chloroform and cleared in terpineol.

Sections were cut at six microns on a rotary microtome in median vertical (sagittal), nasal- and temporal-tangential planes of one eye and median horizontal, upper- and lower-tangential planes of the other eye of each specimen.

Several methods of bleaching the retinal pigment were tried with varying degrees of success. Although nascent chlorine bleached the pigment adequately, subsequent staining with hematoxylin was impaired. It was found that the pigment could be bleached rapidly and thoroughly in a solution of

approximately 1% hydrogen peroxide, 0.1% ammonium hydroxide and 20% alcohol. This mixture was conveniently formulated in a Syracuse watch glass by adding about 2 ml of 3% peroxide and a drop or two of ammonia to the 30% alcohol during the penultimate step of hydration. Bleaching was complete in 2-4 hours, the time varying somewhat with peroxide concentration and temperature. Attempts to use this technique on paraffin sections has resulted in the loss of sections, even when coated with thin celloidin. Experimentation with weaker solutions may prove more successful. O'Connell (1963) bleached fish retinae with 1% hydrogen peroxide in 8-12 hours, but no reference to the use of hydrogen peroxide with ammonium hydroxide as a bleach for the retinal pigment, fuscin, has been found.

Both bleached and unbleached sections of all species were stained in Heidenhain's (1892, fide Gray 1954) iron hematoxylin. The bleached sections stained readily and by mordanting and staining for 8-12 hours, details of the rods and cones became clearly visible. Eosin was used as a counterstain on some sections, but its addition to the bleached sections was of little value. Several other stains were tried but the results were inferior to the hematoxylin preparations.

The cone, rod, bipolar, amacrine and ganglion cell nuclei in a measured length of section were counted in different regions of the retina. The counts were repeated on additional sections of each specimen until approximately 200 of each cell type had been counted in each region. For convenience, the average number per 90 microns length of section was then calculated and used to determine cell ratios. Since all sections were cut at six microns and the counts were made for determining ratios only, it did not seem expedient to correct mathematically for the differences in cell size. The errors introduced by such a method would be nearly equal for each

species, thereby having little significance.

All measurements were made with a filar micrometer. The average size of the cone pattern in tangential sections from dorsal, ventral, nasal and temporal regions of the retinae was determined by a method similar to that of Lyall (1957b). The size of a cone pattern is the distance between the centers of two single cones taken across the axis of a twin cone. The pattern is not always a perfect square, so that at least three measurements were made across ten patterns along each dimension to determine the average pattern size in each region. The figures thus obtained can be used to calculate cone densities for any area, thereby permitting comparison with published data for other species. To minimize discrepancies introduced by the change in pattern size accompanying growth, the four pattern sizes of each specimen were summed and the pattern size of each region expressed as a percentage of the total.

The thickness of the retina and each of its layers and the dimensions of the photoreceptors were measured in the dorsal, ventral, nasal, central and temporal regions in several species. These measurements have some descriptive value, but since they change with growth they are of little taxonomic use.

Measurements referred to as "retinal size" were taken from horizontal sections and represent the greatest nasal-temporal distance between the outer margins of the pigment epithelium layer. Detailed explanations of some other measurements are included with the general description of the retina.

The species included in this study are listed under the subgenera proposed by Bailey and Gosline (1955). Only the specimens from which data were collected are listed; however, specimens from additional areas were

examined in several instances. Abbreviations: SL, standard length; K, Kolmer's fluid; P, Perenyi's fluid; L, light adapted; D, dark adapted.

Genus Percina

Subgenus Alvordius

P. maculata (Girard). Okla., Latimer Co., Fourche Maline Cr. SL 52 mm, K,D.

P. pantherina (Moore and Reeves). Okla., Pushmataha Co., Little R. SL 53 mm, K,D; SL 52 mm, K,L.

Subgenus Hadropterus

P. sciera (Swain). Okla., McCurtain Co., Mountain Fork R. SL 35 mm, P,D: SL 62 mm, K,L; SL 63 mm, K,D; SL 79 mm, P,L; Pushmataha Co., Little R. SL 42 mm, P,L.

Subgenus Swainia

P. phoxocephala (Nelson). Okla., McCurtain Co., Mountain Fork R. SL 52 mm, K,L; Cherokee Co., Illinois R. SL 65 mm, P,L; SL 65.5 mm, K,D; Kay Co., Chikaskia R. SL 42.5 mm, K,L; SL 43mm, K,D.

P. nasuta (Bailey). Okla., Sequoyah Co., Lee Cr. SL 54 mm, K,L.

Subgenus Imostoma

P. shumardi (Girard). Okla., Bryan Co., Red R. SL 30 mm, K,L.

Subgenus Cottogaster

P. copelandi (Jordan). Okla., Adair Co., Tyner Cr. SL 44.5 mm, K,L.

Subgenus Percina

P. caprodes (Rafinesque). Okla., Marshall Co., House Cr. SL estimated over 70 mm, K,L; LeFlore Co., Poteau R. SL 52 mm, K,L.

Genus Ammocrypta

Subgenus Ammocrypta

A. vivax Hay. Texas, Hardin Co., Village Cr. SL 39 mm, K,D.

A. clara Jordan and Meek. Texas, Hardin Co., Village Cr. SL 41 mm, K,D; Okla., Bryan Co., Red R. SL 42.5 mm, K,L.

Genus Etheostoma

Subgenus Boleosoma

E. nigrum Rafinesque. Okla., Pushmataha Co., Little R. SL 37 mm, K,L.

E. chlorosomum (Hay). Okla., McCurtain Co., Waterfall Cr. SL 31 mm, K,L.

E. stigmaeum (Jordan). Okla., Cherokee Co., Illinois R. SL 38 mm, K,D; SL 41 mm, K,L.

Subgenus Etheostoma

E. zonale (Cope). Okla., Cherokee Co, Barren Fork R. SL 45.5 mm, K,L.

E. blennioides Rafinesque. Okla., Cherokee Co., Illinois R. SL 60.5 mm, K,L.

E. histrio Jordan and Gilbert. Okla., McCurtain Co., Mountain Fork R. SL 40 mm, K,D; SL 34 mm, K,L.

Subgenus Oligocephalus

E. radiosum (Hubbs and Black). Okla., Johnston Co., Blue R. SL 49.5 mm, K,L; McCurtain Co., Yashau Cr. SL 33.5 mm, K,L.

E. whipplei (Girard). Okla., Latimer Co., Fourche Maline Cr. SL 52 mm, K,L.

E. punctulatum (Agassiz). Okla., Mayes Co., Little Spring Cr. SL 45 mm, K,L; Cherokee Co., Fourteen Mile Cr. SL 34.5 mm, K,D.

E. parvipinne Gilbert and Swain. Okla., McCurtain Co., Mountain Fork R. SL 33mm, K,L.

E. cragini Gilbert. Okla., Mayes Co., Little Spring Cr. SL 39 mm, K,L.

Subgenus Catonotus

E. flabellare Rafinesque. Okla., Cherokee Co., Fourteen Mile Cr. SL 36 mm, K,L.

Subgenus Hololepis

E. gracile (Girard). Okla., McCurtain Co., Forked Lake SL 28 mm, K,L.

E. fusiforme barratti (Holbrook). Okla., McCurtain Co., Forked Lake SL 38 mm, K,D; SL 47 mm, K,L.

Subgenus Microperca

E. proeliare (Hay). Okla., McCurtain Co., Forked Lake SL 20 mm, K,L; SL 19 mm, K,L.

E. microperca Jordan and Gilbert. Okla., Mayes Co., Big Spring Cr. SL 32 mm, K,L.

OBSERVATIONS

Description of Generalized Darter Retina

To serve as a basis for the following descriptions of the various species and to clarify the terminology used, the general structure of the darter retina is discussed. The organization of the retina is very similar in all the species examined. The major differences between species involve the sizes and densities of the cells in some regions. The general types of variation are also included in this description.

The retina is cup-shaped as is typical of most vertebrates (Fig. 1). The optic nerve head (papilla) is ventro-temporad from the retinal center. A chorioid fissure extends from immediately below the optic nerve head across the lower retina, angling slightly nasad, to the mid-ventral ora. Ventrally the retina tends to flatten in some species, whereas the upper region has a curvature of shorter radius and is frequently foreshortened (Fig. 2). In a horizontal plane the temporal region frequently has a curvature of shorter radius than the central and nasal regions. The ventral retina is typically the thinnest and either the central (fundus), dorsal or temporal region is the thickest.

The convergence of ganglion cell axons toward the optic nerve results in a progressively thicker nerve fiber layer toward the nerve head. This tends to obscure local variations in thickness produced by differing cell densities indicative of differences in visual activity. Therefore, unless specifically stated as "total", the thickness of the retina will refer to the perpendicular distance from the inner margin of the ganglion cell layer

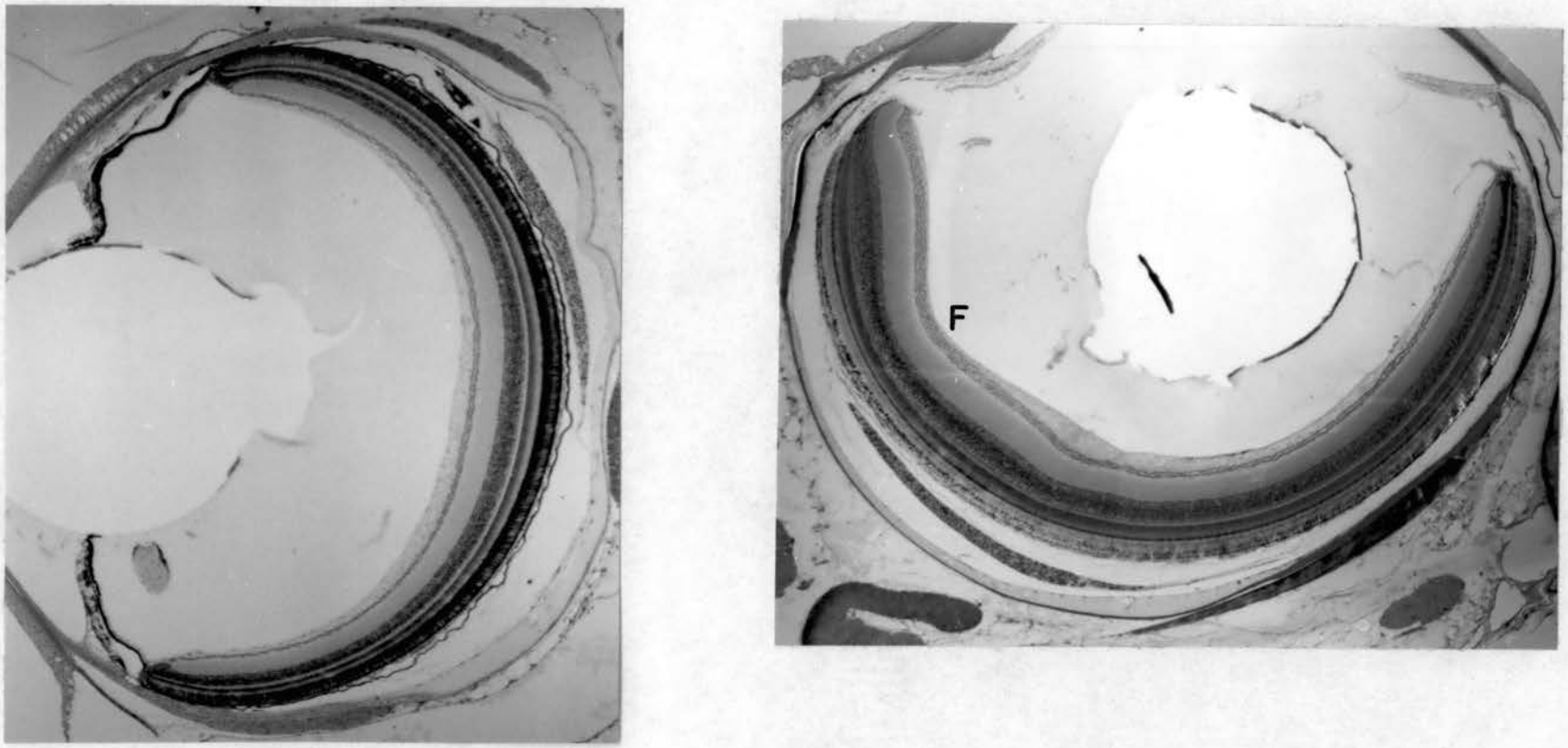

Fig. 1. Retinal sections of E. microperca. Left: unbleached vertical section showing smooth curvature and nearly equal dorsal and ventral regions. Right: bleached horizontal section showing temporal fovea (F) and relatively thick nasal region in comparison to dorsal and ventral regions.

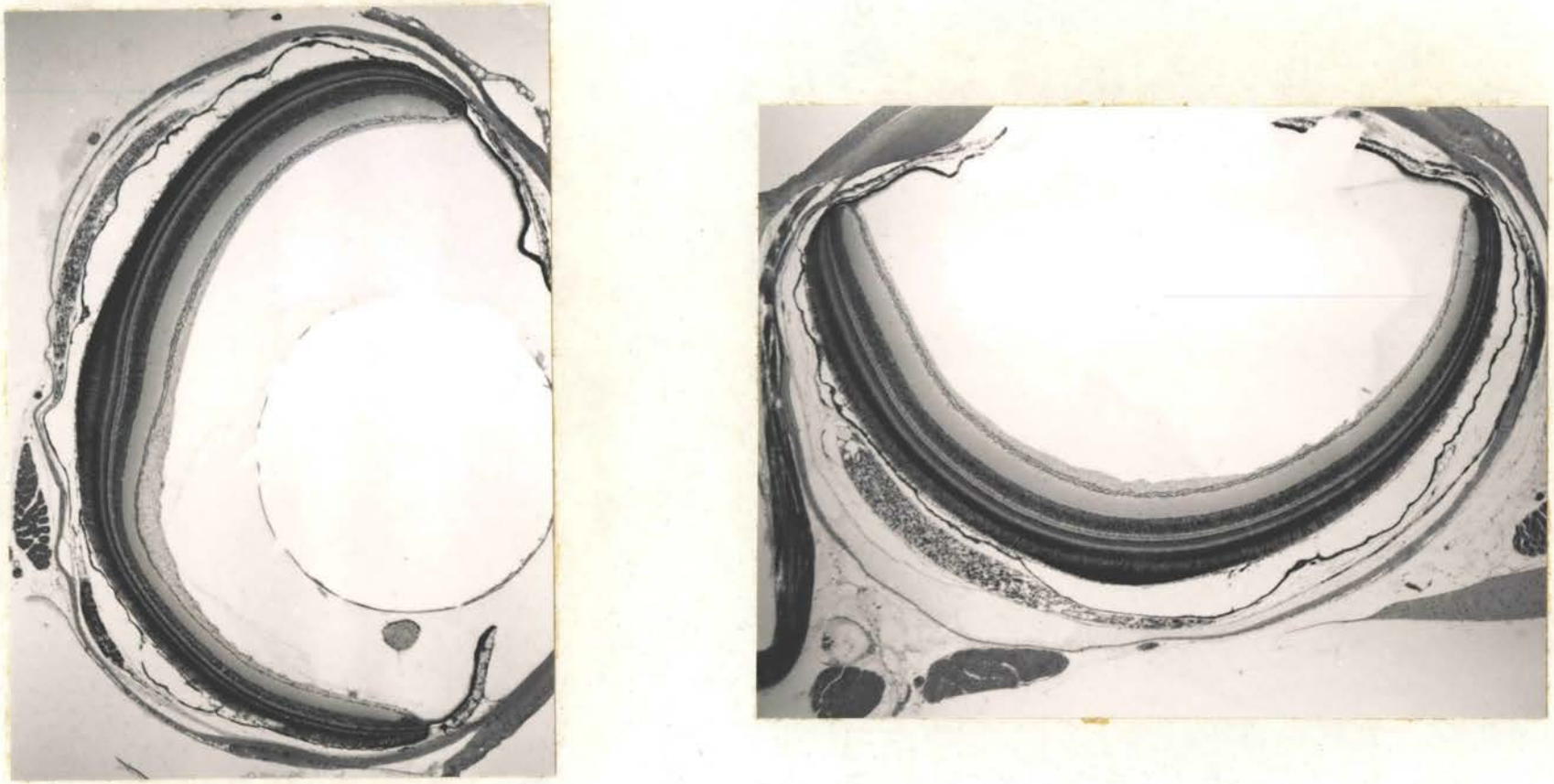

Fig. 2. Retinal sections of E. chlorosomum. Left: vertical section showing the thicker and foreshortened dorsal region and slightly flattened, thin ventral region. Right: horizontal section showing the thickened but afoveate temporal region and thin nasal region. Note the concentration of pigment in the central region of both sections.

to the outer margin of the pigment cells.

The ganglion cell layer contains cells differing in size and nuclear appearance. Some have small, densely-staining nuclei similar to bipolar cells and others have moderate to large nuclei which show a loose reticular chromatin pattern. Although these probably represent different types of ganglion cells, they are considered collectively herein. The layer varies from one to five cells in thickness, usually being most poorly developed in the lower retina where, in some species, the cells are unevenly distributed in small groups with considerable space between.

Little can be said about the inner plexiform layer other than to mention that its thickness usually varies directly with the density of cones. In well-stained sections Müller fibers can be seen traversing the layer in typical fashion. Occasionally an ectopic nucleus, apparently ganglionic, may be seen.

Several types of nuclei lie in the inner nuclear layer. Amacrine nuclei of different sizes constitute the inner one-third to one-half of this layer. These nuclei have a diffuse chromatin arrangement similar to those of the larger ganglion cells. The small, dense nuclei of the bipolar cells make up most of the layer. The majority are located external to the amacrines, but some are scattered among them and a diffuse layer of bipolars is frequently seen along the inner margin of this layer. A few nuclei, intermediate in size and chromatin arrangement between amacrines and bipolars, are usually present and are included with the amacrines in counts. Vertically-elongated Müller fiber nuclei are interspersed among the bipolars. Horizontal cells form a sparse layer external to the bipolars, with elongate nuclei and cytoplasmic processes extending horizontally. They vary in size with the species, but differences in densities were not noticed.

A single layer of epithelium-like cells, forming a neat row in cross-sections, lies between the horizontal cells and cone pedicles (foot-pieces). In areas with numerous cones these cells are cuboidal with spherical nuclei, becoming more flattened in areas with few cones (Fig. 3). In tangential sections the cells appear nearly square and their arrangement corresponds to that of the overlying single cones so that the distance between two nuclei is equal to the cone-pattern size. The cytoplasm of these cells is comparatively clear and no indications of processes were observed. Engström (1963a) noted a similar relationship between the long single cones and "the large nuclei of the horizontal cells" in tangential sections from Labrus ossifagus, but failed to describe the cells. From the photographs by various authors, e.g. Engström and Ahlbert (1963) and Ali and Hanyu (1963), a similar layer of cells is apparently present in many other fishes, especially those with numerous cones and highly organized retinae. Although these cells are generally considered to be horizontal cells, the apparent absence of processes and their regular arrangement suggests a non-conductive function. Measurements include these cells in the inner nuclear layer.

The outer plexiform layer may best be described by considering separately each of the three zones (Polyak, 1941). An inner zone containing horizontal and bipolar cell processes cannot be recognized because the above-mentioned "cuboidal" cells fill the space it usually occupies. The middle zone is readily recognizable as a discrete row of cone pedicles whose bases form a distinct line along the outer margin of the "cuboidal" cells. An indistinct, poorly-stained structure, possibly a group of synaptic vesicles (Sjöstrand, 1961), is in the inner, central part of each cone pedicle. The inner fibers of the photoreceptor cells, constituting the outer zone of this layer, vary in length and direction from one region of the retina to another.

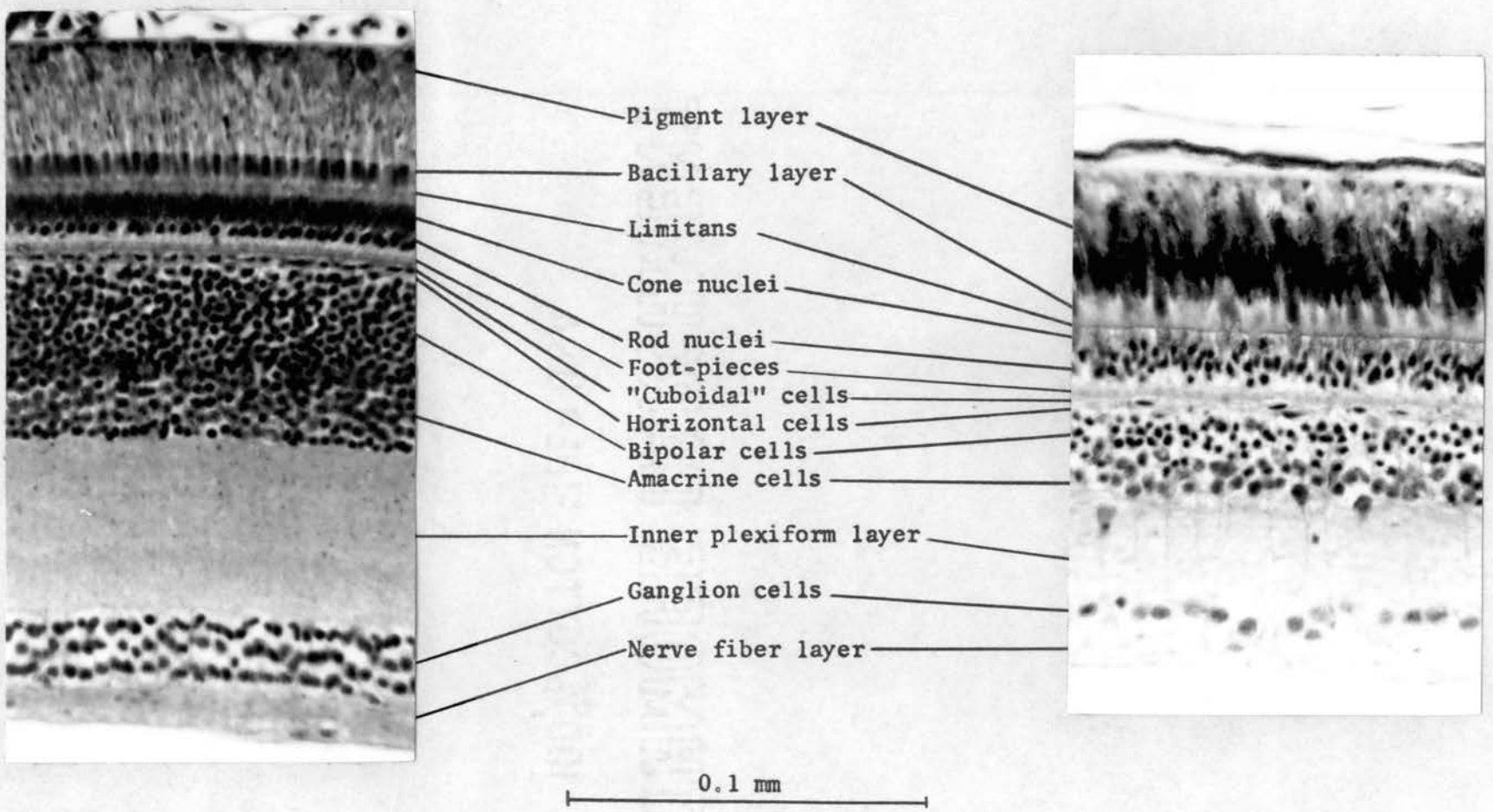

Fig. 3. Cross sections of darter retinae showing variations in layer thicknesses and cell densities. Left: upper central region of E. chlorosomum, bleached, light adapted. Right: ventral region of P. maculata, unbleached, light adapted.

In unmodified regions they are short and extend straight out. As a region of high cone density, i.e. an area or fovea, is approached the fibers angle toward its center in a manner similar to that described by Polyak (1941) for primate retinae. Measurements of the outer plexiform layer were not taken because the inner zone is absent and the outer margin is somewhat irregular. Instead, the distance from the inner margin of the cone pedicles to the external limiting membrane was measured. This distance can be measured with precision and is a more natural unit of the retina than the outer plexiform layer. It also reflects variations in the retina better than either the outer plexiform layer or the outer nuclear layer. This measurement will be referred to as the thickness of the outer nuclear layer.

The nuclei in the outer nuclear layer vary greatly in different regions of the retina. The rod and cone nuclei usually differ in size, shape, position and staining reaction. Rod nuclei typically are smaller, more darkly stained and more irregular in shape than cone nuclei (Fig. 3). In most species they form only one or two irregular rows, being least abundant and sometimes absent in the dorsal retina and fovea. In regions of low cell density the rod nuclei may approach the external limiting membrane between the cone nuclei, but they are usually internal to the cone nuclei. In regions of low density the cone nuclei are nearly spherical and may protrude slightly through the external limiting membrane. They become terete and move inward as their density increases. As an areal or foveal region is approached, the cone nuclei become inclined toward its center, reassuming a vertical position within its center.

The external limiting membrane (limitans) is clearly evident throughout the retina in all species.

One type of rod and two types of cones constitute the bacillary layer.

The density of rods and the lengths of their outer segments vary considerably, whereas their diameters and ellipsoid lengths remain nearly constant. Rods are usually most numerous in the ventral retina. The lengths of the rod myoids change as light intensity changes in typical teleost fashion. This is also generally true of the cone myoids, except in a few species the cones in the ventral region constantly remain in a light-adapted position. Throughout most of the retina, single cones surrounded by four double cones form the square pattern usually found in percids (Engström, 1963b), but in poorly developed regions near the ora a row pattern is found. The two elements of the double cones are equal in size and staining qualities and are considered as twins. The inner segment of a single cone is usually slightly smaller than its counterpart in one element of a neighboring twin. Both cone types vary in size and density in different regions, becoming longer and slimmer as density increases. The inner ends of the cone ellipsoids are indistinct and measurements of their lengths lack precision. The outer segments of all photoreceptors in perifoveal and periareal regions bend toward the center of density where the outer segments are straight.

The term area, in reference to an area centralis, area temporalis or area lateralis, has several connotations and definitions. The most satisfactory and widely-used definition is also the simplest, and merely refers to an area as a localized thickening of the retina containing a higher density of photoreceptor cells than the extra-areal regions. This definition permits the presence or absence of rods or cones and foveae, and though implied, increased acuity is not a requisite condition of an area. Neither the shape nor the position of the area is delimited by definition. The variability of the areae in darters dictates the usage of this

definition. In most species the area is a horizontal, equatorial band that is most highly developed in the temporal region, whereas in others it occupies a central-dorsal position.

Although the term "fovea" usually implies the absence of rods, it will be used here to refer to a region within an area that is marked by a depression in the inner retinal surface and a reduced total thickness (Fig. 1). The darters show varying degrees of foveal development and, although usage of the term is at times quite arbitrary, in the absence of a better term its use becomes necessary. The surrounding photoreceptor cells are always inclined toward the fovea. Although some rods are usually in the fovea they are few and scattered. Foveae are limited to the temporal region of the area and are present in about one-half of the species considered herein.

The pigment epithelium fits the description usually given for this layer in teleosts, with distal rod-shaped and proximal granular fuscin. Guanin was not seen in any species examined. Although this layer received only casual consideration, some apparent differences between species in the distribution of pigment were noted.

Descriptions of Retinae, Habits and Habitats by Species

The following descriptions of the retinae include only those features which indicate specialization. Aspects not included here may be considered typical and covered by the previous general description. For comparative purposes, ratios of various cell counts are included in a later section and, although they have descriptive value, they are referred to only briefly in this section.

Percina caprodes, logperch

In comparison with the other darters the logperch has a generalized retina. The poorly defined area forms a horizontal band that is better developed temporally, with no indication of a fovea. As indicated by the thickness of the retinal layers, the central and nasal regions are very similar (Table I). The ventral region contains the lowest cell densities, although it is thicker than the dorsal region. Most of the difference in the thickness of the two regions is found in the bacillary-pigment and outer nuclear layers. As is evident here, the dorsally thicker, inner plexiform layer correlates with a higher density of cones and better organization of the retina in general, and its thickness may be a better index of development than the thickness of the retina or any one of the cellular layers. Although the inner nuclear layer is slightly thinner dorsally, the cell density is greater there than in the ventral region (Fig. 5). Dorsal/ventral cell ratios indicate higher densities dorsally of all cell types except rods (Fig. 9a).

The tendency for the density of rods to decrease progressively above the ventral region is evident in this darter, but it is not as pronounced as in some of the other species (Fig. 9a and 9b).

TABLE I

P. CAPRODES. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. Standard length over 70 mm, retinal size 3.5 mm, measurements in microns.

Retinal layer	Region				
	Dorsal	Ventral	Nasal	Central	Temporal
Bacillary-Pigment	37.1	50.9	68.6	67.5	65.3
Outer Nuclear	11.9	21.2	25.3	22.1	22.7
Inner Nuclear	27.4	29.9	36.8	36.6	38.1
Inner Plexiform	41.6	31.7	45.9	41.0	54.5
Ganglion	7.9	7.2	11.3	11.5	19.8
Thickness of Retina	126	139	188	178	200

Cone pattern sizes in different parts of the retina indicate the presence, but relatively poor differentiation, of the area. The cone pattern sizes, in microns, and the corresponding numbers of cones per square millimeter in four regions of a 3.5 mm retina were: ventral, 14.9, 13,500; dorsal, 12.3, 19,800; nasal, 11.1, 24,300; temporal, 10.1, 29,400. These figures vary greatly as the size of the eye changes, e.g. comparable figures for the ventral region of a 2.8 mm retina were 12.4, 19,500. Comparison of the dorsal/ventral and central/ventral cell ratios also indicates the weakness of the areal differentiation.

Measurements of some parts of the photoreceptor cells illustrate further the differences in various retinal regions (Table II). Elongation and thinning of the parts in the areal band (nasal, central and temporal columns of Table II) is noticeable, but not as striking as in some other species. Cones in the nasal and temporal regions are about equal in size, but are fewer in number nasally. This may be a modification to accommodate the higher rod density in the nasal region. The similarity in the thickness of the inner nuclear layer in the nasal and temporal regions and the thinner ganglion layer

TABLE II

P. CAPRODES. SIZES OF RODS AND CONES IN DIFFERENT REGIONS OF THE RETINA. Light adapted, standard length over 70 mm, retinal size 3.5 mm, measurements in microns.

	Region				
	Dorsal	Ventral	Nasal	Central	Temporal
Single cone					
Inner segment					
length	16.6	17.0	18.0	17.2	18.5
diameter	4.1	5.0	3.4	3.2	3.4
Outer segment					
length	14	9	17	18	18
Twin cone					
Inner segment					
length	18.9	18.4	20.3	19.8	21.3
diameter	6.9	6.7	4.5	3.6	4.5
Outer segment					
length	16	11	20	17	22
Rod					
Ellipsoid					
length	3.1	5.4	4.3	4.7	4.0
diameter	1.8	1.2	1.1	1.6	2.0
Outer segment					
length	17	17	30	28	29
Cone nucleus					
length	5.5	6.9	10.1	8.0	8.4
diameter	3.8	4.2	3.4	3.4	4.0
Rod nucleus					
length	3.4	4.9	6.1	6.9	5.5

nasally (Table I) indicate a higher rod density and a greater summation of neuronal pathways in the nasal region.

In the light-adapted condition the pigment is located in the long processes and very little remains near the bases of the processes, especially in the central region of the retina. A thin layer of apparently non-migrating granular pigment remains however, near the outer cell-margins. The inner margin of the pigment is near the middle of the cone inner segments throughout the retina. In a dark-adapted eye the retracted pigment forms a thin, dense layer that surrounds only the outer segments of cones. The myoids of single cones elongate more than those of twins.

Habitat. - This wide ranging species has been collected from such a diversity of habitats, small rapid streams to the depths of lakes (Trautman, 1957), that it may be considered ubiquitous.

Habits. - Copepods constitute most of the diet of young logperch, but adults feed largely on aquatic insects, primarily chironomid larvae (Turner, 1921; Dobie, 1959). The reproductive behavior of the logperch is considered to be generalized and primitive (Winn, 1958). It shuns bright light by moving to deep water and hiding under rocks or burying itself in sand, leaving only the eyes exposed (Trautman, 1957).

Percina maculata, blackside darter

The general shape of the retina is slightly modified in the well-developed temporal region where the curvature is decreased. The dorsal region is noticeably foreshortened. Although the horizontal band-shaped area is distinct throughout, there is an obvious nasal-to-temporal complexity gradient that culminates in a mid-temporal fovea. The thickness of the retina and each of its layers reflects the structural complexity in each region (Table III).

The outer ends of the cones, and their nuclei, in the perifoveal area are inclined toward the fovea so that it is structurally distinct. The bipolar nuclei show a similar arrangement, being aligned in rows inclined toward the fovea. The retina is only slightly thicker medial and lateral to the fovea (temporal column of Table III), but a change in the curvature of the retina at the fovea accentuates the depression. The retinal structure and the presence of comparable modifications in other species indicate that the rather sharp bend at the fovea is not an artifact of shrinkage.

TABLE III

P. MACULATA. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 52 mm, measurements in microns.

Retinal layer	Region					
	Dorsal	Ventral	Nasal	Central	Foveal	Temporal*
Bacillary-Pigment	27.5	44.3	51.3	67.5	49.1	45.0
Outer Nuclear	14.9	19.4	21.8	25.7	27.9	26.3
Inner Nuclear	23.2	27.7	38.7	47.9	65.9	74.5
Inner Plexiform	27.5	27.9	46.1	59.0	69.8	76.5
Ganglion	7.9	9.9	11.3	16.9	26.8	24.8
Thickness of Retina	101	129	169	218	239	247

*About mid-way between fovea and ora.

The increased thickness of the inner nuclear and inner plexiform layers in the perifoveal region may be associated in part with the higher density of rods, but most of the increase in thickness is probably the result of some displacement of cells from the fovea.

The ventral retina is a little thicker than the dorsal and, in contrast to the logperch retina, the increase in thickness is represented in all layers. The densities of all cell types are greater ventrally than dorsally. The cone pattern in the ventral region of a 52 mm (SL) specimen measured 12.7 microns as opposed to 14.4 microns in the dorsal region. These measurements are in sharp contrast to 8.4 microns nasally and 5.2 microns temporally, the latter representing 110,000 cones per square millimeter.

A dark-adapted specimen was not available. Pigment in the light-adapted condition is similar to that in the logperch.

Habitat. - The blackside darter is associated with moderate current in pools and raceways between riffles in moderate-sized, clear-water streams (Trautman, 1957; Winn, 1958).

Habits. - P. maculata was observed rising to the surface for insects by Trautman (1957). They spawn over sand or gravel in pools and raceways (Winn, 1958; Petravicz, 1938).

Percina pantherina, leopard darter

The retina of this species is very similar to that of P. maculata, but there is an apparent difference in the size and density of cones. They are smaller and more numerous in P. pantherina where the ventral cone pattern measured 11.2 microns in a 53 mm (SL) specimen as opposed to 12.7 microns in a P. maculata retina of approximately equal size.

Pigment covers the outer halves of the cone ellipsoids in both dark- and light-adapted specimens.

Habitat. - The relatively few collections of the leopard darter indicate that it is limited to clear, swift water (Moore and Reeves, 1955).

Habits. - Unknown.

Percina sciera, dusky darter

The shape of the retina is not modified by the moderately developed, horizontal area. There is some inclination of cones toward a mid-temporal region, but the modification is inadequate to justify the term fovea. The bacillary-pigment layer, and consequently the retina, is thickest in the central region (Table IV), but the thicknesses of the inner plexiform and ganglion layers clearly indicate a temporal center of visual acuity.

Measurements of retinal layers in the dorsal and ventral regions are nearly equal, the latter being slightly thicker. Cone pattern sizes also indicate a slight dorsal-ventral difference: dorsal, 13.0 μ; ventral, 12.4 μ; nasal, 10.4 μ; temporal, 9.1 μ; SL 79 mm. The dorsal/ventral ratios show

TABLE IV

P. SCIERA. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 62 mm, measurements in microns.

Retinal layer	Region				
	Dorsal	Ventral	Nasal	Central	Temporal
Bacillary-Pigment	35.8	41.4	64.8	63.7	38.5
Outer Nuclear	17.3	17.1	20.7	27.7	18.9
Inner Nuclear	18.9	22.7	35.3	43.9	45.9
Inner Plexiform	27.5	28.2	38.7	39.6	50.6
Ganglion	10.1	9.9	12.4	14.4	26.1
Thickness of Retina	107	116	172	212	180

that all types of cells are more numerous ventrally (Fig. 9a). The central/ventral ratios indicate at least twice as many of each cell type in the central areal region except for the rods, which show no change in density.

Variations in the thickness of the bacillary-pigment layer and in cone densities are almost directly correlated with the lengths and diameters respectively of the cones and their nuclei (Table V).

TABLE V

P. SCIERA. TWIN CONE SIZES IN DIFFERENT REGIONS OF THE RETINA. SL 62 mm, light adapted, measurements in microns.

	Region			
	Dorsal	Ventral	Nasal	Temporal
Outer segment length	8	11	25	15
Inner segment length	18.6	16.1	18.0	14.4
Inner segment diameter	8.9	7.0	4.0	3.0
Nucleus length	5.5	7.4	8.7	8.1
Nucleus diameter	5.0	3.9	3.1	3.0

Pigment covers the outer halves of the ellipsoids in the light-adapted condition. The migrating granular pigment leaves a conspicuous clear space in the cell bases. The non-migrating granular pigment forms a distinct layer at the outer margins of the cell bases in the upper half of the eye, but is absent from the lower half. Only the outer segments are covered in dark-adapted eyes.

Habitat. - In Ohio the dusky darter occupies areas with vegetation or debris in streams of moderate size and gradient (Trautman, 1957). This is in agreement with my observations in Oklahoma. The presence of a comparatively well-developed swim bladder may tend to restrict this species to moderate currents.

Habits. - In an aquarium the dusky darter was readily distinguished from other darters by its ability to swim with apparent ease for extended periods. When white worms or other food organisms were introduced, the dusky darters, apparently able to see the food, swam from distances exceeding eight inches and fed ravenously at all levels from the surface to the bottom. They approached food without hesitance, in a head-on direction. This behavior is quite different from that observed in some species.

Percina phoxocephala, slenderhead darter

A thickened temporal region modifies the shape of the retina only slightly, producing a condition intermediate between those of P. maculata and P. sciera. A foveal region is suggested by a slight change in the curvature of the inner surface and a decreased rod density in the temporal area. The distinctiveness of the horizontal area decreases nasally. In the central part of the area the cell densities are three or more times greater than in the dorsal and ventral regions (Fig. 9a).

The density of cells in the ventral retina is greater than in the dorsal region. This is partly attributable to the larger number of rods ventrally (Fig. 9a), and partly the result of more cones, as shown by their pattern sizes: dorsal, 12.0 μ; ventral, 11.0 μ; nasal, 9.5 μ; temporal, 7.0 μ; SL 42.5 mm.

The distribution of pigment is essentially the same as in P. sciera, except the outer halves of the cone ellipsoids are covered in the dark-adapted condition.

Habitat. - The slenderhead darter is most frequently found in pools and riffles of moderately large streams. Its preference for clean sand or gravel, mentioned by Trautman (1957), has been noted in the deeper pools of the Verdigris R. in Oklahoma.

Habits. - Stomachs have been found containing midge and mayfly larvae, and copepods (Turner, 1921).

Percina nasuta, longnose darter

The retina of this species closely resembles that of P. maculata. The fovea is not quite as obvious, but on the basis of the thickness of the layers the area is more distinct (Table VI). This is particularly noticeable in the nasal area where the thickness is comparable to that in the central area. The cone outer segments are exceptionally long in the fovea, approximately 35 microns as opposed to 20 microns in the nasal area.

As in all species discussed thus far, except the logperch, the retina is better developed ventrally than dorsally. This is suggested by the thickness of the layers, even though the inner plexiform layer is a little thicker dorsally. The cone pattern sizes also indicate a higher density ventrally: dorsal, 15.3 μ; ventral, 13.4 μ; nasal 9.2 μ; temporal, 6.3 μ; SL 54 mm.

TABLE VI

P. NASUTA. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 54 mm, measurements in microns.

Retinal layer	Region				
	Dorsal	Ventral	Nasal	Central	Foveal
Bacillary-Pigment	36.2	41.2	61.0	58.0	79.7
Outer Nuclear	11.5	13.8	29.0	30.5	30.4
Inner Nuclear	18.1	24.3	45.0	46.5	70.2
Inner Plexiform	21.2	19.6	51.8	49.0	75.8
Ganglion	8.1	9.2	18.9	19.4	31.7
Thickness of Retina	92	103	206	202	288

In the light-adapted eye the pigment covers about one-half of the cone ellipsoids, but covers only the outer segments when dark adapted. In contrast to the two preceding species, the layer of non-migrating granular pigment is present around the entire retina. This condition prevails in many other species, and only the exceptions will be mentioned hereafter.

Habitat. - Collection records are inadequate to establish a preferred habitat for this species. It has been recorded from both quiet water and riffles (Bailey, 1941; Blair, 1959). The specimens used in this study came from a very fast, large-rock riffle.

Habits. - Unknown.

Percina shumardi, river darter

The shape of the retina resembles that of P. caprodes, with the dorsal and ventral halves being nearly symmetrical. The horizontal area contains a rather indistinct fovea temporally, is thinner in the central region and is well developed nasally.

There is a marked decrease in rod density from the ventral to dorsal retina. Otherwise, cell densities are higher dorsally than ventrally (Fig. 9a). The low dorsal/ventral ratio of bipolars may be attributable to the large number of bipolars associated with the higher density of rods in the ventral region.

Cone pattern sizes in four regions of the retina have a relationship that is also similar to that of P. caprodes.

A dark-adapted specimen was not available for study. The pigment covers about half of the cone ellipsoid in the ligh-adapted condition and is slightly concentrated in the central region.

Habitat. - As its vernacular name implies, this is a fish of the larger streams where it frequents riffles. Trautman (1957) associated its presence in shallow water with turbid conditions, and implied that it may shun bright light. Structural modifications of the retina to support this have not been recognized. The single specimen examined was taken from a riffle in clear water approximately one foot in depth.

Habits. - Unknown.

Percina copelandi, channel darter

The retina is foreshortened dorsally and flattened ventrally. The radius of the temporal curvature is shorter than that of the nasal. Most of the dorsal half of the retina is more highly developed than the ventral half and may be considered as the area. A fovea is present dorso-temporally and the dorso-nasal region is relatively thin. Sections from additional planes will be necessary to evaluate fully these regions.

In sagittal sections an obvious thickening near the center of the retina is accented through the inclined condition of rod and cone nuclei above and

below this part of the area. In the previously-described retinae similarly modified regions have constituted the areae, with all layers thinning dorsally and ventrally. But in this species, all layers except the bacillary-pigment layer retain their thickness for some distance dorsad, so that the modified central region is only the ventral part of the area.

Measurements show little difference in the thickness of the retina in the horizontal plane, but the inner nuclear and ganglion layers suggest a temporal predominance in cells (Table VII). This is substantiated by the cone pattern sizes: temporal, 8.4 μ; nasal, 9.5 μ; dorsal, 8.9 μ; ventral, 14.3 μ; SL 44.5 mm. The dorsal cone-pattern measurement was taken from the areal region and would be slightly larger if it had been taken nearer the ora. The greater thickness of the bacillary-pigment layer in the central and nasal regions corresponds to the elongated cone outer-segments in these regions (Table VIII). There is a similar correlation between the thickness of the outer nuclear layer and the length of cone nuclei.

TABLE VII

P. COPELANDI. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 44.5 mm, measurements in microns.

Retinal layer	Region				
	Dorsal	Ventral	Nasal	Central	Temporal
Bacillary-Pigment	40.1	38.5	68.2	71.3	60.3
Outer Nuclear	14.9	16.9	26.7	29.7	26.4
Inner Nuclear	28.7	20.3	43.3	43.8	47.3
Inner Plexiform	47.0	26.3	56.7	61.0	64.4
Ganglion	9.7	10.6	15.5	18.9	23.2
Thickness of Retina	141	115	211	224	221

TABLE VIII

P. COPELANDI. TWIN CONE SIZES IN DIFFERENT REGIONS OF THE RETINA. SL 44.5 mm, light adapted, measurements in microns.

	Region				
	Dorsal	Ventral	Nasal	Central	Temporal
Outer segment length	14	15	27	25	15
Inner segment length	17.2	15.3	16.9	17.0	17.0
Inner segment diameter	4.7	5.4	2.9	3.0	3.7
Nucleus length	6.2	7.2	12.0	11.3	12.1
Nucleus diameter	2.8	3.4	3.0	3.3	2.8

The uppermost region is noticeably thinner and questionably part of the area, yet it is thicker than the ventral retina (Table VII). The small difference in the thicknesses of the ganglion layer in the dorsal and ventral regions is misleading since the cell density is about three times greater dorsally (Fig. 9a).

As in other species, the number of rods decreases dorsally (Fig. 9a); however, the ratio of cones to rods is greater in the dorsal region of this species than in any of the other Percina.

Pigment distribution and migration is similar to that of P. nasuta.

Habitat. - The channel darter inhabits relatively deep water, either quiet or fast, in larger streams and lakes and is seldom found in riffles (Trautman, 1957; Blair, 1959). It may be found in shallow water at night (Trautman 1957).

Habits. - Breeding occurs over gravel in a moderate current at depths of two or three feet. Food consists of bottom organisms, mainly chironomid larvae (Winn, 1953).

Ammocrypta vivax, southwestern sand darter

The shape of the retina resembles that of the channel darter, but with the dorsal foreshortening and ventral flattening more extreme, and the nasal and temporal curvatures more nearly equal. The resemblance also extends to the area, which occupies the upper half of the retina, but the fovea is absent. The nasal, dorsal and temporal regions are distinctly better developed than the ventral region.

In the ventral margin of the area and a little temporad of center there is a nearly-circular, specialized region that resembles the thickened central region of the channel darter. Rod and cone nuclei are inclined toward this region on its ventral margin only. The thicknesses of the layers in this region, listed under the central region in Table IX, are similar to those in the nasal region. Although the bacillary-pigment layer is thickened considerably in the central and nasal regions, the pigment cells in the central portion are strikingly modified. Their nuclei lie vitread to concentrations of non-migrating, granular pigment in the thickened bases which reduce the space available to rods and cones. This specialized central region cannot be considered as the region of most acute vision for several reasons. The inner nuclear, inner plexiform and ganglion layers are thicker dorsally (mid-dorsal column of Table IX) and temporally. Although the amacrine cell density remains nearly constant dorsally there is a marked increase in the density of bipolars (Fig. 9b). This increase is not associated with the density of rods because they are widely scattered dorsally, and more numerous in the central region. The high densities of bipolar and ganglion cells in the mid-dorsal region are accompanied by an increase in cone density, so that the region of greatest acuity is above the modified central region.

TABLE IX

A. VIVAX. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 39 mm, measurements in microns.

Retinal layer	Region					
	Ventral	Dorsal	Mid-dorsal	Central	Nasal	Temporal
Bacillary-Pigment	26.6	28.1	33.1	57.2	56.7	35.8
Outer Nuclear	11.7	10.8	17.8	19.4	19.8	17.3
Inner Nuclear	19.1	53.8	69.8	48.8	40.3	69.1
Inner Plexiform	18.7	44.6	49.7	45.5	41.0	50.6
Ganglion	9.2	20.0	22.1	17.1	14.6	19.4
Thickness of Retina	85	157	192	188	172	192

The thin ventral region (Table IX) contains much larger cones than the other parts as is indicated by the cone pattern sizes: ventral, 10.8 μ; dorsal, 5.1 μ; nasal, 7.2 μ; temporal, 5.1 μ; SL 39 mm.

Although the ventral cones are rather bulky, adequate space exists between them for the rods to reach the limitans without cone migration during dark-adapation. Cones, rods and pigment migrate in typical fashion in and around the modified central region, but only the rods migrate in the dorsal and ventral regions. The pigment covers only the outer segments of the cones throughout most of the retina.

Habitat. - A. vivax and the other sand darters require fine sandy areas in clear, flowing water. The size of the stream seems insignificant, but silt is apparently an excluding limiting factor.

Habits. - Limited field observations indicated that A. vivax might be active diurnally and bury itself in the sand at night. This was at least partially affirmed through a study of the behavior of this species in aquaria by Catherine Hale (unpublished) at the University of Oklahoma Biological

Station. She found that they usually buried themselves at night but would emerge readily when exposed to light. Feeding was limited to live organisms on the surface of the sand. Burying occured through a head-first, swimming-wriggling action. This, and the feeding habits, agree with my observations of A. clara and A. beani in aquaria. Tail-first burying, as mentioned by Trautman (1957) for A. pellucida, has not been observed.

Ammocrypta clara, western sand darter

This species differs from A. vivax in retinal structure only in the relative cell densities (Fig. 9b).

Habitat. - The few records available indicate that A. clara inhabits larger streams and may be less tolerant to silt than A. vivax.

Habits. - A. clara has habits similar to those of A. vivax, but is apparently most active during twilight periods. The most successful collection for this investigation was made between daybreak and sunrise. Aquarium specimens did not react to lighting changes as readily as did A. vivax. Instead, A. clara was frequently buried in light and one specimen remained buried in one place for longer than 18 hours under natural light conditions. Their metabolic rate is apparently lower than that of most darters, for they feed very casually and never display the voracious appetite characteristic of other species.

Etheostoma chlorosomum, bluntnose darter

The retina of the bluntnose darter is a less-specialized version of an Ammocrypta retina. It is slightly longer dorsally and more curved ventrally. A fovea is absent and the area occupies the dorsal half of the retina, with greater cell densities temporally and lesser densities nasally. The circular,

specialized region in the center also resembles that of Ammocrypta.

Most of the retinal layers are thin in the ventral region (Table X), where the cell densities are low. Although the temporal region has the greatest thickness, cell densities seem to be higher in the dorsal region (Fig. 2). This is indicated by the following cone pattern sizes: ventral, 10.6 μ; dorsal, 6.6 μ; nasal, 8.2 μ; temporal, 7.3 μ; SL 31 mm. However, densities in the central region are nearly as high as dorsad (Fig. 9a).

Rods are numerous throughout the retina, but decrease dorsad (Fig. 9a).

Rods, cones and pigment in all regions migrate in typical fashion with changes in light intensity. The non-migrating granular pigment is concentrated in the central region but absent from part of the ventral retina. Pigment covers about half of each cone ellipsoid in both light- and dark-adapted eyes.

TABLE X

E. CHLOROSOMUM. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 31 mm, measurements in microns.

Retinal layer	Region				
	Ventral	Dorsal	Central	Nasal	Temporal
Bacillary-Pigment	38.7	32.2	66.4	34.2	71.1
Outer Nuclear	12.2	12.1	22.2	9.9	23.7
Inner Nuclear	21.2	41.8	47.5	27.8	47.1
Inner Plexiform	27.0	45.0	45.0	33.1	52.0
Ganglion	9.9	17.6	17.6	10.4	17.3
Thickness of Retina	109	150	197	116	212

Habitat. - E. chlorosomum inhabits backwaters of sluggish streams, oxbow lakes and swamps. It seems to prefer areas strewn with organic debris.

Habits. - Limited observations of specimens in aquaria indicate that they will come without hesitation from about two inches to take food that is directly in front of them. Linder (1955) found that aquarium specimens will eat non-living food items and suggested, on the basis of their tolerance to turbidity, some dependency on the sense of taste in feeding.

Etheostoma nigrum, johnny darter

The retina of the johnny darter is so similar to that of the bluntnose that only one apparent difference warrants comment. Although the retina is thicker and has higher densities of cells, this may not be a true difference because it is influenced by growth. However, the cone pattern sizes are smaller in a johnny darter with a standard length of 37 mm (ventral, 9.7 μ; dorsal, 5.9 μ; nasal, 7.0 μ; temporal, 6.4 μ) than in the 31 mm bluntnose darter, thereby suggesting a true difference.

Habitat. - Johnny darters tolerate a variety of conditions including silt (Trautman, 1957). They are known from small brooks and lakes, but are most frequently found in streams that are moderate in size and gradient. They seem to prefer pools, but are also found in riffles (Speare, 1960).

Habits. - The reproductive behavior of E. nigrum has been studied, but it has not been associated with vision (Atz, 1940; Winn, 1958). Copepods and cladocerans are frequently eaten by the young, but adults feed largely on midge larvae and include some bottom debris (Turner, 1921). In experiments the feeding response was primarily elicited by visual cues of movement (Roberts and Winn, 1962).

Etheostoma stigmaeum, speckled darter

In general, the retina of the speckled darter closely resembles those of the previous two species, but the region of greatest cell density is

distinctly temporal. A well-defined fovea is not present, although there is some indication of one. The dorsal half of the retina is considered to be an area. This is supported by the cone pattern sizes: ventral, 11.4 μ; dorsal, 7.4 μ; nasal, 6.4 μ; temporal, 5.5 μ; SL 41 mm.

Habitat. - The speckled darter inhabits the clear streams of moderate size and current. This species may be associated with a silty bottom (Blair, 1959), but it is also found in rocky riffles.

Habits. - Unknown.

Etheostoma zonale, banded darter

The retina of E. zonale forms a cup with comparatively uniform curvatures except for the sharper curve in the temporal fovea. A thickened area, in the shape of a horizontal, equatorial band, clearly separates the nearly-equal dorsal and ventral region (Table XI). As in other species with a distinct fovea, some of the retinal layers are thicker in the area surrounding the fovea. The area progressively thins toward the nasal region as cell densities decrease. The following cone pattern sizes correlate well with regional variations in retinal thickness: ventral, 10.7 μ; dorsal, 10.5 μ; nasal, 7.2 μ; temporal, 6.2 μ; SL 45.5 mm.

The area in the central part of the retina is modified by a concentration of non-migrating pigment in a manner similar to the central retina of A. vivax.

Pigment surrounds the outer halves of the cone ellipsoids in both dark- and light-adapted eyes.

Habitat. - In Oklahoma the banded darter is found most frequently in riffles of moderate to large, clear streams.

Habits. - Unknown.

TABLE XI

E. ZONALE. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 45.5 mm, measurements in microns.

Retinal layer	Region				
	Dorsal	Ventral	Nasal	Central	Temporal
Bacillary-Pigment	47.3	49.3	53.1	80.8	84.2
Outer Nuclear	15.5	17.1	24.6	34.2	25.3
Inner Nuclear	26.4	27.0	42.5	58.3	59.4
Inner Plexiform	36.0	36.5	50.2	64.1	76.3
Ganglion	14.4	12.4	17.6	16.7	36.2
Thickness of Retina	140	142	188	252	283

Etheostoma blennioides, greenside darter

The ventral region of the retina is somewhat flattened; otherwise, the shape is unmodified. The horizontal, band-shaped area is a little dorsad from the equator and although it is better developed temporally, the length of the cones is increased nasally. In sagittal sections a thickening of the bacillary-pigment layer distinctly marks part of the area, but the thickened ganglion and inner nuclear layers extend dorsad, producing an indistinct, upper areal margin. The thick region of the bacillary-pigment layer differs from the comparable region in E. zonale by lacking the concentration of pigment and thick pigment-cell bases.

The cellular arrangement in the inner nuclear layer is unusual in the extra-areal regions in that a narrow space, containing fibers, tends to separate the amacrine and bipolar nuclei. Additional preparations will be necessary to evaluate the relationship of this space to cellular ratios.

Though higher than in the ventral region, the cone density in the dorsal region does not approach that within the area. Cone pattern sizes in a 60.5 mm

specimen were: ventral, 11.1 μ; dorsal, 10.0 μ; nasal, 7.9 μ; temporal, 6.9 μ.

Pigment covers the outer halves of the cone ellipsoids in the light-adapted eye, but surrounds only the tips of the outer segments when dark adapted.

Habitat. - The preference of E. blennioides for the deeper, rocky riffles of moderate to large streams is well documented (Fahy, 1954; Trautman, 1957).

Habits. - Although Fahy (1954) conducted an extensive study of the life history and others have studied the reproductive behavior (e.g. Winn, 1958), a minimum of information is available on visual-associated habits of the greenside darter. They were observed feeding on insect larvae attached to rocks, but the role of vision in feeding was not mentioned (Fahy, 1954). Fahy did observe a high sensitivity to moving objects and white, artificial light. Stomach analysis indicated midge larvae to be the main food item, with bottom debris frequently present (Turner, 1921).

Etheostoma histrio, harlequin darter

In E. histrio the retina shows very little specialization. Its curvature is nearly uniform, but slightly flatter ventrally. The horizontal area is most highly developed temporally, with no indication of a fovea. The central region is not distinctly modified, but contains a slight concentration of granular pigment.

The area is wide in the central and temporal regions. Its ventral margin is below the equator and the upper margin grades imperceptably into the thinner dorsal region. That the high cell densities of the temporal area decrease in the central area and remain nearly constant through the nasal region is indicated by the thicknesses of the cellular layers (Table XII).

TABLE XII

E. HISTRIO. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 34 mm, measurements in microns.

Retinal layer	Region				
	Dorsal	Ventral	Nasal	Central	Temporal
Bacillary-Pigment	38.0	44.3	59.2	56.3	50.6
Outer Nuclear	12.0	16.1	22.4	23.7	25.0
Inner Nuclear	24.5	18.8	33.6	39.2	38.2
Inner Plexiform	30.8	26.1	41.9	40.3	47.5
Ganglion	11.0	9.2	11.3	11.3	17.1
Thickness of Retina	115	116	168	171	180

The thicknesses of the layers indicate a greater nasal-temporal difference than is shown by the cone pattern sizes: ventral, 13.1 μ; dorsal, 10.9 μ; nasal, 9.7 μ; temporal, 9.2 μ; SL 40 mm.

The harlequin darter has a higher density of rods (41 per 90 μ length of section) in the ventral retina than any of the other species in which rods were counted. The next highest rod density (34) was found in a P. caprodes specimen approximately twice the size of the 40 mm E. histrio. Since rod densities increase with growth, the high number in E. histrio seems significant. As in all species discussed previously, the rod density decreases progressively toward the dorsal region.

The pigment-cone relationship is similar to that in E. blennioides.

Habitat. - This poorly-known species seems to prefer the riffles of moderate to large streams.

Habits. - Unknown.

Etheostoma radiosum, orangebelly darter

The dorsally foreshortened and ventrally flattened retina of E. radiosum is modified by a temporal fovea. The area is extensive in the temporal region but narrows centrally and almost disappears nasally. In contrast to previously discussed species that have the ventral region flattened, the ventral retina is as well developed as the dorsal region, as indicated by the thicknesses of the layers (Table XIII) and the cone pattern sizes: ventral, 10.8 μ; dorsal, 10.9 μ; nasal, 7.9 μ; temporal, 6.0 μ; SL 33.5 mm. The following cone pattern sizes of a larger specimen (SL 49.5 mm) show similar relationships and the effects of growth on cone density: ventral, 13.7 μ; dorsal, 13.9 μ; nasal, 9.5 μ; temporal, 7.3 μ.

Although the thicknesses of the layers in the nasal area are considerably less than those in the fovea and central area, the lengths of the cones in these three regions are remarkably uniform (Table XIV). The inner-segment diameters and cone nuclei proportions reflect cone densities much better than the lengths of the inner or outer segments.

TABLE XIII

E. RADIOSUM. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 33.5 mm, measurements in microns.

Retinal layer	Region				
	Dorsal	Ventral	Nasal	Central	Foveal
Bacillary-Pigment	43.0	41.6	65.0	79.4	79.4
Outer Nuclear	10.7	15.2	19.0	28.2	33.9
Inner Nuclear	22.8	24.7	33.2	49.9	61.3
Inner Plexiform	32.2	30.6	39.8	47.9	69.7
Ganglion	8.6	10.1	11.0	15.8	21.6
Thickness of Retina	119	121	145	221	265

TABLE XIV

E. RADIOSUM. SIZES OF RODS AND CONES IN DIFFERENT REGIONS OF THE RETINA. Light adapted, SL 33.5 mm, measurements in microns.

	Region				
	Dorsal	Ventral	Nasal	Central	Foveal
Single cone					
Inner segment					
length	9.9	10.7	11.1	9.9	11.2
diameter	4.2	3.5	2.6	2.0	2.0
Outer segment					
length	14	10	16	16	16
Twin cone					
Inner segment					
length	11.0	12.2	12.3	10.8	11.7
diameter	4.6	3.8	3.0	2.5	2.2
Outer segment					
length	14	10	16	16	16
Rod					
Ellipsoid					
length	4.4	6.4	4.3	3.3	2.2
diameter	2.2	2.0	1.8	2.1	1.5
Outer segment					
length	26	20	35	40	30
Cone nucleus					
length	5.0	5.5	7.1	11.1	13.6
diameter	3.7	4.0	3.6	2.3	2.5
Rod nucleus					
length	4.2	4.8	5.6	4.3	6.9

E. radiosum has comparatively large rods (compare Tables II and XIV), but their density is near the average for darters. In contrast to all aforementioned species, the rod density is greater centrally than in the ventral region. A decreased number in the dorsal region is typical of all darters.

A slight concentration of granular pigment in the central area disrupts the uniform distribution of pigment. It covers the tips of the cone ellipsoids in light-adapted retinae, but only the outer halves of the cone outer segments in the areal regions when dark-adapted. In the dorsal and

ventral regions the cone-pigment relationship remains the same regardless of light conditions.

Habitat. - E. radiosum prefers rocky and gravelly riffles of moderately fast gradient in clear, small to large streams (Moore and Rigney, 1952).

Habits. - In aquaria, this species tended to hide among rocks from which they emerged readily when food was introduced. White worms were approached in short, darting movements. Each worm was carefully scrutinized with one eye from about a one-inch distance before it was engulfed during an anterio-lateral dart.

Etheostoma whipplei, redfin darter

The retina of E. whipplei closely resembles that of E. radiosum, but differs in some respects. The dorsal-ventral difference is greater, with the ventral region containing more cells (Fig. 9b). The cone pattern sizes indicate a more distinct area and temporal fovea: ventral, 12.9 μ; dorsal, 13.6 μ; nasal, 8.5 μ; temporal, 6.7 μ; SL 52 mm.

An obvious difference from E. radiosum is seen in the pigment layer within the area. The pigment cells are nearly devoid of granular pigment so that a clear region occurs outside of the rod-like pigment that is in the processes when the eye is light adapted. The rods in the area migrate extensively and occupy the pigment-free space beyond the ends of the pigment-surrounded cones. When dark adapted, the pigment is concentrated in the cell bases, leaving the less-migratory cones exposed except for the tips of their outer segments.

Habitat. - The redfin darter tolerates silt and may be found over mud or sand in the backwater and slow-current regions of large streams, but it

also inhabits riffles and small streams (Moore and Rigney, 1952; Blair, 1959).

Habits. - Unknown.

Etheostoma punctulatum, stippled darter

The retina of the stippled darter shows very little specialization. The curvatures are rather uniform except in the somewhat flattened, ventral region. The slight increase in cell densities along the horizontal equator hardly justifies the term area, and there is no indication of a fovea.

The preparations available do not permit critical measurement of the photoreceptors, but the cone ellipsoids appear more stocky and the rods longer than in most darters of comparable size. There is no indication of crowding or elongation of the cones in any region.

The cone pattern sizes (ventral, 13.3 μ; dorsal, 11.8 μ; nasal, 9.4 μ; temporal, 9.0 μ; SL 45 mm) indicate a higher density dorsally than ventrally, but counts from sagittal sections show these two regions to be nearly equal (Fig. 9b).

In some regions a thin, fibrous layer tends to separate the amacrine and bipolar cells as in E. blennioides.

The uniformly distributed pigment approaches the limitans in light-adapted eyes, but covers less than half of the cone outer segments in the dark-adapted condition. The typical, granular layer is present throughout.

Habitat. - E. punctulatum is found in the shallow riffles of cool, clear brooks, but shows some preference for the quiet, vegetated pools of spring-fed streams (Moore and Paden, 1950).

Habits. - Unknown.

Etheostoma parvipinne, goldstripe darter

The smooth, cup-shaped retina of the single specimen available is not flattened ventrally. The curvature is not modified by a fovea, but there is a definite center of high visual acuity in the thickened temporal region of the distinct, horizontal area.

The ventral retina is a little thicker and contains higher cell densities than the dorsal region (Fig. 9b). The dorsal-ventral difference and the temporal specialization is reflected by the following cone pattern sizes: ventral, 7.8 μ; dorsal, 8.9 μ; nasal, 7.5 μ; temporal, 5.6 μ; SL 33 mm.

The density of rods is higher in the central area than in the ventral region and is lowest dorsally (Fig. 9b). The rods show an extensive migration similar to those of E. whipplei, but the distribution of pigment is rather typical.

Habitat. - The goldstripe darter hides among vegetation over a sand, gravel or mud bottom in the smaller, spring-fed streams. Although the specimen used in this study was collected near the mouth of the comparatively large Mountain Fork River, its apparently optimal habitat was afforded by a small, cool spring at the river's margin. Because of the relative scarcity of this species, its ecology is poorly known, and the statement above is founded on limited observations.

Habits. - Unknown.

Etheostoma cragini, Arkansas darter

The retina of the Arkansas darter is so strikingly similar to that of E. parvipinne that only one apparent difference will be mentioned. The densities of cones seem to be less in E. cragini, but since the individual was

larger the difference may be correlated with growth. The cone pattern sizes in a 39 mm specimen were: ventral, 11.4 μ; dorsal, 13.0 μ; nasal, 11.2 μ; temporal, 9.0 μ.

Habitat. - E. cragini is found almost exclusively in the vegetated pools of clear, spring-fed brooks (Blair, 1959).

Habits. - Unknown.

Etheostoma flabellare, fantail darter

The ventral region of the retina is flattened and the temporal region is modified by a conspicuous fovea. A broad area occupies the temporal region and, though less well-developed, it extends as a band through the central and nasal regions. Beginning at the lateral margin of the fovea, all retinal layers, except the bacillary-pigment layer, increase in thickness until a maximum is reached about equidistant from the fovea and lateral ora, and then decrease in thickness toward the ora. This produces an inward bulge in the retina lateral to the fovea. A similar thickening does not occur on the fundal side of the fovea; instead, the layers remain nearly constant in thickness throught the central area and decrease nasad (Table XV).

The thicknesses of the layers in the ventral region indicate that it is slightly better developed than the dorsal region. This is verified by the dorsal/ventral cell ratios (Fig. 9b) and by the cone pattern sizes: ventral, 12.3 μ; dorsal, 12.6 μ; nasal, 10.1 μ; temporal, 8.3 μ; SL 36 mm.

The rod density is high in the central region, intermediate ventrally and low dorsally.

The uniformly distributed pigment in the light-adapted position covers the ellipsoids of cones in the ventral region, but only their outer halves in the dorsal retina. In the dark-adapted condition, the cone outer segments

TABLE XV

E. FLABELLARE. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 36 mm, measurements in microns.

Retinal layer	Region					
	Dorsal	Ventral	Nasal	Central	Foveal	Temporal*
Bacillary-Pigment	45.0	42.5	60.8	70.4	72.9	66.6
Outer Nuclear	13.5	14.9	17.6	21.6	19.6	26.8
Inner Nuclear	22.5	21.8	25.9	38.7	38.0	61.7
Inner Plexiform	35.8	37.4	38.3	47.5	54.9	70.4
Ganglion	7.0	8.6	11.0	12.8	19.4	21.2
Thickness of Retina	124	125	153	191	205	245

*About mid-way between fovea and ora.

are completely covered in the ventral region and partially covered dorsally.

Habitat. - The fantail darter prefers to hide in gravelly riffles of small streams.

Habits. - The reproductive behavior of this species has been observed (Winn, 1958; Lake, 1936), but habits of value to this study were not recorded. Turner (1921) considered this species to be highly active and specialized for feeding on bottom organisms such as mayfly and midge larvae without including bottom debris.

Etheostoma gracile, slough darter

The temporal fovea is very similar to that in E. flabellare, but the ventral retina is only slightly flattened. A wide area occupies all of the retina except the strictly dorsal and ventral regions. It is best-developed temporally, but still quite obvious nasally.

Cell densities in the dorsal and ventral regions are unusual in that the cones, rods and bipolars are more numerous ventrally, whereas the amacrine and ganglion cells are more abundant dorsally. The higher ventral density of cones is verified by the cone pattern sizes: ventral, 8.4 μ; dorsal, 9.3 μ; nasal, 7.5 μ; temporal, 6.6 μ; SL 28 mm. Rod densities remain nearly constant through the ventral and central regions and decrease dorsally.

The pigment is uniformly distributed in most of the retina, with a small, central region containing a concentration of granular pigment. Only the outer segments of the cones are covered by pigment in light- and dark-adapted eyes.

Habitat. - E. gracile is tolerant to the silt that is frequently present in the muddy-bottom, low-gradient streams and backwaters to which it is restricted (Collette, 1962). The specimens used herein were collected from among organic debris in the clear, dark water of an oxbow lake.

Habits. - Linder (1955) suggested, on the basis of their tolerance to turbidity, that E. gracile may depend upon the sense of taste in feeding but he was probably influenced by his observation that this species, as well as E. chlorosomum, will eat prepared food, e.g. dog food, in aquaria. Collette (1962) also found that E. gracile will eat non-living food.

Observations of specimens in clear aquarium water indicate that they can see white worms from a distance of several inches. They approach the worms rapidly and ingest them, without hesitation, from a "head-on" position.

Etheostoma fusiforme barratti, scalyhead darter

The retina forms a more open, or shallow, cup in E. f. barratti than is found in most darters. This results from a flattening of the ventral and

temporal regions and apparently some foreshortening in the nasal, dorsal and temporal regions. There is a similarity to E. gracile in the distribution of cells and associated variations in thicknesses of layers. However, the fovea is more dorsad and appears to be less well-developed because the lateral thickening is not as great. However, the following cone pattern sizes indicate a better developed temporal region in E. f. barratti: ventral, 11.1 μ; dorsal, 11.7 μ; nasal, 9.7 μ; temporal, 6.6 μ; SL 47 mm.

In the light-adapted condition the pigment covers the outer halves of the cone ellipsoids, but only the outer segments of the cones in the dark-adapted position. There is some concentration of pigment centrally, and the granular pigment is absent ventrally.

Habitat. - The scalyhead darter inhabits the quiet, vegetated areas of lakes, swamps and stream backwaters (Collette, 1962).

Habits. - The habit of perching in vegetation noted by Collette (1962) for E. f. fusiforme has been observed in E. f. barratti in aquaria and natural environments, but the habit of scrutinizing food with one eye has not been noticed in this subspecies. That feeding is not limited to bottom-dwelling organisms, as in some darters, is supported by the predominant presence of Chaeborus and Chydoras in their stomachs (McLane, 1950).

Etheostoma proeliare, cypress darter

The retina of E. proeliare forms a deep cup with a uniformly smooth curvature except in the temporal region where it is modified by a fovea. As in E. gracile, the area is wide and occupies most of the retina with the thinner, extra-areal part being limited to the dorso-nasal and ventral regions.

The ventral region has slightly higher cell densities than the dorsal

portion (Fig. 9b), as indicated by the cone pattern sizes: ventral, 7.7 μ; dorsal, 8.3 μ; nasal, 7.1 μ; temporal, 4.6 μ; SL 20 mm.

The pigment is similar to that in E. gracile.

Habitat. - E. proeliare occupies the same habitat type as E. f. barratti.

Habits. - Limited field and laboratory observations indicate some similar habits for cypress and scalyhead darters, but E. proeliare seems to spend less time perched in vegetation. Differences in their feeding habits were not noticed.

Etheostoma microperca, least darter

The retina of this species closely resembles that of E. proeliare, with some differences in cell densities. The cone pattern sizes indicate higher densities of cones in E. microperca: ventral, 8.4 μ; dorsal, 8.1 μ; nasal, 6.1 μ; temporal, 4.4 μ; SL 32 mm. The temporal density here is the highest encountered, and represents about 155,000 cones per square millimeter. This high density may be considered significant because the specimen showing the next highest density, E. proeliare, had a somewhat shorter standard length, assuming that the changes in cone density with growth are not atypical in these species.

The retina is a little thicker on the medial side of the fovea and considerably thicker laterally, resulting in an inward bulge on each side of the fovea. Most of the difference in thickness involves the inner nuclear layer (Table XVI). Within the fovea there are some unusual undulations that involve the outer margin of the inner nuclear layer and inner margin of the outer nuclear layer. This was only observed in one specimen and although it does not seem to be a shrinkage artifact, it will require

TABLE XVI

E. MICROPERCA. THICKNESS OF RETINAL LAYERS IN DIFFERENT REGIONS. SL 33 mm, measurements in microns.

Retinal layer	Region					
	Dorsal	Ventral	Nasal	Central	Foveal	Temporal*
Bacillary-Pigment	45.2	34.7	54.9	62.3	59.6	49.7
Outer Nuclear	16.0	13.3	26.1	29.9	33.1	36.5
Inner Nuclear	33.1	31.3	47.3	77.6	53.1	81.2
Inner Plexiform	46.1	39.2	54.5	58.5	69.3	80.8
Ganglion	14.2	11.0	14.0	18.5	30.6	29.9
Thickness of Retina	155	131	194	224	244	278

*About mid-way between fovea and ora.

verification in additional specimens. A similar condition has been found in birds (Polyak, 1941, 1957).

In contrast with the preceding species, the cell densities are higher dorsally than ventrally (Fig. 1). This is indicated by the thicknesses of the retinal layers (Table XVI) and the smaller cone pattern size in the dorsal region.

The pigment distribution is similar to those of E. proeliare and E. gracile.

Habitat. - The least darter is found almost exclusively in heavily vegetated regions of clear lakes or streams where the current is slight.

Habits. - E. microperca spends much of its time among the branches of vegetation. In aquaria they ate live crustaceans but refused artificial food (Petravicz, 1936).

The Effects of Growth on the Retina

The greatest problem in quantitatively comparing the retinae of different species is associated with the progressive changes that occur during growth. To obtain some concept of the rate and degree of change, cell densities in ventral retinae of different sizes were compared in four species (Figs. 4 and 5). It is readily apparent that the actual number of cells has little comparative value; however, some species differences are indicated. The tendency for the densities of all cells, except rods, to decrease as the retina becomes larger is observable in all four species.

Deferring consideration of rods, the greatest change in density occurs in bipolars and the least in ganglion cells. However, the percentages of change are more nearly equal, for example in P. sciera the bipolars decrease 52.0% and the ganglion cells 51.4% from the 2.0 mm to the 3.1 mm retina. Similarly, E. punctulatum shows a 29.9% decrease in bipolars and a 35.0% decrease in ganglion cells.

Changes in rod densities follow a somewhat different pattern. In the earlier growth stages there is a decrease that is followed by an increase in later stages (Table XVII). Many more specimens will be required to establish mimimum rod densities for these species.

Counts in the central-areal and dorsal regions were made in two specimens of P. caprodes to check the possibility of different growth-changes occurring in these regions. The same general pattern of lower densities in the large eye, except for the rods, is evident in all three regions (Fig. 5). A possible explanation for the failure of the rod density to increase in the central-areal region is suggested by the higher cone density there. A comparison of the number of cones with the amount of change in rod density

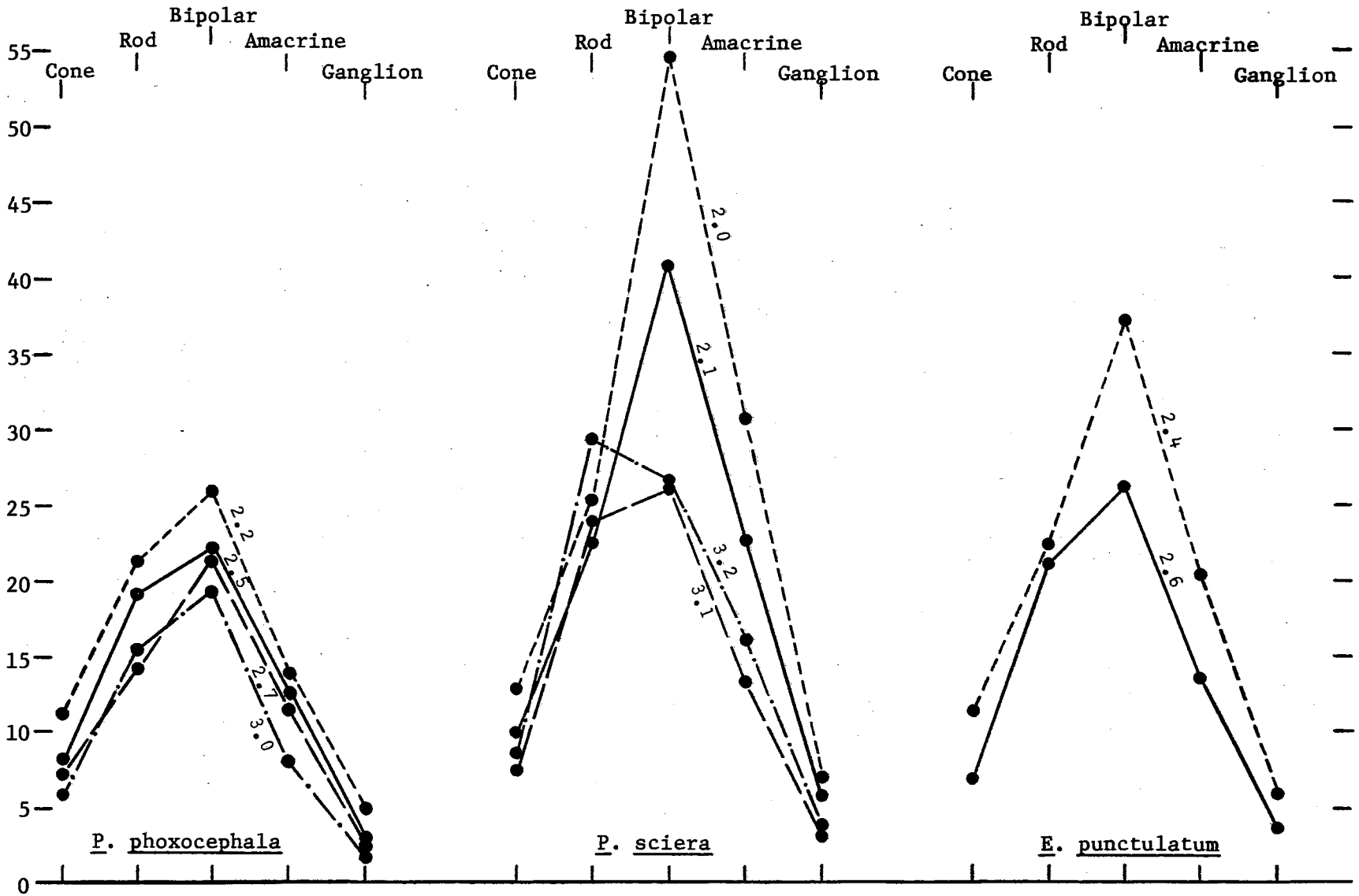

Fig. 4. Average number of nuclei per 90μ length of section in ventral retinae of different sizes. Numbers on lines denote retina size in millimeters.

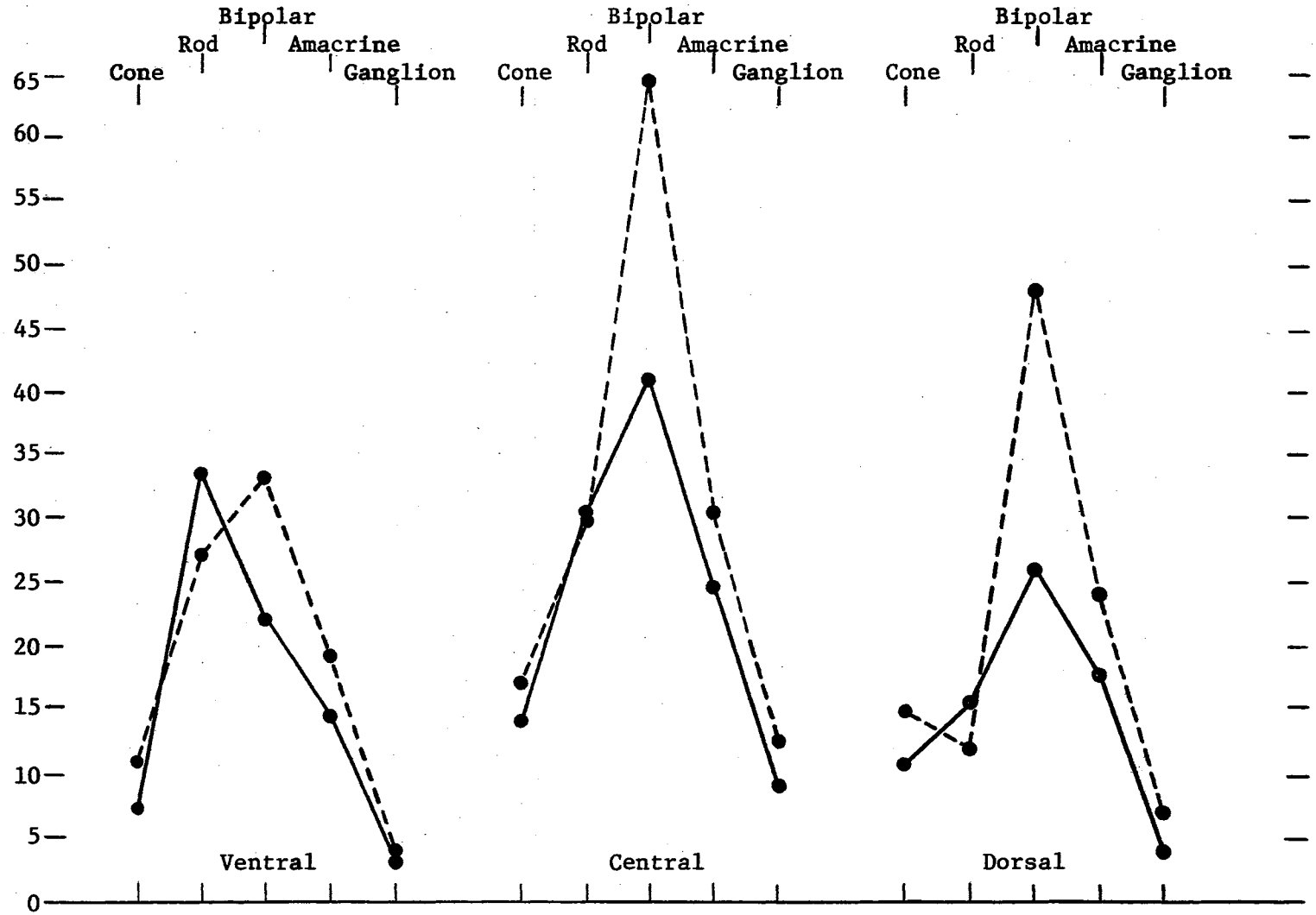

Fig. 5. Average number of nuclei per 90μ length of section in three retinal regions of P. caprodes of different sizes. Retina size: 2.8 mm (---); 3.5 mm (——).

TABLE XVII

CHANGES IN THE AVERAGE NUMBER OF ROD NUCLEI PER 90 μ OF SECTION IN VENTRAL RETINAE OF DIFFERENT SIZES

P. phoxocephala		*P. sciera*		*P. caprodes*	
Retina size (mm)	Rod nuclei number	Retina size (mm)	Rod nuclei number	Retina size (mm)	Rod nuclei number
2.2	21.3	2.0	25.2	2.8	27.2
2.5	18.8	2.1	22.5	2.9	24.9
2.7	14.2	3.1	23.7	3.5	33.6
3.0	15.4	3.2	29.3		

in each region shows a relationship that indicates space as a limiting factor in rod density. This agrees with generally accepted concepts (Walls, 1942).

To evaluate further the effects of growth in different parts of the retina, cell densities in both the dorsal and central regions were compared with corresponding densities in the ventral retina. Although ratios were determined for only two *P. caprodes* of different sizes, there is surprisingly little variation between them (Table XVIII).

In view of the similarity of the changes occurring with growth in different regions of the retina, within a species as well as in different species, it seems reasonable to assume that ratios of the densities of cell types within each retinal region, with the possible exception of the rods, can validly be used to compare species regardless of eye size. However, comparisons of several ratios from retinae of different sizes show considerable variation (Table XIX). Since the variations do not fit a pattern, most of them may be attributed to the methods employed and to human error. Some natural variation is to be expected, but a great many

TABLE XVIII

RATIOS OF DORSAL AND CENTRAL CELL DENSITIES TO VENTRAL CELL DENSITIES IN *P. CAPRODES* RETINAE OF DIFFERENT SIZES.

Ratio and Retinal size	Cell Type				
	Cone	Rod	Bipolar	Amacrine	Ganglion
Dorsal/Ventral					
2.8 mm	1.4	0.4	1.4	1.4	2.1
3.5 mm	1.4	0.4	1.2	1.2	1.4
Central/Ventral					
2.8 mm	1.6	1.1	2.0	1.7	3.6
3.5 mm	1.9	0.9	1.9	1.7	3.1

specimens would be required to determine its extent. The same is true for any changes in cell ratios that may accompany changes in rod density. In any event, the range of variation shown in Tables XVIII and XIX may serve as a basis for evaluating differences between ratios in different species.

TABLE XIX

RATIOS BETWEEN CELL TYPES WITHIN VENTRAL RETINAE OF DIFFERENT SIZES IN *P. PHOXOCEPHALA* AND *P. SCIERA*

Ratio	*P. phoxocephala*				*P. sciera*			
Retina Size (mm)	2.2	2.5	2.7	3.0	2.0	2.1	3.1	3.2
Cone/Rod	.50	.40	.51	.38	.50	.45	.31	.27
Bipolar/Cone	2.43	2.82	3.03	3.34	4.28	4.03	3.55	3.14
Bipolar/Rod	1.23	1.14	1.56	1.26	2.17	1.81	1.11	.85
Bipolar/Amacrine	1.87	1.71	1.87	2.43	1.79	1.80	1.99	1.60
Bipolar/Ganglion	5.26	7.64	8.40	9.24	7.83	6.95	7.74	7.25
Amacrine/Cone	1.30	1.64	1.62	1.38	2.39	2.24	1.78	1.96
Amacrine/Rod	.65	.66	.83	.52	1.21	1.00	.56	.53
Amacrine/Ganglion	2.81	4.46	4.48	3.81	4.38	3.88	3.88	4.53
Cone/Ganglion	2.15	2.71	2.77	2.76	1.83	1.72	2.18	2.31
(Bipolar + Amacrine)/Ganglion	8.07	12.11	12.88	13.04	12.21	10.82	11.62	11.77
(Bipolar + Amacrine)/Cone	3.73	4.46	4.64	4.72	6.67	6.26	5.34	5.10
Bipolar/(Cone + Rod)	.82	.81	1.03	.92	1.44	1.25	.85	.69

Comparison of Cone Densities

A figure that would express the acuity of vision in a species would be highly desirable for comparative purposes. Cone densities express, to some extent at least, the degree of visual acuity, but actual cone densities have little comparative value because they change with growth. If enough individuals were examined to establish the limits of variation in cone densities for each species, these limits would provide a basis for comparison. Or, an acurate measurement of eye size combined with the cone density would serve the same purpose. O'Connell (1963) circumvented the problem of accurately measuring the eye by using the lens diameter, on the basis of Matthiessen's (1882) ratio, as a proportional measurement, but he apparently did not consider the possibility that shrinkage during fixation might be disproportional in lenses that differ in size or species. Other methods of accurately measuring eyes require that the retinae have the same shape, and this is not applicable to darters.

In view of the problems associated with attempts to express cone densities quantitatively for comparative purposes, a method was devised to express intraretinal differentiation in a manner suitable for comparing species. The cone density value (cone pattern size in this instance) for each region of the retina (dorsal, ventral, nasal and temporal here, but others could be used) is expressed as a percentage of the total of these values. This method is based on the assumption that relative densities remain nearly constant during growth. This assumption has not been thoroughly tested, but significant deviations have not been encountered. With the small eyes of darters, where cone densities change rapidly over a short distance, variations in the calculated percentages are more apt to

be the result of sampling different regions of the retinae than of differential growth.

The figures obtained by this method do not express visual acuity, but they provide a reasonably valid means of comparing species. The values obtained for the retinal regions are plotted in the same sequence for each species in Figure 6, where greater percentages denote lower densities. Examination of the resulting species patterns reveals three general groups of similar patterns, each representing a different distribution of cone densities in the retina.

Pattern Group I. - This group has a stair-step pattern that represents a retina with a progressive regional decrease in the density of cones in the sequence: temporal, nasal, dorsal, ventral. P. shumardi has the most evenly spaced "steps", although P. caprodes and E. blennioides are similar. A relatively high cone density in the dorsal retina, but not high enough to fit the group II pattern, results in the moified pattern of E. stigmaeum. The E. histrio and E. punctulatum patterns indicate weakly-developed areae with little differentiation between nasal and temporal regions. The six members mentioned above do not have distinct foveae, although P. shumardi has some indication of one. The remaining two members of this group, E zonale and E. microperca, have similar patterns and well developed foveae. Their dorsal and ventral cone densities are nearly equal and, in view of the arbitrary limits of these groups, they might fit better in group III.

Pattern Group II. - The distinctive pattern of this small group indicates nearly equal densities of cones in the dorsal and temporal regions, an intermediate density nasally, and a poorly-developed, ventral retina. The patterns of A. clara and A. vivax indicate a greater difference between

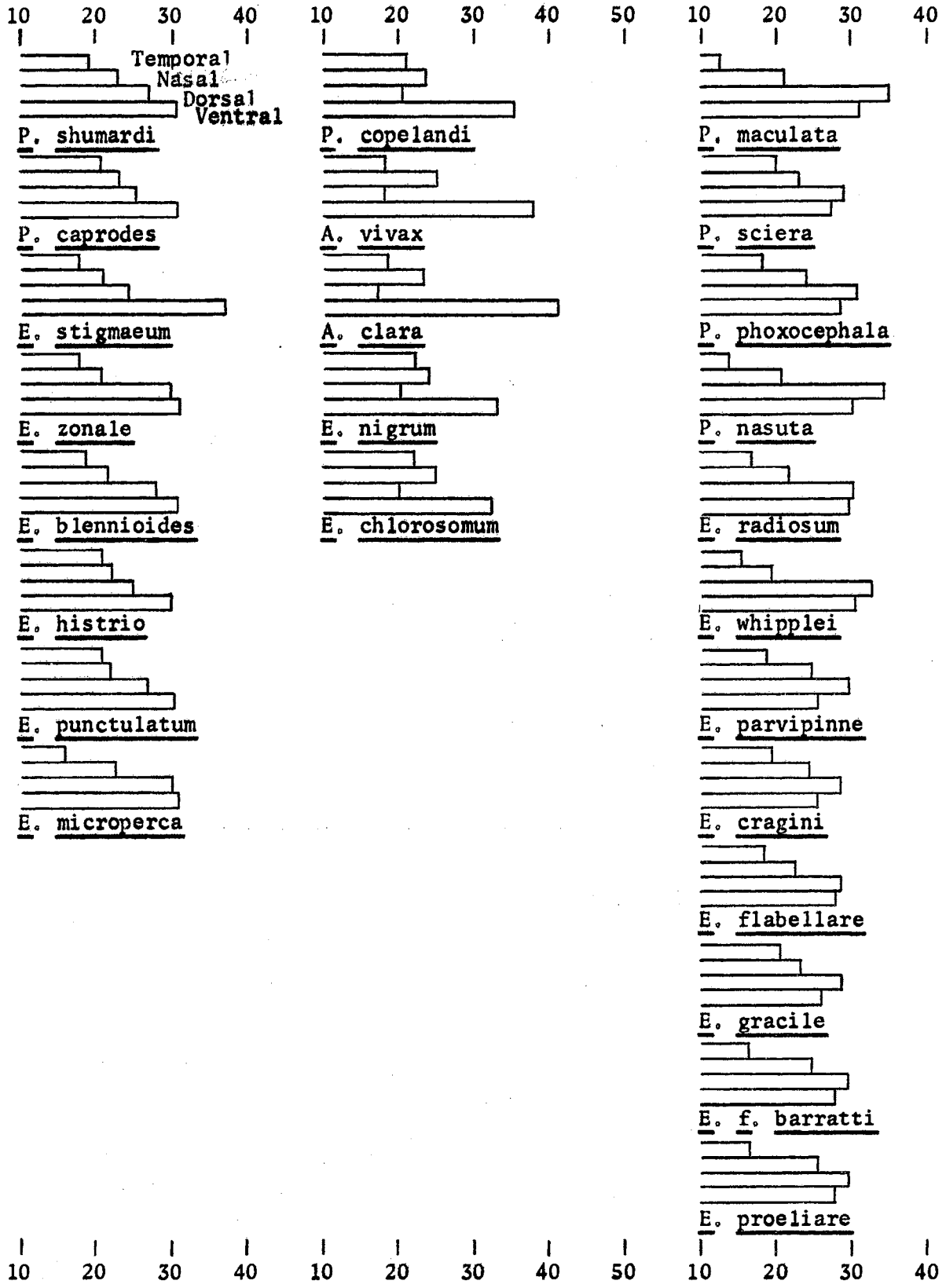

Fig. 6. Regional percentages of cone pattern sizes.

the temporal and ventral regions than those of the other members: P. copelandi, E. nigrum and E. chlorosomum. Otherwise, the patterns are very similar within this group and distinctive from those of other species. The only member of this group with a fovea is P. copelandi, and its dorso-temporal position is unique.

Pattern Group III. - This large group has the lowest cone density in the dorsal region. Considerable variation is seen in the patterns in this group, indicating species differences in relative densities in the four retinal regions. It is possible to pick out a few patterns that show close similarity, e.g. P. maculata and P. nasuta, but there are enough intermediate patterns to make subdivision of the group unrealistic. Nine of the members of this group have a fovea; P. sciera, E. parvipinne and E. cragini do not.

As a possible means of clarifying the species relationships indicated by similarities in the cone-density patterns, the ratios of temporal to nasal cone-pattern sizes were plotted against the ratios of dorsal to ventral cone-pattern sizes (Fig. 7). The resulting arrangement shows the members of cone-density pattern group I occupying a central position between the members of group II below and those of group III above. The position of E. stigmaeum indicates a closer relationship with group II. Likewise, the close association of E. zonale and E. microperca with group III is readily apparent. The sand darters are clearly separated from the other members of group II, but group III will require additional clarification.

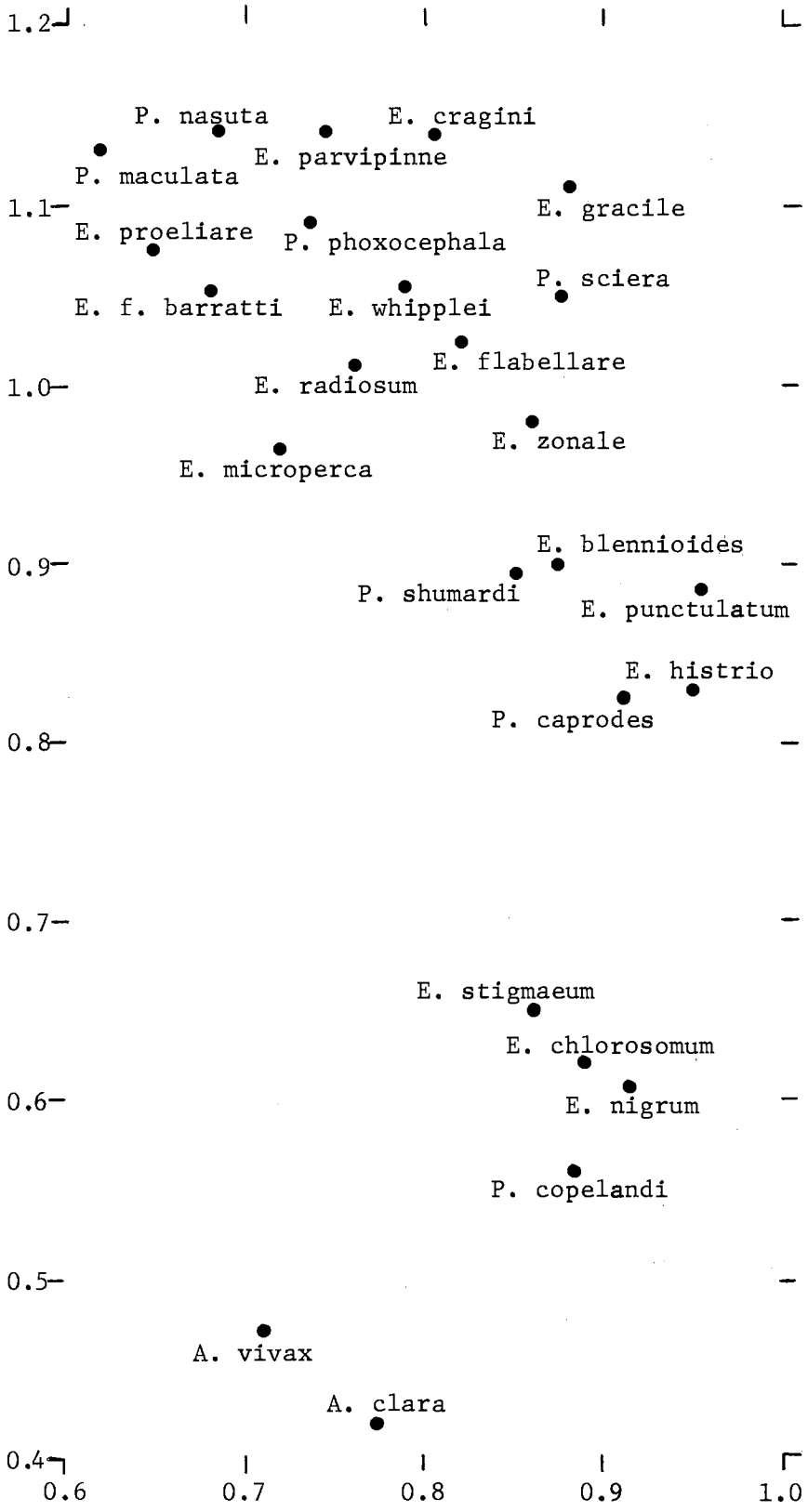

Fig. 7. Ratios of cone pattern sizes from different regions of the retina.

Comparison of Cell Ratios

Several relationships between the densities of the five main types of cells, and combinations thereof, were computed for 16 species. At first, ratios of cell types were determined for the ventral retinae only. This line of investigation was based on the following premises: (i) Each cell is an integral component of a neuronal pathway, and cell ratios are generalized expressions of neuronal pathways. (ii) Neuronal pathways are basically constant within a species and do not change with growth. They are genetically controlled, and closely related species have similar pathways and, therefore, similar cell ratios. (iii) In darters, the ventral retina shows the least specialization, and therefore shows ancestral relationships rather than species specializations.

The second premise was neither supported very strongly by the investigation of changes with growth, nor shown to be false. The third premise is apparently true, as most of the ratios obtained from the ventral retinae show very little difference between species (Table XX). Most of the variations are within the range of error attributable to the method. This may be interpreted as indicative of a common ancestry for all species.

Since the ventral-retina ratios failed to divide the species into groups, cell ratios from the dorsal and central regions were determined. Some of the ratios from these regions show very little difference in the species, e. g. amacrines/cones, whereas others vary so greatly that they fail to indicate species relationships, e. g. (bipolar + amacrine)/ganglion (Table XX). Several ratios are less extreme and show distinctive differences between groups of species. The two species of Ammocrypta and E. chlorosomum have particularly distinctive bipolar/rod ratios.

TABLE XX

CELL-DENSITY RATIOS IN DIFFERENT REGIONS OF THE RETINA

Species	Ratio:	Cones/Rods			Bipolars/Cones			Bipolars/Rods		
	Region:	Ventral	Dorsal	Central	Ventral	Dorsal	Central	Ventral	Dorsal	Central
P. caprodes		.2	.7	.5	3.0	2.5	2.9	.7	1.8	1.4
P. maculata		.4	.8	1.0	3.2	2.5	3.5	1.3	1.9	3.6
P. sciera		.3	.4	.6	3.6	3.3	3.7	1.1	1.2	2.2
P. phoxocephala		.4	.6	1.0	3.3	2.5	3.4	1.3	1.4	3.5
P. shumardi		.4	1.0	1.3	3.9	3.5	3.5	1.5	3.6	4.5
P. copelandi		.3	1.7	.9	3.4	2.9	3.8	1.1	4.9	3.5
A. vivax		.6	6.3	2.6	3.4	10.0	4.8	2.0	62.7	12.4
A. clara		.7	14.2	10.1	3.6	6.5	4.4	2.4	93.1	44.0
E. chlorosomum		.5	2.2	.9	3.5	6.0	5.0	1.7	13.2	4.4
E. histrio		.2	.7	.7	3.7	3.6	3.5	.7	2.4	2.6
E. whipplei		.7	.8	1.0	3.1	2.7	3.2	2.2	2.1	3.1
E. punctulatum		.3	.4	.5	3.8	3.4	3.6	1.2	1.3	1.9
E. parvipinne		.8	.9	1.2	3.8	3.6	3.5	3.0	3.4	4.3
E. flabellare		.7	.8	1.1	3.4	3.4	3.6	2.4	2.5	4.0
E. gracile		.9	1.2	1.6	3.7	3.8	4.0	3.2	4.6	6.1
E. proeliare		1.0	1.4	1.7	4.3	4.0	4.1	4.4	5.8	7.0

TABLE XX (Continued)

Species	Ratio:	Bipolars/Amacrines			Bipolars/Ganglion			Amacrines/Cones		
	Region:	Ventral	Dorsal	Central	Ventral	Dorsal	Central	Ventral	Dorsal	Central
P. caprodes		1.5	1.5	1.7	7.6	6.4	4.6	2.0	1.7	1.7
P. maculata		1.7	1.9	2.1	7.4	5.8	5.5	1.9	1.3	1.7
P. sciera		2.0	1.8	1.7	7.7	7.3	4.7	1.8	1.8	2.2
P. phoxocephala		2.4	2.2	2.1	9.2	6.2	5.0	1.4	1.1	1.6
P. shumardi		2.1	1.6	2.5	7.2	4.3	5.0	1.9	2.2	1.4
P. copelandi		1.9	1.9	2.3	8.2	5.3	5.1	1.8	1.5	1.7
A. vivax		2.1	5.0	2.9	6.2	6.5	4.1	1.7	2.0	1.7
A. clara		2.5	3.3	2.7	9.1	6.1	4.3	1.5	2.0	1.6
E. chlorosomum		2.3	3.7	2.9	5.8	5.7	4.4	1.5	1.6	1.7
E. histrio		1.8	1.6	2.3	6.8	4.1	3.7	2.1	2.2	1.5
E. whipplei		2.0	1.9	2.2	6.0	6.1	4.4	1.6	1.4	1.5
E. punctulatum		1.9	2.1	2.9	6.8	7.0	5.7	2.0	1.6	1.3
E. parvipinne		1.6	1.6	1.9	4.4	5.0	4.7	2.4	2.3	1.9
E. flabellare		1.9	1.8	2.5	4.9	3.9	3.8	1.8	1.9	1.5
E. gracile		2.4	1.7	2.2	6.4	3.9	3.9	1.6	2.2	1.8
E. proeliare		1.8	1.7	2.2	3.4	3.4	4.3	2.3	2.4	1.9

TABLE XX (Continued)

Species	Ratio:	Amacrine/Rod			Amacrine/Ganglion			Cone/Ganglion		
	Region:	Ventral	Dorsal	Central	Ventral	Dorsal	Central	Ventral	Dorsal	Central
P. caprodes		.4	1.2	.8	5.0	4.4	2.7	2.5	2.6	1.6
P. maculata		.8	1.0	1.7	4.5	3.0	2.5	2.3	2.3	1.5
P. sciera		.6	.7	1.3	3.9	4.0	2.7	2.2	2.2	1.3
P. phoxocephala		.5	.6	1.7	3.8	2.8	2.4	2.8	2.5	1.5
P. shumardi		.7	2.3	1.8	3.5	2.7	2.0	1.8	1.2	1.4
P. copelandi		.6	2.5	1.5	4.4	2.8	2.2	2.4	1.8	1.3
A. vivax		1.0	12.5	4.3	3.0	1.3	1.4	1.8	.7	.8
A. clara		1.0	28.0	16.5	3.7	1.8	1.6	2.5	.9	1.0
E. chlorosomum		.7	3.6	1.5	2.5	1.6	1.5	1.7	.9	.9
E. histrio		.4	1.5	1.1	3.9	2.5	1.6	1.9	1.2	1.1
E. whipplei		1.1	1.1	1.5	3.0	3.2	2.0	1.9	2.3	1.4
E. punctulatum		.6	.6	.7	3.5	3.3	2.0	1.8	2.1	1.6
E. parvipinne		1.9	2.2	2.3	2.7	3.2	2.5	1.2	1.4	1.3
E. flabellare		1.2	1.4	1.7	2.5	2.2	1.5	1.4	1.2	1.1
E. gracile		1.4	2.7	2.8	2.7	2.3	1.8	1.8	1.0	1.0
E. proeliare		2.4	3.4	3.2	1.8	2.0	2.0	.8	.8	1.0

TABLE XX (Continued)

Species	Ratio:	(Bipolar + Amacrine)/Ganglion			(Bipolar + Amacrine)/Cone		
	Region:	Ventral	Dorsal	Central	Ventral	Dorsal	Central
P. caprodes		12.6	10.7	7.3	5.0	4.2	4.7
P. maculata		11.9	8.8	8.0	5.1	3.9	5.2
P. sciera		11.6	11.3	7.5	5.3	5.1	5.8
P. phoxocephala		13.0	8.9	7.4	4.7	3.6	5.1
P. shumardi		10.7	7.0	7.0	5.8	5.7	4.9
P. copelandi		12.7	8.0	7.3	5.2	4.4	5.5
A. vivax		9.2	7.7	5.5	5.1	11.9	6.5
A. clara		12.8	8.0	5.9	5.1	8.5	6.0
E. chlorosomum		8.3	7.2	6.0	5.0	7.7	6.8
E. histrio		10.7	6.7	5.3	5.8	5.8	5.0
E. whipplei		9.0	9.3	6.4	4.7	4.0	4.7
E. punctulatum		10.3	10.3	7.7	5.8	5.0	4.9
E. parvipinne		7.2	8.2	7.2	6.2	5.9	5.3
E. flabellare		7.4	6.1	5.3	5.2	5.3	5.0
E. gracile		9.1	6.2	5.6	5.2	6.0	5.8
E. proeliare		5.2	5.3	6.3	6.6	6.4	6.0

To facilitate interpretation and to combine the ratios from the three retinal regions into a single unit, the values from the cell ratios were plotted on a graph and the three values for each species were joined by a line to form ratio-figures. The ratio-figures for two of the more useful ratios are shown in Figure 8. Whereas some of the cell ratios provide little or no information concerning visual capacity, the figured ratios give some measure of relative retinal development. A high value in the bipolars/(cones + rods) ratio can be considered indicative of high visual acuity. This statement is usually made in reference to the bipolar/cone ratio (Table XX), but since some of the bipolars are associated with rods only (Ali, 1959), inclusion of the rods in the ratio should give a better figure for comparing acuity. This argument can also be applied to the other figured ratio, (bipolars + amacrines)/cones × ganglions, but in view of the uncertain relationships of the amacrine cells in neuronal pathways, the omission of the rods seems insignificant; high values are presumed to indicate high visual acuity. With the possible exceptions of the two Ammocrypta and E. chlorosomum, the maximum visual acuity of each species is not represented because ratios for the temporal regions are not included.

Both sets of ratio-figures, as well as several of the ratios in Table XX, can be divided into groups of similar figures, denoting species relationships (premise ii). Considering both sets of figures simultaneously, A. vivax, A. clara and E. chlorosomum form a distinct group; P. shumardi, P. copelandi and E. histrio are similar, with P. caprodes showing some similarities to this group; P. maculata, P. sciera and P. phoxocephala are very much alike, whereas E. whipplei, E. punctulatum, E. flabellare, E. parvipinne and E. proeliare seem to form a progressively diverging sequence from them; and E. gracile has some similarity to the preceding group, but

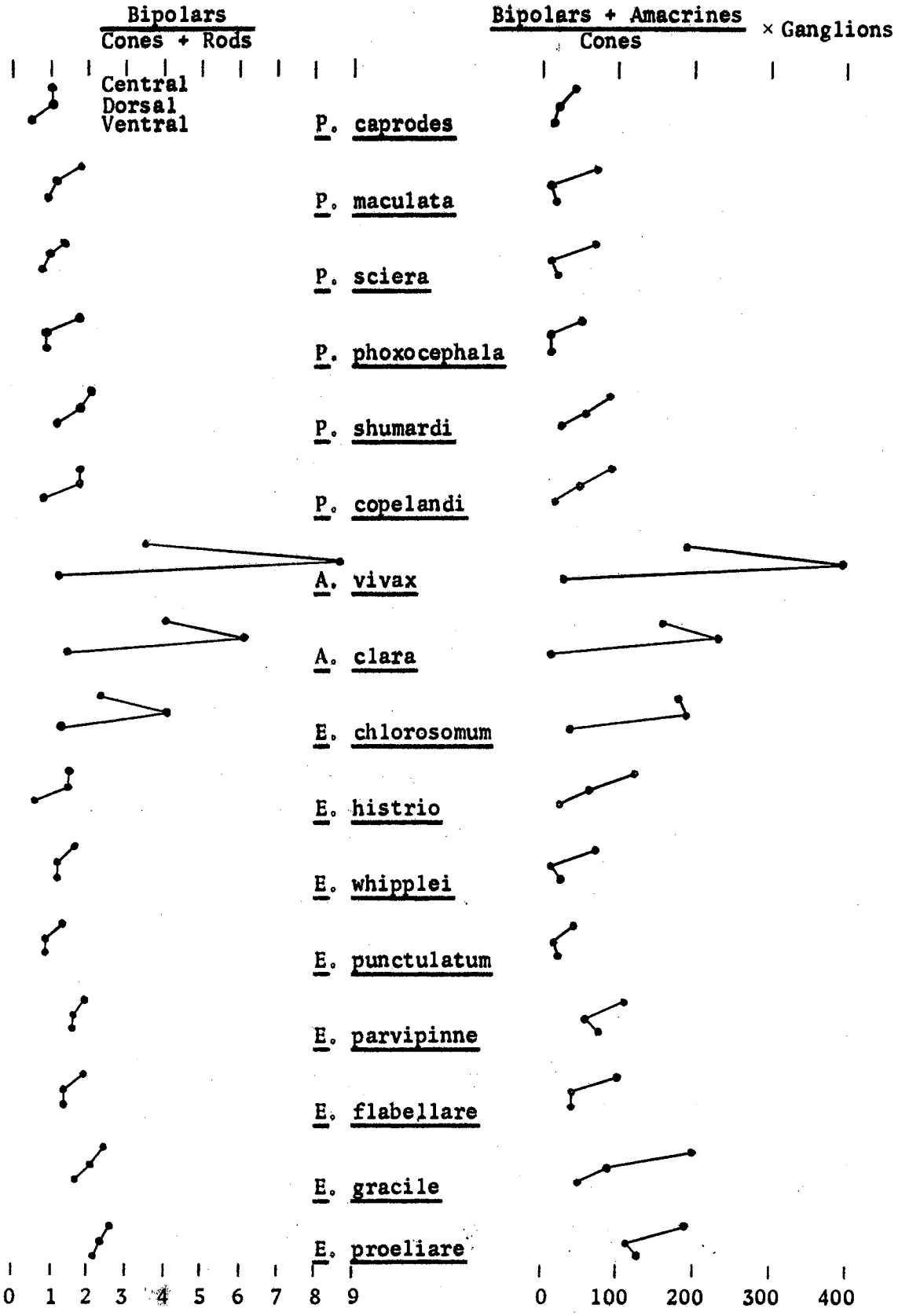

Fig. 8. Cell density ratios in the central, dorsal, and ventral regions of the retina.

differs enought to be separated. On the basis of some of the other ratios, E. whipplei and E. punctulatum tend to form a separate group, and E. flabellare, E. parvipinne and E. proeliare may each stand alone.

The relationships indicated by the ratio-figures above coincide rather well with the groups based on cone-density patterns. Only two species are grouped differently; P. copelandi is placed with the members of group I, and E. punctulatum is placed with group III.

To illustrate better the relative regional differences in retinal development, and possibly to elucidate the relationships of some species, one additional treatment was applied to the cell-density data. The ratios of each cell type in the dorsal and central regions to the corresponding cell type in the ventral region were computed and illustrated in Figure 9a and b. Again, consideration of the general patterns facilitates the grouping of the species. The greater the proximity of the lines to each other and to the value one, the poorer the differentiation of the regions. The greatest differentiation is seen in A. clara, while A. vivax has a similar but less extreme pattern. E. chlorosomum has a pattern resembling Ammocrypta, but differentiation is so much less that it perhaps resembles P. copelandi equally well, although the latter shows a greater difference between the dorsal and central regions. The dorsal retina is less well developed in E. histrio, but otherwise it is similar to the preceding species, and not greatly different from P. shumardi.

By including P. caprodes, a group of species is formed with dorsal/ventral ratios above 1.0 for all cell types except rods. P. caprodes shows the least differentiation, and P. shumardi, E. histrio, E. chlorosomum and P. copelandi form a series with progressively greater differentiation that culminates in the distinct Ammocrypta. These species were grouped in a

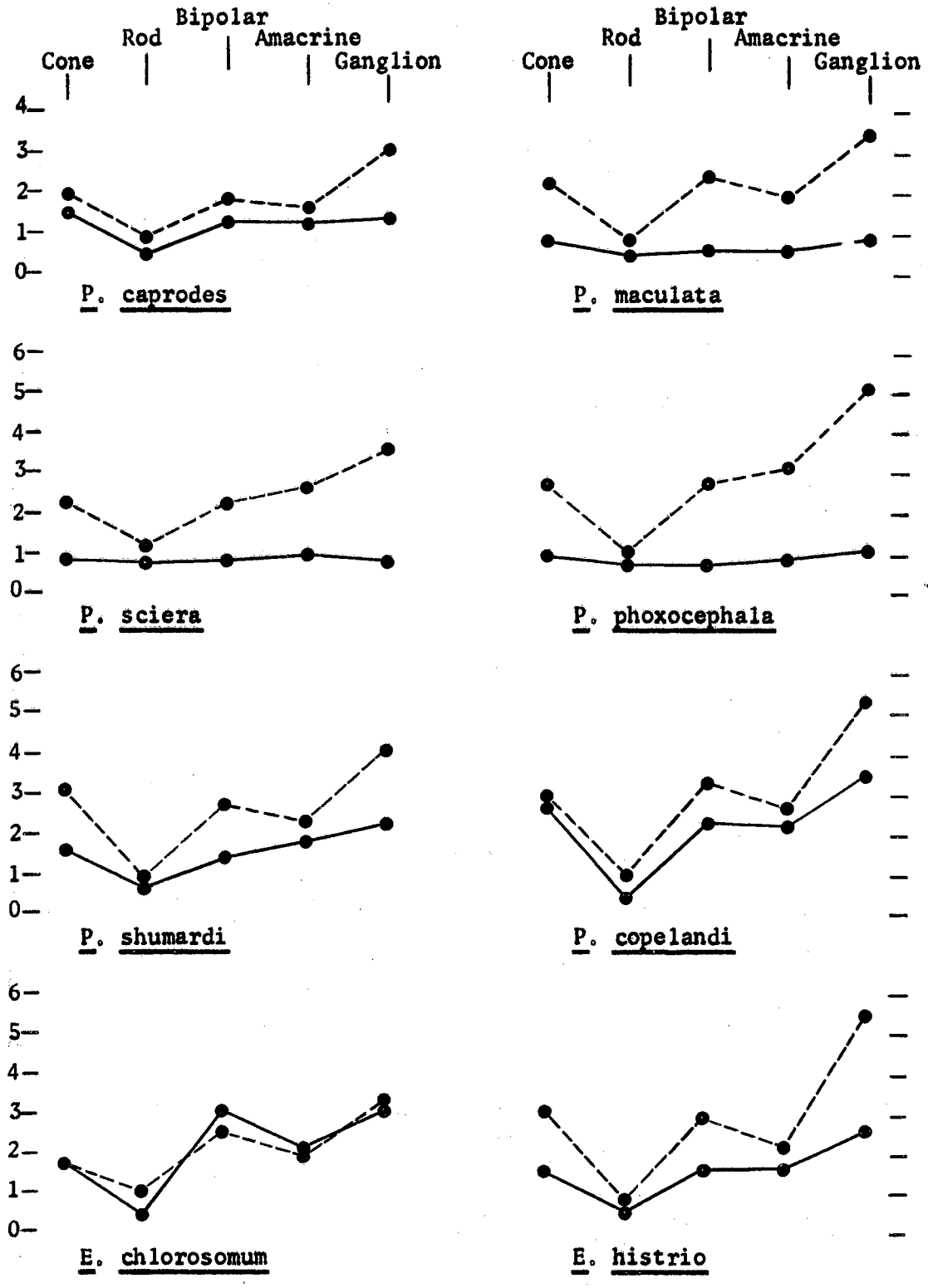

Fig. 9a. Density ratios of cell types in different regions of the retina. Dorsal/ventral (——); central/ventral (---).

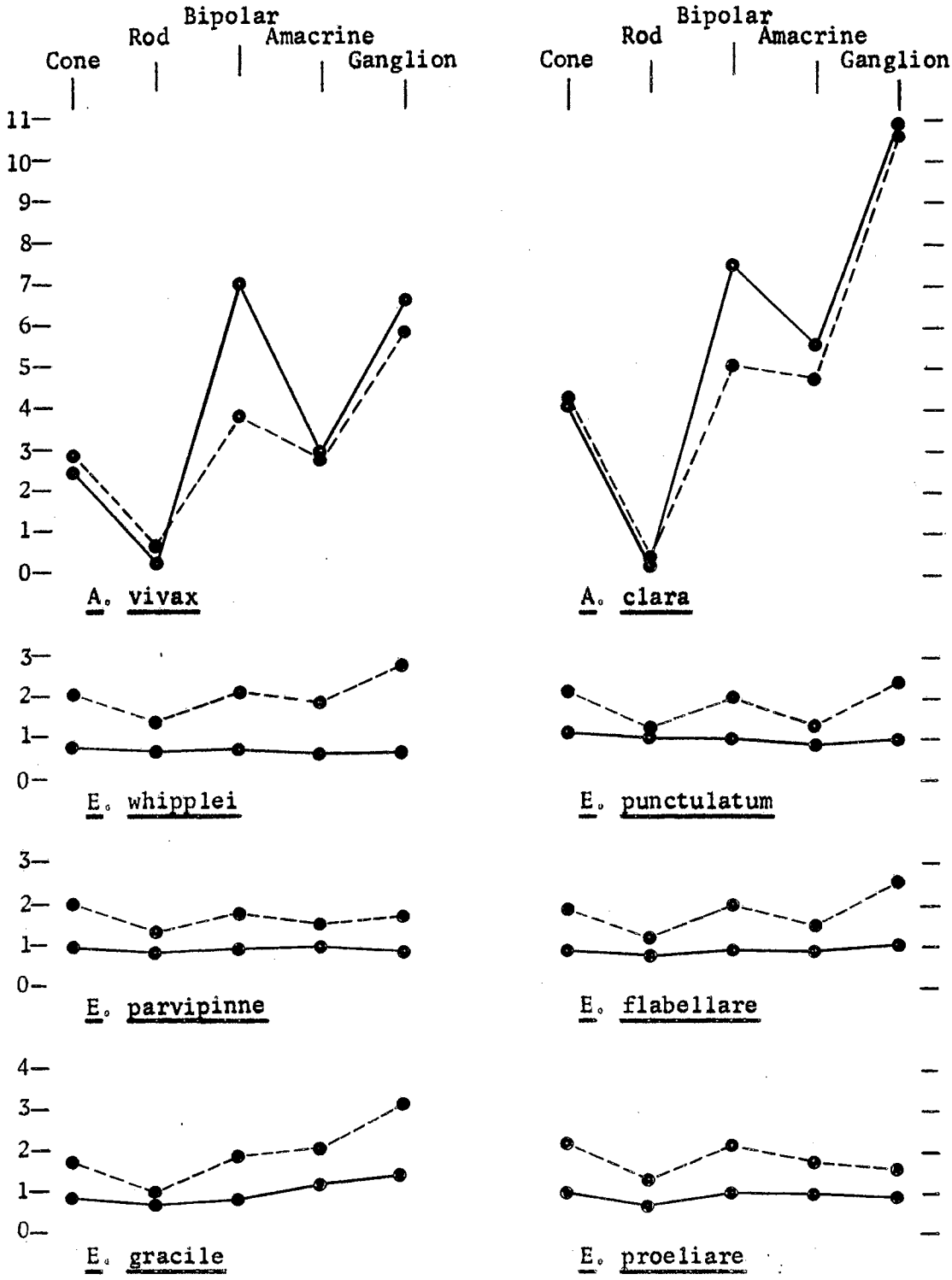

Fig. 9b. Density ratios of cell types in different regions of the retina. Dorsal/ventral (——); central/ventral (- - -).

similar manner on the basis of ratios between cell types, but a greater difference between E. chlorosomum and Ammocrypta is shown here.

Separation of the remaining species into groups is difficult. P. sciera, P. maculata and P. phoxocephala again show similarities with relatively high cell densities, except for rods, in the central region, but the likeness of E. gracile and E. flabellare to these Percina species cannot be denied. The high rod density in the central retina excludes E. whipplei from the group. The meagerly-differentiated species, E. punctulatum, E. parvipinne, and E. proeliare tend to form a sub-group showing some similarities to the three preceding species.

Phylogeny and Taxonomy

The uncertainty of the interspecific relationships of the darters is partially indicated by the numerous and frequent changes made in their classification, particularly at the generic level. More than 30 once-recognized genera were gradually combined until Bailey (in Bailey, Winn and Smith, 1954) finally lumped them into the three genera currently recognized by most workers. Bailey (in Bailey and Gosline, 1955) subsequently erected eight subgenera under Percina, two under Ammocrypta, and 12 under Etheostoma. Some of these subgenera represented previously recognized genera, whereas others contained new combinations of species. These revisions were based on forthcoming but as yet unpublished studies. However, some indication of possible relationships of the subgenera was provided by the sequence in which they were presented. The authors mentioned however, that phyletic lines could not be shown linearly.

With few exceptions, the sequence of the species presented herein follows that of Bailey (in Bailey and Gosline, 1955). The retina of Percina (Percina) caprodes was described first, primarily for convenience since it is relatively unspecialized and herein considered to be primitive. A preliminary scheme of the phylogeny of some of the darters prepared by Bailey and based on unpublished morphological data (Winn, 1958), seems to show some inconsistencies with his previously-indicated relationships. Consequently, in the absence of published explanatory material, the currently-used classification scheme and the indicated phylogenetic relationships of the darters cannot be fully evaluated. Therefore, the following taxonomic considerations are based on retinal structure only.

Each of the treatments of the cell density data has permitted the division of the species into groups with similar retinal characteristics.

Since all of the groups thus produced are not identical, they do not necessarily represent logical taxa. It is therefore desirable to devise a possible phylogeny based on the retinae while considering taxonomy.

The three groups based on the distribution of cone pattern sizes contain obviously artificial assemblages of species, but some rather basic similarities and differences between species are indicated. The scatter-diagram of cone-pattern-size ratios (Fig. 7) is more informative because it tends to rank the species and partially subdivides the previous groups. It also indicates some possible lines of phylogeny. A hypothetical, ancestral retina with a uniform distribution of cones would have a value of 1.0 on both coordinates. Assuming that the ancestral darter was modified slightly for seeing food organisms in an antero-ventral position, the values on both coordinates would be less than 1.0, and the distribution of cone densities would produce a group I figure.

Among the typical representatives of group I, P. caprodes and E. punctulatum show the least specialization. Though poorly developed in P. shumardi, a fovea is considered to be an advanced condition. Cell density ratios in the central retina of E. histrio indicate considerable specialization. Cell ratios were not computed for E. blennioides, but the high density of cones distinguishes it from the less modified forms. All of the treatments applied here indicate greater uniformity in the retina of E. punctulatum than in P. caprodes, thus suggesting that the ancestral darter may have been "Etheostoma-like." On the basis of osteological and other morphological characters, it is generally agreed that Percina is the ancestral genus (Collette, 1963), and this view is acceptable here. E. punctulatum may be looked upon as an early derivative of the ancestral Percina that has undergone less specialization than P. caprodes.

From the relatively unmodified forms of Percina and Etheostoma, retinal evolution has diverged in two general directions resulting in cone-density pattern groups II and III with better developed dorsal and ventral regions respectively. The presence of foveae in both lines of Percina evolution suggests its appearance prior to the divergence and after the development of the forms that gave rise to P. caprodes and P. sciera. However, in view of the similarities in the cell ratios of P. sciera, P. maculata and P. phoxocephala, the independent origin of foveae in each group seems more plausible than the parallel evolutionary processes that would have been required to maintain these cell-ratio similarities. The presence of basically similar foveae in relatively unrelated groups of vertebrates with no phylogenetic continuity supports the hypothesis of independent foveal development.

The accompanying dendrogram (Fig. 10) is intended to express a possible sequence of phylogeny in addition to degrees of difference between species of Percina (Mayr, 1965). Each species represents a different subgenus in Bailey's classification. Although densities of cells other than cones were not computed for more than one representative of each subgenus, cursory examination of an additional species from each of two subgenera revealed only minor differences within each subgenus. It is therefore assumed that retinal variation within these subgenera is less than that between subgenera.

The retinae of P. phoxocephala and P. maculata are sufficiently alike to be included in the same subgenus[1], whereas P. sciera differs enough to remain separate. As a means of indicating the close relationship of these

[1]In view of the new and incomplete nature of this study, problems of nomenclature are ignored.

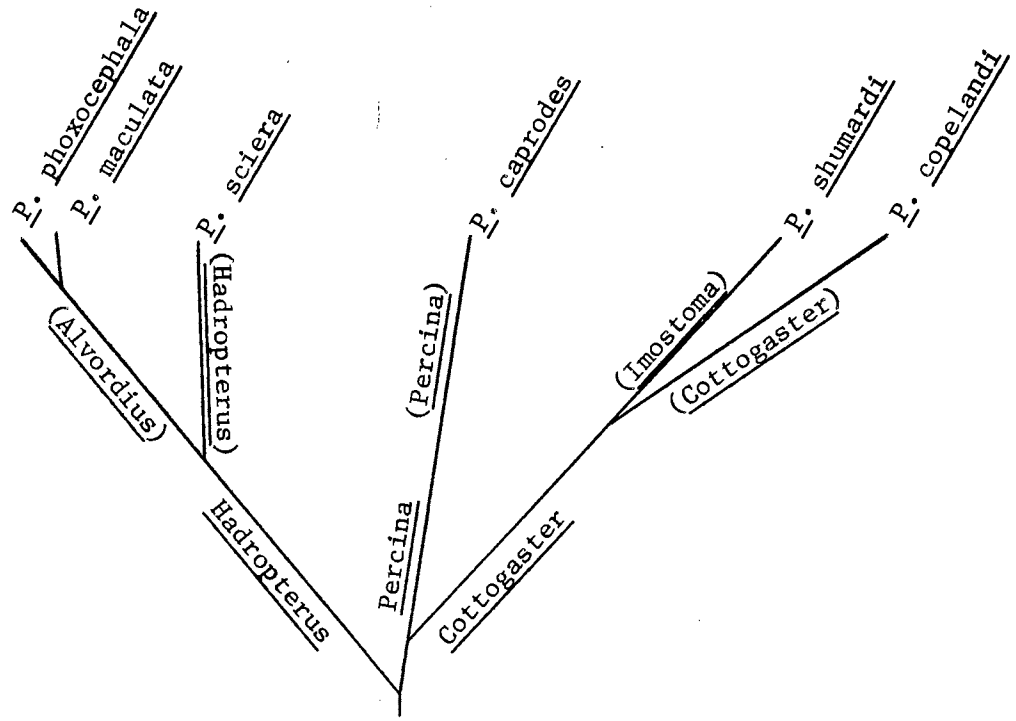

Fig. 10. Dendrogram of Percina based on retinal structures.

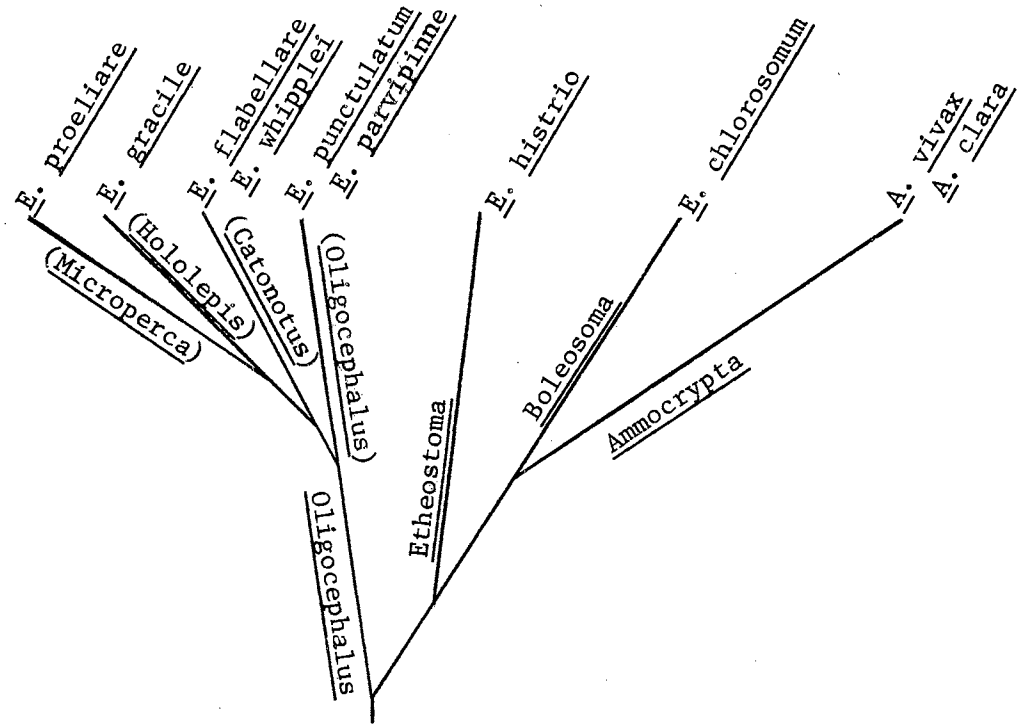

Fig. 11. Dendrogram of Etheostoma and Ammocrypta based on retinal structures.

two subgenera, the designation of this evolutionary line as a genus, Hadropterus, seems justified. Although the distribution of cones in P. caprodes shows little differentiation, the dorsal decrease in rod density is considered a specialization that has been retained by P. shumardi and P. copelandi while other cell densities increased. In general, the cell ratios indicate a closer relationship of P. caprodes to these latter two species than to the Hadropterus group. The ancestral form is therefore considered to have been somewhat intermediate between P. caprodes and Hadropterus. The distinctiveness of the relatively unspecialized retina of P. caprodes warrants a separate subgenus. The difference in the shape of the retina and the distribution of cones is adequate for retaining P. shumardi and P. copelandi in separate subgenera, but the smilarities in cell ratio figures, which are distinct from those of P. caprodes, dictates separate generic designations for the Imostoma-Cottogaster taxon and the subgenus Percina.

Construction of a dendrogram of the genus Etheostoma (Fig. 11) presents some difficulties, and the resulting diagram should perhaps be termed a cladogram, but the two main lines of evolution are distinct. One line leads to the specialized dorsal retina as seen in E. chlorosomum. On the basis of the cone-density patterns, E. nigrum and E. chlorosomum are very similar and belong in the same subgenus, whereas E. stigmaeum, with some indication of a fovea, may represent another subgenus. In either case, these species are sufficiently modified to be considered as a separate genus, Boleosoma.

The cell-density ratios of E. histrio, representing the subgenus Etheostoma, are strikingly similar to those of P. shumardi. This is suggestive of a common ancestor, and an indication of the evolutionary line

of Percina (s.l.) that may have given rise to the genus Etheostoma. It is possible that the similarity is the result of convergent evolution, but in view of the relationships indicated by Bailey, the possiblity above seems more plausible. The inclusion of E. histrio and E. blennioides in one subgenus is indicated by the general structure of the retina, but the position of E. zonale is questioned because of its distinct fovea. Analyses of the retinae of additional species in this subgenus should help clarify these relationships. Until then, the distinctiveness of E. histrio, as a representative of a major evolutionary line, justifies the recognition of another genus, Etheostoma.

The relationships of the remaining Etheostoma are not clearly expressed by the treatments employed. Analyses of additional species, and the inclusion of cell ratios from the nasal and temporal regions, may help to clarify the relationships in this large group of darters. The data available indicate a close relationship of E. punctulatum, E. parvipinne, E. whipplei and E. flabellare, but they vary greatly in their degree of specialization. E. punctulatum shows little regional differentiation, whereas the latter two have well-developed foveae. On the basis of the fovea they can be separated into two subgenera, Oligocephalus containing E. punctulatum and E. parvipinne, and the foveate forms arbitrarily designated Catonotus. The cell ratios indicate specialization leading to greater visual acuity with little dorsal-ventral differentiation in E. gracile and E. proeliare. While there are differences between these two species that may warrant subgeneric designation, they seem to fit a cline of specialization with E. punctulatum at the lower and E. proeliare at the upper end. Consequently, all of the species on this phyletic line are considered congeneric on the basis of the available data. The origin of this genus (Oligocephalus, for

convenience) is also controversial. It has a closer resemblance to Hadropterus than to Boleosoma or Etheostoma, thus suggesting a dual origin for the species that Bailey assigned to Etheostoma.

The genus Ammocrypta is clearly distinguished from the other darters by its highly specialized dorsal retina. The differences between A. vivax and A. clara are considered to be at the species level only. The possible relationship of Ammocrypta with P. copelandi indicated by the cone-pattern figures is not substantiated by the cell-ratio figures. The figures produced by all treatments for Ammocrypta closely parallel those for E. chlorosomum, thus suggesting a common origin of Ammocrypta and Boleosoma.

In an attempt to express the generic and subgeneric relationships of the taxa considered herein in a two-dimensional dendrogram (Fig. 12), it was necessary to misrepresent the Hadropterus line, which would be in the same plane as the Oligocephalus line in a three dimensional figure.

The impracticality of attempting to establish an acceptable scheme of phylogeny on the basis of the retina only, is well recognized. In this instance it seemed advisable to exceed the limits of practicality for two reasons: i) In an endeavor to evaluate the possible use of the retina as a taxonomic tool, it is necessary to consider any limitations to its usefulness. Although the phylogeny of the darters has not been adequately established, there are enough indications of phylogeny based on morphological and behavioral evidence to permit some evaluation of a phylogeny based on retinal structure. ii) Since the phylogeny is not well established, the retinal evidence may be of value in indicating some possible relationships, and taxa that might be critical to the establishment of an acceptable phylogeny.

The retinal indices developed herein show differences between most of

Fig. 12. Dendrogram of genera and subgenera of darters based on retinal structure.

the species that are considered to be closely related, but some refinement of the methods, a more critical evaluation of the changes associated with growth, and consideration of the range of variation will be necessary before these retinal indices can be relied upon for species determinations. The value of the retina as an effective taxonomic tool is indicated by the high correlation between the subgeneric designations based on retinal structure and those of Bailey. The retinal figures failed to distinguish P. (Alvordius) maculata from P. (Swainia) phoxocephala, and E.(Oligocephalus) whipplei from E. (Catonotus) flabellare, but otherwise, the 13 subgenera under consideration were distinguishable. This is considered to be clear evidence that the retinal structure is controlled through phylogeny, and is not merely a plastic reflection of the environment.

The designation of genera is highly subjective, but it should suggest the relationships of species whenever possible. The recognition of at least six genera is necessary to express effectively the suggested relationships of the 11 subgenera. With the exception of the admittedly questionable combination of taxa included under Oligocephalus, the groupings suggested here have been considered as genera by previous workers.

Likewise, much of the suggested phylogeny has been expressed previously. Ammocrypta has been listed between Cottogaster and Boleosoma Bailey, (in Bailey and Gosline, 1955), so that its suggested derivation from the Boleosoma line may not be totally unexpected. The specialization of Boleosoma indicated here seems compatible with findings based on their reproductive behavior (Winn, 1958). There is a striking similarity between the phylogeny based on retinal structure and the view of Jordan, Evermann and Clark (1930:282): "From Percina two lines diverge in different directions; the allies of Crystallaria and Vigil to Ammocrypta toward a

quiescent life, buried in sand; the other through Poecilichthys, Nothonotus and Oligocephalus for life in weedy brooks, culminating in Microperca...." They then listed, "in as natural sequence as our present knowledge permits", the following genera with those not represented here omitted: Percina, Alvordius (including phoxocephala), Serraria (sciera), Cottogaster, Imostoma, Etheostoma, Ulocentra (histrio and stigmaeum), Boleosoma, Vigil (clara and vivax), Nanostoma (zonale), Nivicola (cragini and punctulata), Claricola (whipplei and parvipinne), Catonotus, Boleichthys (gracile), Hololepis and Microperca. This sequence almost duplicates that indicated by Figure 12, except for the Hadropterus line.

Correlation of Retinal Structure with Habitat and Habits

Some rather distinct correlations between retinal structure and habitat types (riffle, backwater, etc.) might be expected, but attempts to find such correlations were futile. This does not imply that there is no correlation, but merely that the criteria used here to evaluate retinal structure and habitat were inadequate for that purpose.

Relationships between retinal structure and habits are apparent in some species. In darters the eyes are instrumental in feeding and, in the few instances where they are known, the food habits can be correlated with retinal structure. Those darters that feed largely on relatively stationary food items, such as chironomid larvae in quiet water or attached larvae in fast water have poorly-differentiated, afoveate retinae (e.g. P. caprodes and E. blennioides). A food-habit study of E. parvipinne or E. cragini should reveal a diet of relatively large, non-swimming organisms. A well-developed retina with a fovea permits feeding on faster moving organisms; E. f. barratti and E. microperca capture active swimmers, and P. copelandi eats chironomid larvae dislodged by the current.

The highly specialized dorsal region of the sand darter's retina correlates well with its habit of feeding on the bottom, presumably on organisms being swept by the current. The bottom-dwelling habit can be associated with the flattened ventral retina and the foreshortened condition of the dorsal retina; its extension would view only the sand adjacent to the body and would be subject to dazzlement by reflection from the sand. The poorly developed ventral retina is apparently limited to the detection of potential enemies under both photopic and scotopic conditions. The paucity of rods in the more dorsal "food-detection" region of the retina dictates photopic feeding habits. Although several species have similar

retinal modifications indicative of a bottom-dwelling habit, most are less extreme and more difficult to correlate.

Species that perch in vegetation, e.g. E. f. barratti, and E. microperca, are at the opposite end of a graded series of retinal modifications from the sand darters. The nearly equal dorsal and ventral regions may function primarily in detecting enemies that might approach from either above or below, but their cell densities suggest some capacity for detecting food organisms.

A more detailed analysis of the rods and cones in darters, coupled with additional details of their habits and habitats, should reveal more subtle correlations. Some apparent differences among species in the sizes and densities of rods and cones have been noticed, but they were not evaluated in terms of function because of the unknown effects of growth. Detailed information about rods and cones could probably be correlated with light intensity factors, such as tolerence to silt, and shade or water-depth requirements, and with diel activities.

DISCUSSION AND CONCLUSIONS

The darters, Etheostomatini, apparently originated from the Percini (Collette, 1963) rather recently, and through adaptive evolution have invaded and become specialized for many freshwater habitat types in North America. In the process, the feeding and reproductive habits have become modified (Winn, 1958). Examination of the retina shows that it has also undergone specializations that can be correlated more closely with feeding habits than with characteristics of the habitat. This was unexpected, since investigators of other species have frequently found retinal specializations indicative of habitat type preferences. Retinal structures have been associated with diel and seasonal activities and with highly specialized habits such as those of the archer fish, Toxotes jaculatrix (Lüling, 1958). Correlations with more subtle differences in feeding habits similar to those suggested for darters were found in several marine fishes (Tamura, 1957). If further study verifies a correlation of retinal structure with differences in the diets of darters, it will certainly confirm the following statement by Detwiler (1943:60): "So closely correlated is the mode of life of the animal with the structure of the retina that, from a histological section, one can predict something of the habits of the animal, as well as its visual ability."

The retinae of fishes are specialized in so many different ways that visual abilities cannot be compared in a quantitative manner unless their structure is similar and size differences can be equated. Most of the described retinae of teleosts have comparatively large photoreceptors with

rods numerically predominating (Detwiler, 1943). Rods are absent in the areae of some clupeids, but in other parts of their retinae rods may approach 100 times the number of cones (O'Connell, 1963). Several teleosts are known to have pure-rod retinae, but descriptions of pure-cone forms have not been found. Although ratios of rods to cones may be suggestive of bright- or dim-light habits, they may be misleading unless factors of sensitivity and acuity are considered. In view of the high cone, bipolar, and ganglion cell densities, and the near absence of rods in some areae and foveae, the relatively high cone/rod ratios indicate that darters are most active under photopic conditions. The cones of some fishes, including Perca fluviatilis, contract and supposedly become functional at light intensities below the color threshold of humans (Wunder, 1926b; Brunner, 1934) so the statement above does not necessarily exclude twilight periods.

An indication of the retinal structure in the ancestral darter may be obtained from the extant Percini. Among the species for which retinal descriptions are available, Perca fluviatilis is considered the most typical (Engström, 1936b). The limited information available on the retina of P. fluviatilis agrees with the hypothetical ancestral condition proposed earlier. The retina is thicker dorsad than ventrad (Wunder, 1925), suggesting higher cell densities dorsally. Counts supplied by Wunder (1925) for the dorsal retina give a cone/rod ratio of 0.32, which is lower than any found in the dorsal retinae of darters (Table XX). The P. fluviatilis eye was probably larger than the darter eyes and, since rod numbers increase during growth, a lower ratio is expected. Each of the main evolutionary lines of darter retinae has involved a progressive increase in the cone/rod ratio, so a low ratio value would be expected in the ancestral form.

Densities of bipolar, amacrine, and ganglion cells are rarely found in descriptions of teleost retinae, and since published data of cell ratios, except rods/cones, are almost nonexistent, these data for darters cannot be compared with other species at this time. High densities of cones, bipolars, and ganglion cells suggest a diurnal eye with high acuity (Walls, 1942). The relationship of the bipolar/cone ratio to acuity was questioned when data indicated that this ratio increased with eye size (O'Connell, 1963). The value of including rods in the ratio is thus emphasized, for O'Connell was apparently led astray. The density of cells in the inner nuclear layer varies in closer proportion to rod than to cone density in the guppy (Müller, 1952). Bipolar/cone ratios in the darters do not increase with eye size, and the range of variation in this ratio in different regions of an Ammocrypta vivax retina is almost as great as the maximum difference between the species considered by O'Connell. Bipolars/(cone + rod) ratios computed with O'Connell's data show no correlation with eye size.

The ratios between cones, rods, bipolars, and ganglion cells indicate high acuity in the darters. A neuronal path from one cone through a single bipolar to a ganglion cell without summation has been illustrated for trout (Ali, 1959). This type of pathway is usually considered to produce the maximum acuity possible for a given cone density. The high bipolar/cone ratio in the nearly pure-cone regions of Ammocrypta suggests that each cone may be associated with several bipolars. A scheme of divergence from a cone to three bipolars was suggested for a lizard on the basis of cell ratios (Vilter, 1949), but mention of this type of neuronal pathway for teleosts is unknown. In darters a cone may make connections with eight or more bipolars, but additional study will be necessary to

establish this and to determine its functional significance.

Many fishes have a retinal region modified for better visual acuity that involves a higher photoreceptor density. These regions vary in position and degree of differentiation, and have received various appellations. The hesitancy of some authors to use the term "area" seems unwarranted, especially when accompanied by descriptive data. Areae usually occupy some part of the temporal retina, but may be dorsal or ventral (Tamura, 1957; O'Connell, 1963; Vilter, 1948). Nasal and temporal areae were found in Salvelinus fontinalis, Esox lucius and Labidesthes sicculus (Polyak, 1957), and Engraulis mordax (O'Connell, 1963), but horizontal band-shaped areae, as found in darters, have not been described for other fishes. Investigation of the functional significance of the nasal portion of the area in darters is anticipated.

Distinct foveae were known previously from marine species only, but comparatively few fresh-water fishes have been examined. The presence of foveae in darters is not surprising, in view of their reliance on vision to capture minute food organisms.

A thorough analysis and comparison of visual acuity was not the objective here, but some factors to be considered in such a study have been disclosed. As a means of indicating the degree of areal specialization for comparison of species representing 18 families, Tamura (1957) used cone densities from seven retinal regions and computed the ratio of the highest density to the average of the densities in the other six regions. Since the seven regions were not equally spaced over the retina, a bias against broad temporal areae was introduced that may have influenced his results. To be valid, comparison of the degree of areal specialization based on cone density ratios can only be made when neuronal

pathways are similar in all species. Different degrees of summation may accompany identical cone densities, producing different degrees of acuity. From various cell ratios in darters it is apparent that neuronal pathways vary considerably between species within a tribe. Variation between families is expected to be much greater, and it should be considered in acuity evaluations.

The absence of any correlation between the indices of areal specialization and the minimum separable angles further suggests that Tamura (1957) was dealing with different degrees of summation. However, the apparent ommission of a factor for lens shrinkage in his minimum separable angle determinations may be significant.

Usage of retinal structures in taxonomy involves the same problem that is associated with virtually all other characters, namely, variation. Usually the published descriptions of fish retinae give data for a single specimen, and the extent of variation within and between populations is unknown for most species. Sexual differences in the retina are unlikely, but have not been investigated. The presence of allometric growth presents special problems that will require additional study. The use of intra-type cell ratios is believed to be of particular value as an index of regional differentiation because only minor changes in these ratios are expected with growth, especially in small-eyed forms such as darters. The effects of growth on the inter-type cell ratios were briefly considered in two darters, P. phoxocephala and P. sciera (Table II), with some conflicting results that suggest species differences in growth patterns. The bipolar/cone ratio increases with eye size in P. phoxocephala, but decreases in P. sciera. Differences of this type seem illogical and must be investigated more thoroughly. It is quite possible that sections from

incomparable retinal regions were used, and the method of measuring retina size was certainly inaccurate.

To be of taxonomic value a character must be less variable within a taxon than between taxa. Although the extent of retinal variation has not been thoroughly evaluated, the differences found between some species are so much greater than the variation observed within a species, that retinal structures can be considered useful in distinguishing taxa of darters. The value of a taxonomic character is increased in proportion to any additional information it may convey. In darters the retinal structure is suggestive of some possible phylogentic relationships, and has some predictive value with regard to some aspects of behavior. Although the conclusions here are based on a comparatively small number of species, and the examination of additional forms may markedly alter the suggested relationships and phylogeny, it is concluded that retinal structures of darters have a positive taxonomic value.

The close similarity of most of the generic groupings and phylogenetic relationships suggested on the basis of retinal structures to pre-existing classification and phylogenetic schemes further substantiates the usefulness of the retina. Furthermore, since the retinal structures clearly indicate the divergence of darters into evolutionary lines leading to the sedentary Ammocrypta and the vegetation-dwelling E. microperca as proposed by Jordan, Evermann, and Clark (1930), the reclassification of the darters into at least seven genera is strongly suggested on the basis that the currently-used generic designations fail to express their relationships.

In addition to the previously mentioned areas needing further study, some serendipitous observations concerning extraretinal structures of the eye were made. The unusual morphology and histologic nature of the muscles

of accommodation are being considered and will be discussed elsewhere. Vitreal blood vessels are limited to the ventral half of the eye in most darters, but extend into the dorsal region in E. cragini, thus suggesting that a comparative study of intraocular vascularization in darters might be fruitful. The cornea is exceptionally thick in some species and seems to contain an undescribed layer in E. zonale. Analysis of the corneal structure may have physiological and taxonomic significance.

SUMMARY

1. The retinae of 26 species of darters were investigated to determine their general structure and possible value in taxonomy. Representatives of thirteen subgenera and three genera, Percina, Ammocrypta and Etheostoma, as currently defined, were used.

2. Tangential sections from four retinal regions were used to determine the cone pattern and density. Vertical and horizontal sections were used for general structure and cell density determinations.

3. Hydrogen peroxide with ammonium hydroxide effectively bleached fuscin.

4. Descriptions of retinal shape and general structure have been presented with habitat and habit data for each species. The retinae are basically similar, but regions of specialization vary in degree and position. The variations are correlated more closely with feeding habits than habitat.

5. Darter retinae are generally modified for acute photopic vision. Areae are dorsal in strictly bottom-dwelling forms, becoming temporal and frequently forming a horizontal band in those less restricted to the bottom. Foveae vary in extent of development and are limited to temporal regions.

6. Cell densities change with growth in a manner similar to those described for other teleosts, and cannot be used directly for species comparisons. Several types of intraretinal density ratios minimize size differences and permit the comparison of species.

7. Distribution patterns of cone densities indicate three general categories of retinal specialization, each containing species of Percina and Etheostoma. From the relatively unspecialized forms, two diverging evolutionary lines leading to either dorsal or temporal retinal specialization are suggested.

8. Density ratios between cell types in the ventral retina are similar in all species, suggesting a common ancestry. By including ratios from dorsal and central regions the species are divisible into several groups suggesting species relationships.

9. Density ratios between dorsal, central and ventral regions for each cell type indicate regional specialization and suggest species relationships.

10. Some of the cell ratios may be useful in considerations of visual processes, but they have not been fully evaluated here.

11. By using combinations of ratios it was possible to group the species into higher taxa and propose a possible scheme of phylogeny.

12. The taxa and phylogenetic scheme based on retinal structure closely parallel some pre-existing concepts based on other characters.

13. Retinal structures are considered valuable tools in darter taxonomy.

14. The recognition of at least seven genera would express the relationships of the darters better than the three generic groupings currently employed.

15. Additional investigations of darter retinae in the following areas are considered worthwhile. (i) A more complete evaluation of the effects of growth on cell ratios. (ii) The range of variation in retinal structure within a species. (iii) The diagnosis of additional species.

(iv) Determination of neuronal pathways by silver impregnation in regions where divergence is suspected. (v) Comparisons of photoreceptor sizes in relation to densities and habitats.

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