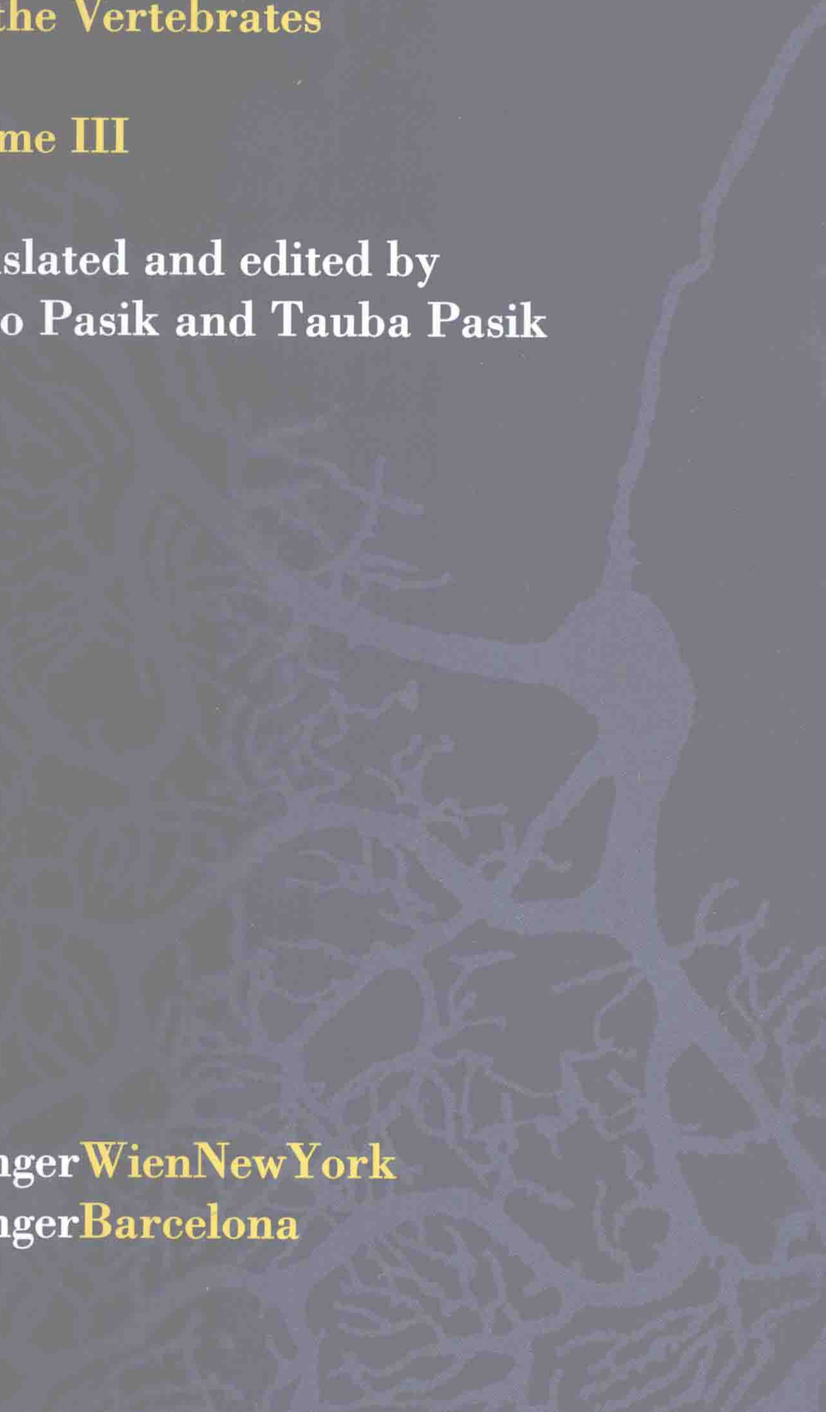
Santiago Ramón y Cajal

Texture of the Nervous System of Man and the Vertebrates

Volume III

Translated and edited by
Pedro Pasik and Tauba Pasik



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Texture of the Nervous System of Man and the Vertebrates

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An annotated and edited translation of the original Spanish text with the additions of the French version by
Pedro Pasik and Tauba Pasik

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PREFACE

The first volume of our annotated and edited translation of Cajal's Texture of the Nervous system of Man and the Vertebrates (the *Textura*) appeared exactly 100 years after the original Spanish text. It is with much pride that we present this third and final volume, which had been published as Volume II Part 2 in 1904, in joyous celebration of the 150th birthday of Don Santiago Ramón y Cajal.

As stated in the prefaces of our first two books, we have tried to preserve the original Spanish of Cajal's language and style, and ask the readers for indulgence toward the sometimes not so elegant English rendition. The advantages are evident in that interpretative statements are avoided in the text, being restricted to pertinent annotations at the end of each chapter, for which we are fully responsible.

Additions from the French version, the *Histologie*, increase the text by approximately 10% of the entire work, and appear in brackets in the present version. The *Histologie* contributed also 142 extra figures bringing the total to 1012.

Cajal's original art work was used to produce 670 figures, i.e. about two thirds of the total. The remainder are reproductions from the *Textura* or the *Histologie*. A special challenge has been to offer our identification of over 90% of the almost 1500 symbols appearing in the illustrations but missing in the original legends. We should like to acknowledge especially the important help obtained from Facundo Valverde's Golgi Atlas of the Mouse Brain, Springer-Verlag Wien New York, 1998, to elucidate some of the forebrain structures in the present volume, which sometimes reinforced our opinions and some others illuminated an obscure point. For identification of symbols in figures of non-mammalian brains we consulted the original publications of Pedro Ramón in the *Revista Trimestral Micrográfica* which contain full legends of the illustrations used by Cajal in the Textura.

A total of 90 different species appear in the Taxonomy Glossaries showing the presently used scientific designations as well as their colloquial English counterparts.

Finally, references were verified, corrected and completed as need it, in over 96% of a total of 1885 citations.

A completely new Subject Index appears at the end of this volume. The selection of entries was based to a large extent on present day interests and, in general, it utilized current nomenclature followed in brackets by corresponding terms used in the *Textura* and/or the *Histologie*. It includes references to all figures.

It has been hard but extremely rewarding work, as if almost having an intimate conversation with the great Master, admiring his foresight in many issues which are today at the forefront of Neurobiological research. Even the concept of inhibition, which on cursory reading appears absent in the *Textura*, and has been so commented upon, is mentioned by Cajal 16 times in various contexts. The thrill of handling so many of the elaborate drawings he prepared to illustrate the book, containing even his own annotations and instructions to the publisher, was indeed a hallmark of our efforts.

It is already with a touch of nostalgia that we offer this third volume with the hope that it will serve the explorers of the nervous system in their pursuit of the understanding of its functions as given in the original by the founder of modern Neuroscience.

We are very pleased to repeat here in the same order the acknowlegements mentioned by name in the previous volumes: János Szentágothai, José Valciukas, Josefina Cano, Alberto Machado, María Ángeles Ramón y Cajal Junquera, Cajal Institute of the Spanish Council of Scientific Research, Alberto Ferrús, María Angustias Pérez de Tudela, the New York Academy of Medicine Library, the Research Library of the American Museum of Natural History, the Gustave L. Levy Library of the Mount Sinai School of Medicine, Rudolf Siegle, Raimund Petri-Wieder, Springer-Verlag Wien New York, Constantino Sotelo, Facundo Valverde, Santiago Ramón y Cajal Junquera, Alexander Pasik, the National Institutes of Health, Ricardo Martínez-Murillo, Miguel A Freire, María A Langa and María C Díaz.

New York, Spring 2002 Pedro Pasik and Tauba Pasik

TEXTURA DEL SISTEMA NERVIOSO

DEL

HOMBRE Y DE LOS VERTEBRADOS

ESTUDIOS SOBRE EL PLAN ESTRUCTURAL
Y COMPOSICIÓN HISTOLÓGICA DE LOS CENTROS NERVIOSOS
ADICIONADOS DE CONSIDERACIONES FISIOLÓGICAS
FUNDADAS EN LOS NUEVOS DESCUBRIMIENTOS

POR

S. RAMÓN CAJAL

Catedrático de Histología en la Universidad de Madrid.

Con numerosos grabados en negro y en color.

TOMO II

SEGUNDA PARTE

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IMPRENTA Y LIBRERÍA DE NICOLÁS MOYA
Carretas, 8, y Garcilaso, 6.

1904

TEXTURE OF THE NERVOUS SYSTEM

OF

MAN AND THE VERTEBRATES

STUDIES ON THE STRUCTURAL PLAN
AND HISTOLOGIC COMPOSITION OF THE NEURAL CENTERS
WITH PHYSIOLOGIC CONSIDERATIONS BASED ON NEW DISCOVERIES

BY

S. RAMÓN CAJAL

Professor of Histology of the University of Madrid

With numerous black and white and color illustrations

Volume II
Second Part

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PRINT SHOP AND BOOKSTORE OF NICOLÁS MOYA
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1904

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CHAPTER I

RETINA (CONTINUATION)

Retina of lower vertebrates (birds, reptiles, amphibians and fish).—Structure of the central fovea of the retina.—Retinal histogenesis.—Connections of retinal cells and physiologic inferences derived from the structure of the visual membrane.

The retina, similar to almost all neural sensory apparatuses and peripheral ganglia of the nervous system, exhibits a remarkable structural uniformity in the vertebrate series. Mammals, birds, reptiles, amphibians and fish, all have the same retinal layers, each with the same neuronal types and connectivity arrangements. Each animal, however, does not collect exactly the same impressions of the external world because of the diverse conformation of the eye and the somewhat different conditions under which vision occurs in each species. It is, therefore, conceivable that each type of vertebrate shows some interesting changes in the structure, conforming to the special physical environment and particular needs for survival. As we shall see promptly, such changes do not alter the essential plan, but they affect the morphology, frequency of occurrence and location of neurons, particularly the shape, size and chemical composition of the receptor cells.

RETINA OF BIRDS

The avian retina is the most perfect and complicated of all. It has been the subject of many careful analyses by almost all early histologists, such as Müller, Schultze, Schwalbe, W. Krause, Dobrowsky, Hoffmann, Schiefferdecker, etc. Among modern investigations, we should cite those of Dogiel with the Ehrlich method, ours with both Ehrlich and Golgi methods, Ressnikoff's, etc. The results of such studies are given in the following summary.

Layer of rods and cones.—Examination of this layer in birds, reveals first the extreme scarcity of rods in all retinal regions. The avian retina, therefore, consists essentially of cones. An interesting case is that of nocturnal birds, where according to our investigations, the occurrence of rods is just as frequent as in mammals.

Rods present, as in mammals, an outer and an inner segment. Both are thin in some birds (nocturnal and small birds), and thick in others (gallinaceans). The visual pigment (photostesin) was discovered in rods of nocturnal birds.

Cones are thinner than in mammals, and are particularly characterized by an interesting feature. There is a colored fatty sphere (Fig. 1*a*) between the two segments, which is not present in mammals. It occupies the entire diameter of the cell, so that only monochromatic light, or at most a light with very small proportion of other spectral components, can reach the outer segment or sensitive portion. The color of such spheres may be red, orange, yellow or green. Blue spheres are rarer and their existence was denied by Schwalbe, but confirmed by W. Krause, Dobrowsky and Greeff. Finally, some cones show colorless fatty spheres. The distribution of colored spheres is not uniform and varies in some birds, as noted by Waelchli (1881). In the pigeon, the postero-superior portion of the retina exhibits a high density of red spheres (red field), whereas yellow spheres predominate in the remaining retina. The same author recognized that spheres of a certain color are present at a different level than those of other hues. According to Van Genderen Stort (1887), there are up to four levels or series of spheres. We should add that even the cones with red spheres may have fine pink granules in the inner segment, as shown also by Schultze, Beauregard and other authors (Fig. 1*a*).

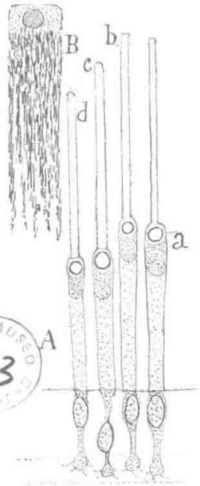

Fig. 1.—Cones of the pigeon retina. Dissociation of fresh tissue. (Semischematic).—A, inner segments of cones; B, pigment epithelium cell; *a*, colored sphere; *b, c, d*, outer segments of cones

Outer granules.—According to our investigations in small birds, pigeons and gallinaceans, the cell bodies of cones and rods are quite different from each other. Whereas the body of the rod is robust, with the nucleus toward the center, and ends in a large foot from which many fine threads emerge in a horizontal direction, the soma of the cone is located at all levels of the layer, and shows a thin descending process, with a conical ending bristled with a few appendages. The contrast between the two visual receptors is well seen in small birds. As observed in Fig. 2*a, b*, the base of the rod ends in a more superficial plane than that of the cone, and in addition, it issues a tuft of long obliquely descending filaments.

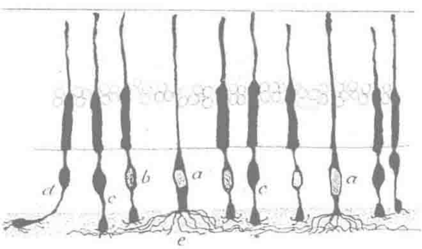

Fig. 2.—Cones and rods; sparrow retina. Golgi method.—*a*, rods; *b, c*, straight cones; *d*, oblique cone[a]

In gallinaceans and pigeons, there is also a variety of cones, discovered by us and confirmed by Ressnikoff. These are the *oblique cones* with a descending oblique or arched process, ending in a thick varicosity at the deepest plane of the plexiform layer (Fig. 2*d*). Occasionally, this process takes a rather long horizontal course issuing some collaterals (Fig. 3*a, e*)

In birds, there are also *twin cones*, i.e. pairs of elements in close longitudinal contact, one smaller than the other (accessory cone). As shown by our investigations, each element of the pair represents an individual conductor, since the varicosity or foot of the descending process resides in a different plane of the outer plexiform layer, and most possibly, becomes in contact with a special type of bipolar cell (Fig. 3*d*).

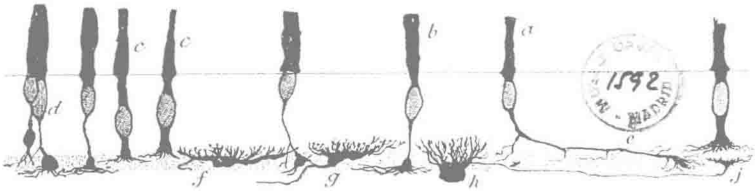

Fig. 3.—Bodies of cones and rods; chicken retina. Golgi method.—*a*, oblique cone; *b*, straight cone; *c*, rods; *d*, double cones; *f, g, h*, horizontal cells[b]

As stated earlier, cones are rare in nocturnal birds, although they are not lacking in the common owl (*Strix otus* Lin.) and the red owl (*Strix flammea* Lin.), which thus resemble diurnal birds. Instead, rods are very abundant and, similar to the homologues in the mammalian retina, they characteristically terminate in the first plane of the plexiform layer as a smooth varicosity (Cajal, 1889c) with no filaments.

Horizontal cells.—They are much smaller than in mammals, and form an irregular row. Two types are found in our preparations. 1st. *Tufted* or *brush-like* type, very abundant, with numerous ascending appendages (Fig. 3*h*) and a horizontal axon that ends at a variable distance in a very characteristic spiny arborization [(Figs. 3*j* and 4*c*)]. 2nd. *Stellate* type, less frequent, with a more flattened shape and longer horizontal dendrites; in small birds, we followed the axon for long distances and observed its termination in a more extensive arborization than that of the preceding type (Figs. 3*g* and 7 I).[c] The existence of the first type has been confirmed by Ressnikoff.

Bipolar cells.—They are also of two types. 1st. *Large* type, rich in cytoplasm, with numerous ascending expansions, but with no Landolt club (Fig. 5*n*). 2nd. *Small* type, abundant, of ovoid shape, scarce cytoplasm, present at various planes of the inner granular layer. The inner process of this cell ends in a varicose tuft at various levels of the inner plexiform layer after issuing collateral arborizations for the overlying planes, as discovered by us in birds, reptiles and amphibians. The

Fig. 4.—Brush-like horizontal cell, flat view; chicken retina. Golgi method.—*a*, dendrites; *b*, axon; *c*, horizontal axonal arborization

outer process forms a horizontal tuft distributed in the outer plexiform layer and, in addition, as noted concurrently by Dogiel (1888a, b, 1895d) and ourselves (Cajal, 1888, 1889c), it gives off an ascending fiber ending freely in a varicosity at the level or beyond the external limiting membrane. This appendage is known as the Landolt club, in honor of the author that first described it in the amphibian retina. It is seen very frequently in the pigeon and gallinaceans, but we have failed to impregnate it in small birds (Fig. 5*m, o, p, q*).

It is possible that, as in mammals, the large and small bipolar types relate to rods and cones, respectively.

Stellate cells.—As noted in a recent publication (Cajal, 1896d), the retina of small birds contains also some stellate, ovoid or triangular cells among bipolar cells. They show no definite orientation, several relatively short descending processes, and some ascending branches ending in complicated arborizations in the outer plexiform

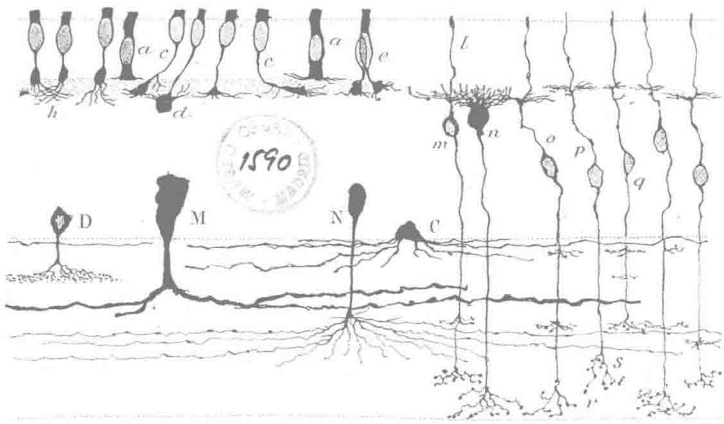

Fig. 5.—Chicken retina. Golgi method.—C, D, M, N, different types of amacrine cells; *a*, rod; *c*, oblique cone; *d*, cone with oblique pedicle; *e*, double cones; *m*, bipolar cell with Landolt club; *n*, large bipolar without a bulb; *l*, Landolt club; *s*, terminal tuft of bipolar cells[d]

layer. We do not know the significance of these cells nor could we find the corresponding axon (Fig. 6*a, b*).

Amacrine cells.—The layer of these cells contains three neuronal types: ordinary amacrine, [giant amacrine], and short axon or association amacrine, in addition to displaced ganglion cells.

The *ordinary amacrine* corresponds to the description given earlier, differing from that of mammals in its abundance and variety, the extraordinary elegance of the types, and the unusual richness of horizontal arborizations, which, in thicker regions of the retina, are arranged in seven planes. We present some varieties of these cells in Figs. 5 and 8. A detailed description can be found in our extensive book on the retina. Note the unistratified amacrines (large, small, with varicose and contracted tuft, with fine, light and extensive tuft, etc.), bistratified amacrines and diffuse amacrines. In some regions, we also found tristratified[e] amacrines (Fig. 6*d*).

The *displaced ganglion cells* were reported by Dogiel and confirmed by us. Such cells, which we shall call *Dogiel cells*, in honor of their discoverer, are few and voluminous, of semilunar or mitral shape, with dendrites and an axon. Dendrites are thick, usually horizontal and distributed in the first plane of the inner plexiform layer. The axon descends perpendicularly without emitting collaterals and continues with a fiber of the optic nerve. The fact that these cells, except for their location, behave substantially as ganglion cells destined to the first plane of the inner plexiform layer, allows the assumption that Dogiel cells are just giant cells of the ninth layer, which become displaced of their usual location, as an adaptation following the law of space economy (Fig. 10A).

Short axon cells or horizontal amacrines [or association amacrines].—These curious cells, which were discovered by us (Cajal, 1895d,1896d), are pyriform in shape, with a descending tuft of short, thick and sparsely ramified dendrites. This tuft is sometimes represented by a single, short, denticulate appendage. The axon, [arising from the inner tip of the descending process, or from one of the dendrites], is robust, horizontal, and courses either within the first plane, or along the outer border of the inner plexiform layer. After a very long itinerary, it resolves in a dense, horizontal arborization within the mentioned first plane, where it becomes related with a group of processes of ordinary amacrine cells (Fig. 7*b*). As we shall see later, Ehrlich preparations show that the soma and dendrites of such interesting cell are surrounded by terminal arborizations of centrifugal fibers[1]

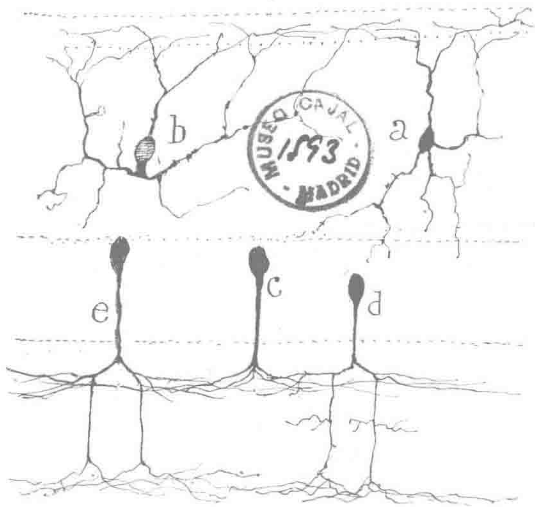

Fig. 6.—Small bird retina. Golgi method.—*a, b*, stellate cells of the layer of bipolar cells; *c*, monostratified amacrine cell; *d*, tristratified amacrine cell; *e*, bistratified amacrine cell

The cited cells must have been seen, although imperfectly, by Dogiel. The methylene blue method used by this author, however, is inadequate to reveal their morphology. Furthermore, the frequent occurrence of staining these cells together with the centrifugal fibers that contact them, leads to possible errors, as noted in another of our publications (Cajal, 1896d).

Dogiel (1895b) mentions in birds, the existence of certain horizontal, small, and semilunar cells located immediately superficial to the plexiform layer, with a short, fine axon ramified within the same plane of this layer. We lack personal observations on such cells, which are very different than the preceding ones. They do not appear in our Ehrlich and Golgi preparations. We are inclined to assume that the Russian savant has taken for short axon neurons, certain semilunar amacrine cells described by us some time ago in the avian retina. The multiple and very long processes of these cells, some of which he may have interpreted perhaps as axons, extend within the first plane of the inner[h] plexiform layer (Fig. 8B).

[*Giant amacrines*. Finally, there is a type of giant amacrine cell, very abundant in birds, with initially thick processes that become gradually thinner resembling axons. We shall described them with the retina of reptiles.]

Ganglion cell layer.—This layer presents an enormous amount of neurons, particularly in small birds. The stratified cells predominate because of their various

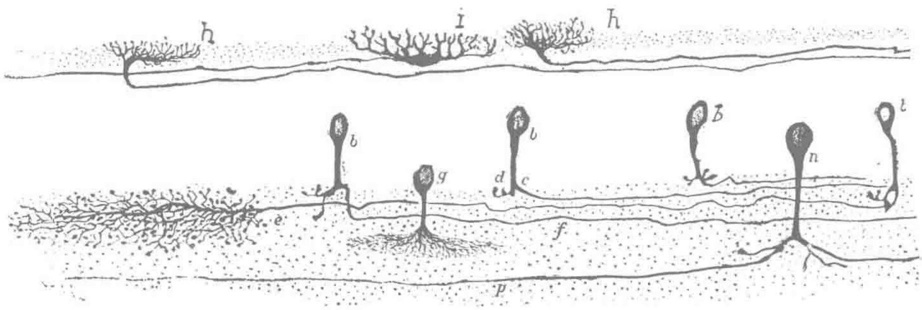

Fig. 7.—Small bird retina (greenfinch, *Ligurinus chloris*, L). Golgi method.—*b*, short axon amacrines or association amacrines; *d*, dendrites of these cells; *c, f*, their horizontal axon; *e*, their terminal axonal arborization; *i*, flattened horizontal cell; *h*, its axonal arborization; *g, n*, amacrines[f]

sizes and shapes, and the exquisite elegance of their terminal horizontal dendritic plexi. Inspection of Fig. 10, where we reproduce some main types of this cell variety, allow us to skip a more detailed description. The unistratified ganglion cells are almost the same as those of reptiles, as drawn in Figs. 13 and 14.

This layer contains also a large number of displaced amacrine cells, with fine ascending stems forming a flattened, very dense, delicate terminal arborization in the third plane of the inner plexiform layer. Branches are so varicose that at low magnifications resemble an accumulation of granules.

Optic fiber layer.—It consists of *centripetal axons*, mostly of medium or small diameter, and *centrifugal axons*, usually more robust and arborized, as in mammals, in the zone of amacrine cells. The latter fibers are easily stained in birds with both the Golgi and Ehrlich methods.

In Figs. 9 and 10, we present the main varieties of *centrifugal fibers* in the retina of the pigeon and small birds, respectively. Note that the fiber proceeds from the optic fiber layer, and after traversing without dividing the inner plexiform layer, it