A TEXTBOOK OF

HISTOLOGY

A TEXTBOOK OF

HISTOLOGY

HARVEY ERNEST JORDAN, A.M., PH.D., SC.D.
Professor of Anatomy, Retired, University of Virginia

NINTH EDITION

APPLETON-CENTURY-CROFTS, INC.
NEW YORK

PRINTED IN THE UNITED STATES OF AMERICA

Preface

An effort has been made in this edition to incorporate important advances during recent years, including certain results of tissue culture and electron microscopy. In order to keep the book within earlier limits, the effort involved extensive revisions and considerable elimination of text and figures. Account has been taken of new material with reference to mitosis, mitochondria, striated muscle, collagen fibers, blood cells, the liver lobule and the endocrine glands. Consideration of the autonomic nervous system has been amplified. Less satisfactory illustrations have been replaced and some new figures have been added.

With a view to stimulating interest in histologic data, the known or believed function dependent upon the structure described is indicated where this seemed desirable; and, to the same end, comparative anatomic facts are frequently presented. Photomicrographs of actual sections, combined with interpretative drawings and diagrams, appear to be the ideal illustrative procedure.

Since Embryology usually constitutes a separate course in the medical curriculum, the development of tissues and organs is discussed only to the extent deemed essential for a better appreciation of structure. Since the anatomy of the nervous system likewise properly constitutes a separate course, only the fundamental nervous tissues are here described, including the microscopic structure of the spinal cord, the cerebral cortex and the cerebellar cortex.

In an attempt to adapt the book to varying teaching conditions, less essential material has been set in smaller type.

References to the literature are appended for the convenience of the student who may wish to pursue the study of particular subjects beyond the restricted practical limits of the textbook.

I wish to acknowledge, with gratitude, my indebtedness to my colleague, Dr. James E. Kindred, for help in the preparation of new material for the ninth edition, and to the publishers for their courteous cooperation with many valuable suggestions.

H. E. Jordan

A TEXTBOOK OF
HISTOLOGY

CONTENTS

A TEXTBOOK OF HISTOLOGY

CHAPTER I

THE PROTOPLASM AND THE CELL

Definition.—Histology is the science of tissue structure, plant or animal. It concerns itself, therefore, chiefly with the structural characteristics and interrelationships of the component elements of tissues. These elements are the *cells,* and the material connecting or separating the cells, the *intercellular substances.* A tissue consists of cells associated in the performance of a specific function. A cell may be defined in a preliminary way as the unit of organic structure and function. The minuter details of histology involve also cell anatomy or *cytology.* Here we meet with the essential substance of the cells, the *protoplasm,* or *bioplasm,* the "material basis of life." We also meet with the chief "organ" of cells, the *nucleus.* A more precise definition of a cell may accordingly be given as a *circumscribed mass of protoplasm containing a nucleus* (Fig. 1). A complete histologic description embraces, therefore, details of the relationships of the component cells of a tissue, and of the protoplasmic structure and nuclear characteristics of the types of cells involved. Histology includes further the data of tissue origin and development, or *histogenesis,* and of cell origin and development, or *cytogenesis.* Cells are the building stones of tissues; tissues combine to form organs; organs are associated into systems. Animal histology is accordingly a part of general anatomy; it is *tissue anatomy;* that part of human histology which considers the relationships between tissues in organs is sometimes spoken of as *microscopic anatomy.*

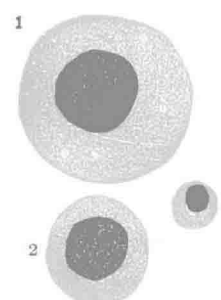

FIG. 1.—VARIOUS SPHEROIDAL CELLS.

1, ovum from ovary of a child; *2,* spermatocyte; and *3,* spermatid, from the testicle of a rabbit. Hematein and eosin. ×750.

Historical Development.—Modern human histology had its origin in the work of Bichat (1771-1801). He did not employ the microscope; but his careful and extensive studies of the minute anatomy of tissues gave the impulse and general outline for later studies by means of the microscope through which mammalian histology has grown to a relatively complete science. Great impetus was given also by the announcement of the cell theory of Schleiden and Schwann in 1839, namely, the statement that all tissues are composed of structural units, or cells.

In less complete form the cell theory had been advanced by earlier investigators, by Mirbel[1] (1808), by Lamark (1809) and by Dutrochet[2] (1824). Other epochal steps in histologic science were the recognition of the nucleus by Robert Brown in 1833, and of protoplasm by von Mohl in 1846. Cytology arose almost as an incident to embryology. It traces its origin to the work of O. Hertwig on the fertilization of the sea urchin's egg (1875) and the substantially identical observations, made independently and simultaneously by H. Fol. It is the infant anatomic science, its late development being due, largely, to its dependence upon the optical and mechanical refinements of the microscope. It deals with fundamental structures within the limits of visibility, and is destined to grow to vast proportions, as the already voluminous literature on mitochondria and Golgi material foreshadows.

Relation to Other Biologic Sciences.—Histology aims to complete anatomic knowledge. It is thus the complement of gross anatomy. It furnishes also essential preliminary data for the understanding of pathology; abnormal structure and function become fully intelligible only in the light of normal histology. It is fundamental also to physiology, the science of normal function.

A certain function demands a specific structure; structure and function sustain reciprocal relationships. Normal function depends upon the normal structure of the cells involved in the function; abnormal function, or disease, is associated with altered cellular structure. Histology gains enormously in interest and value to the student who will keep in mind the function that a certain structure under consideration is called upon to perform. Embryology also to a considerable extent builds upon histologic and cytologic data.

PROTOPLASM

Chemical Constitution.—The unit of both structure and function is the cell. The essential constituent of cells is protoplasm. Protoplasm may be thought of as a physiochemical mechanism. Chemically, it is a very complex aqueous mixture of substances, containing the elements, carbon, oxygen, hydrogen, nitrogen, and small quantities of sulphur, phosphorus, calcium, sodium, chlorine, magnesium, potassium and iron.

The principal compounds of protoplasm are proteins, which furnish the main source of energy expended in function; carbohydrates; fats; water, which constitutes about three-quarters of its weight; and inorganic salts. It is believed by one school of biologists (mechanists) that if we had the formula for the proper stereo-isomeric association of the elements and compounds of protoplasm, life could be artificially produced; another school of biologists (vitalists) assume an additional vital principle as a prerequisite for life.

Physical Constitution.—Physically, protoplasm is a granular semifluid or gelatinous substance. It possesses properties characteristic of both solids and liquids.

---

[1] Gerould, 1922.
[2] Goss, 1937.

It is an aggregate of *colloids* and *crystalloids*. The physicochemical laws which govern the crystalloids and colloids underlie the properties of living matter. An organism is essentially an aqueous solution, holding in suspension colloidal substances of great complexity. Crystalloids are divisible into two groups: electrolytes and nonelectrolytes. The one (salts, acids, bases) in solution conducts the electric current, the other (urea, sugar) does not. Colloids exist in two states, a liquid or *sol* state, and a *semisolid* or *gel* state. There exists no sharp line of division between colloids and crystalloids; these terms designate phases or states rather than substances; between them lie all kinds of intermediate grades. Protoplasm is a sol; and since its fluidity is due to water, it is commonly classed as a *hydrosol*. It passes

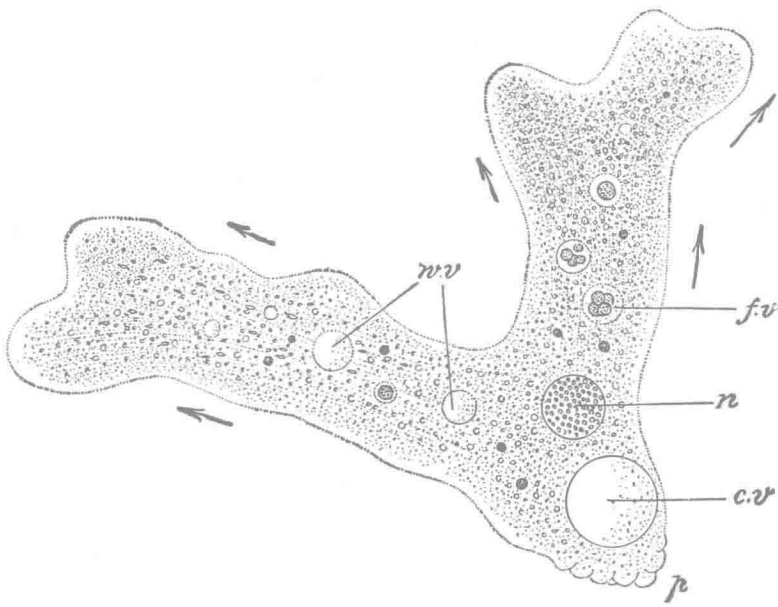

FIG. 2.—AMEBA PROTEUS IN MOTION.

c.v., contractile vacuole; *f.v.*, food vacuole; *n.*, nucleus; *w.v.*, water vacuoles. The arrows indicate the direction of the protoplasmic flow. Note the peripheral nongranular ectoplasm, and the granular endoplasm. (From Calkins, *Biology*, H. Holt & Co., after Sedgwick and Wilson.)

readily into a gel condition, thus becoming a *hydrogel*. In living protoplasm this metamorphosis is a reversible process. Agents which effect an irreversible gelation of protoplasm tend to bring life to a standstill. Fixation, or killing, of tissue for microscopic study consists in a separation of the more solid part of colloidal protoplasm from a more liquid part. Death is histologically such a process of coagulation. Living protoplasm may be studied to good advantage in the one-cell animal forms, ameba (Fig. 2) or paramecium (Fig. 3). These and other equally favorable protozoan forms are readily available from hay infusion cultures, and can be profitably employed for the demonstration also of the simpler modes of proto-

plasmic activity, and of the changes suffered by protoplasm in passing from the living to the dead condition. Since protoplasm is commonly organized into cells, the next step demands a knowledge of a typical or generalized cell.

THE CELL

A *generalized cell* is of spheroidal shape (unmodified by pressure) and contains certain organs and a variety of fundamental and secondary elements (Fig. 4).

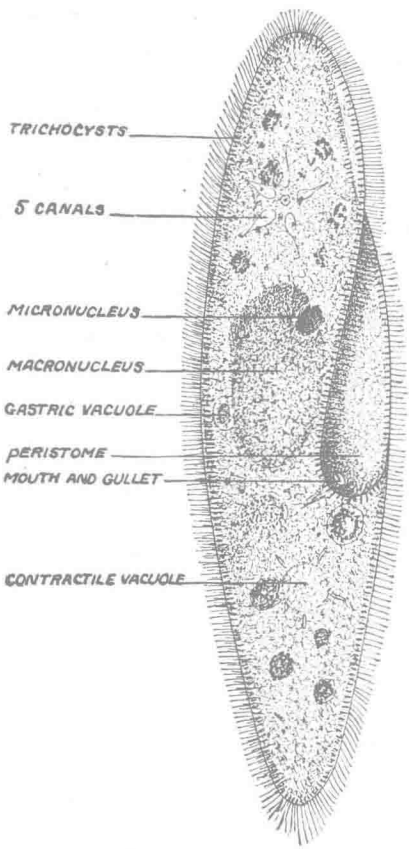

FIG. 3.—PARAMECIUM CAUDATUM.

Note the peripheral cilia and the granulo-alveolar character of the protoplasm. (From Calkins, *Biology*, H. Holt & Co.)

A cell (or protoplast; Hanstein) is a mass of protoplasm endowed with vital properties. The confines of such a cellular mass of protoplasm exist in a *cell membrane*. This represents a differentiation product of protoplasm; when robust as in plant cells, it forms a *cell wall*. In certain cells, *e.g.*, white blood cells, it is apparently lacking; however, in these so-called naked cells the peripheral layer of protoplasm is more condensed and most probably subserves the osmotic function of a distinct membrane. In fact, the surfaces of protoplasm possess the properties of semipermeable lipoid membranes.

An essential organ of the cell is the *nucleus*. It is trophic in function, the center of oxidation processes. In certain protozoa this is represented by scattered nuclear materials or granules (Fig. 5). The shape of the nucleus is spherical; typically it has a central location, but it frequently assumes eccentric positions. It is physically denser and more elastic than the extranuclear protoplasm. Its periphery consists of a membrane, the *nuclear wall*. Whether as a membrane it be complete or reticulated, whether of nuclear, cytoplasmic or composite origin, are undecided points. Certain results of investigations on the nuclear membrane suggest that it is fenestrated; such conditions would permit of an easy escape of nuclear material into the cytoplasm.

Nucleus.—The protoplasm composing the nucleus is known as *nucleoplasm* or *karyoplasm;* that constituting the remainder of the cell, the *cytoplasm*. The nuclear constituents include a more fluid ground substance or *nuclear sap* (*karyolymph;*

paralinin), throughout which extends a delicate reticulum of *linin* threads (Fig. 4). Upon these linin or achromatic threads are supported, more abundantly at the points of intersection of the mesh, granules (*chromioles*) and masses (*net knots*) of a substance staining deeply in the basic dyes, the *chromatin*. Spheroidal net knots are known as *karyosomes*. The linin is said to be achromatic. Whether it is chemically different from chromatin or simply more attenuated chromatin is disputed. The "chromatic" granules themselves undergo changes in stainability: on the basis of reaction to acid and basic dyes, this substance is divided into *oxy-*

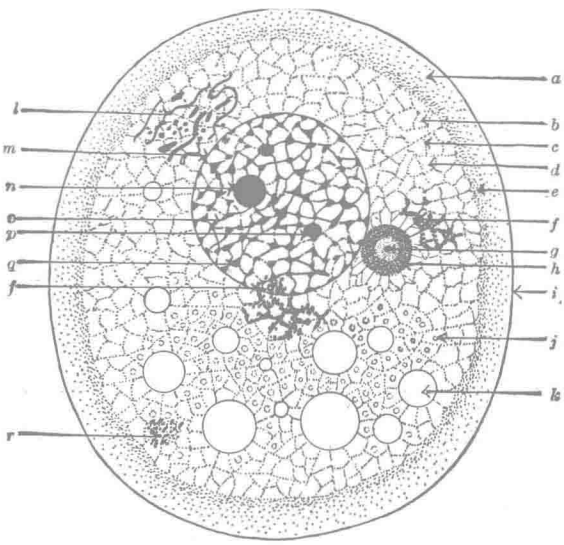

FIG. 4.—A GENERALIZED CELL.

a, exoplasm; *b*, endoplasm; *c*, spongioplasm; *d*, hyaloplasm; *e*, microsomes; *f*, chromidia; *g*, centrosome (centriole); *h*, centrosphere; *i*, cell membrane; *j*, deutoplasmic granule; *k*, fluid vacuole, or oil drop; *l*, mitochondria or plastosomes; *m*, nuclear membrane; *n*, nucleolus; *o*, linin; *p*, karyosome; *q*, chromatin (net knot); *r*, foreign inclusions, pigment, etc. (metaplasm).

chromatin (*lantanine*) and *basichromatin*. Linin and chromatin are regarded by some as different phases in the elaboration of the same substance. The nucleus includes, furthermore, usually one, frequently more, nucleoli. These do not grade into the nuclear sap, like the nuclear network, but are limited by a sharp line of demarcation. They may be achromatic, when they are known as *plasmosomes*, or they may take on chromatin, becoming *chromatin nucleoli*. It is uncertain whether the latter are identical in all cases with the karyosomes. The difference among nucleoli is more probably one of degree of abundance of chromatin. The nucleus is the metabolic organ of the cell; without a nucleus a cell may continue to live for a time, but it can neither grow nor undergo progressive differentiation. All changes in enucleated protoplasm are regressive, leading to death. The nucleus is also largely the reproductive center, as will be described below. The nucleolus

plays the rôle, among other possible functions, of a center of storage, perhaps also elaboration, of chromatin. Nuclear protoplasm, more especially the chromatin, is relatively rich in phosphorus.

Astral System.—Another organ of a typical cell is the aster, *astral system* or *attraction sphere*. Its substance is collectively known as *archoplasm*. It usually lies outside of, but close to, the nucleus; in certain cells it is intranuclear, *e.g.*, spermatocytes of Ascaris. It consists centrally of a granule, the *centrosome* (cytocentrum); in this, in certain instances, may be differentiated centrally a smaller granule, the *centriole;* when the latter appears, the more outlying portion of the centrosome is designated the *centroplasm*. The centrosome may divide into two, becoming a *diplosome*, or in some instances it may become multiple, when it is known as a pluricorpuscular centrosome. Surrounding the centrosome is a clearer, minutely granular sphere, the *centrosphere;* radiating from this peripherally are delicate astral rays, collectively known as the astrosphere (Fig. 6). Structurally the aster is subject to considerable variations in different cells. On account of its relation to cell division, it is regarded as the dynamic center of the cell; viewed thus its substance is known as *kinoplasm*. The attraction sphere may or may not be visibly present; in all living cells it, or its analogue, is generally believed to be potentially present.

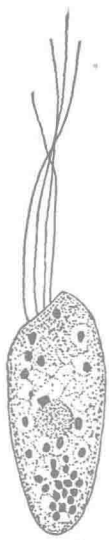

FIG. 5.—A UNICELLULAR FLAGELLATE ANIMAL (TETRAMITUS CHILOMONAS).

The nuclear material is distributed as granules throughout the cell. (Redrawn from Calkins.)

Cytoplasm.—The cytoplasm or *cytosome* may be divided into a thin peripheral or cortical layer of less granular protoplasm, the *exoplasm* (ectoplasm), and the main central mass, the *endoplasm*. In certain highly differentiated cells the exoplasm is not discernible. In others, at certain stages in the development it contains the products of differentiation, when it is known as "deuteroplasm" (Studnicka). The endoplasm is commonly described as consisting of a more fluid, finely granular ground substance, the *hyaloplasm* (*paraplasm, interfilar mass, paramitome, enchylema, cytolymph*), containing a delicate denser reticulum, or *cytoreticulum*, with polygonal or spheroidal meshes. The substance of the reticulum is called *spongioplasm* (*mitome; filar mass*). It is held by some to be continuous with the linin mesh of the nucleus. The granules of the ground substance, both free of and attached to the spongioplasm, are called *microsomes*. According to one interpretation the spongioplasm arises by coalescence of microsomes. A more recent interpretation regards both network and granule as simply more condensed portions of the hyaloplasm. The cytoplasm may contain, besides the aforementioned fundamental constituents, nutritive materials including yolk granules or globules (*deutoplasm*); vacuoles, foreign inclosures, *e.g.*, bacteria, etc., and pigment (*metaplasm*); *plastids* (in plant cells); *chromidia* (Fig. 7), masses of chromatic granules, presumably of nuclear origin, and probably the raw

material for certain differentiation products; *mitochondria* or *plastosomes; trophospongium; Golgi apparatus,* and *tonofibrils.*

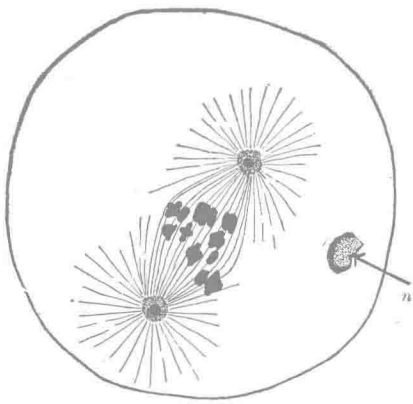

FIG. 6.

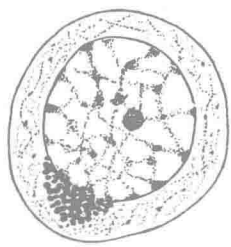

FIG. 7.

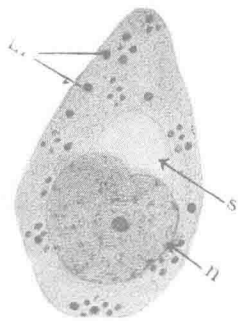

FIG. 8.

FIG. 6.—EGG OF A CLAM (CUMINGIA TELLINOIDES).

The first maturation spindle with centrosomes and chromosomes at metaphase, and the disappearing nucleolus (*n*) at the right. ×1000.

FIG. 7.—PRIMARY SPERMATOCYTE OF A TURTLE (CISTUDO CAROLINA).

Chromatic spherules (chromidia) apparently in process of extrusion from nucleus. × 1500.

FIG. 8.—SPERMATID OF OPOSSUM IN EARLY STAGE OF METAMORPHOSIS INTO A SPERMIUM.

Granular mitochondria; *m,* in the cytoplasm; *n,* nucleus; *s,* archoplasmic sphere. ×2000.

Mitochondria.—Mitochondria are cytoplasmic elements of very variable form and of almost universal distribution. These are destined to bulk very large in immediate cytological investigations. They may prove to be very important elements of the more fundamental protoplasmic structure and function. In the germ cells of vertebrates, as in undifferentiated cells generally, they are for the most part, granular (*chondriosomes*) (Fig. 8); in the somatic differentiated cells filamentous or rod-shaped (*chondriomites; chondrioconts; pseudochromosomes*) (Figs. 9, 10). Both chromidia and *trophospongium* (a canalicular network of the cytoplasm, probably concerned with circulation of nutritive material or secretion products) (Fig. 11) have been identified with mitochondria. Trophospongium at least is a distinct structure, and chromidia more probably also, though by some regarded as the elements from which the filamentous mitochondria are formed. Mitochondria have been credited with a great variety of functions, *e.g.,* formation of presecretion and excretion granules, and the formation of various kinds of fibrils. M. Heidenhain regards the chondriosomes as vegetative organs of the cells subserving metabolism. Our knowledge is as yet too limited to speak with assurance either as to their origin, complete function, or fate. One thing only is certain,

namely, that they are actual constituents of the cytoplasm of practically every type of cells, at certain, perhaps all, stages of development and active function. They

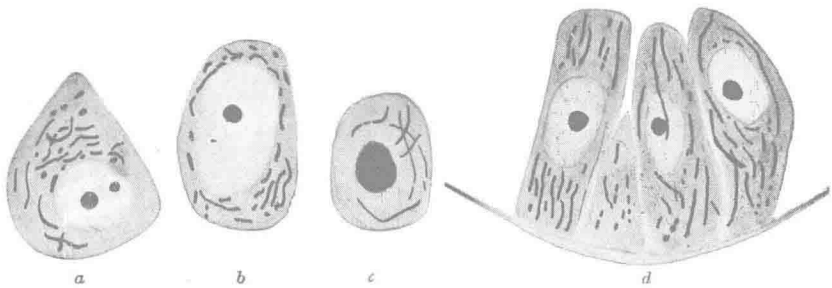

FIG. 9.—CELLS FROM THE NEWLY HATCHED RAINBOW TROUT, TREATED ACCORDING TO MEVES' TECHNIC FOR THE DEMONSTRATION OF MITOCHONDRIA (PLASTOSOMES).

a and *b*, cartilage cells; *c*, young blood cell; *d*, epithelial cells from the intestine. ×2000.

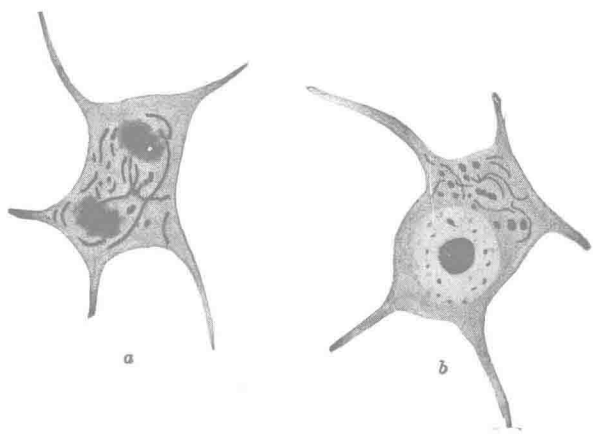

FIG. 10.—TWO CELLS FROM THE MESENCHYMA OF THE NEWLY HATCHED RAINBOW TROUT.

The one to the left (*a*) at late anaphase of mitosis, showing mitochondria (plastosomes). Meves' technic. ×2000.

have been seen and studied in living plant cells,[3] and in animal cells grown in artificial media they have been observed [4] to move, to change shape, to divide into granules and again to reunite into filaments—facts which render inadmissible their interpretation in fixed material as lipoid precipitation products (Faure-Fremiét), and strongly suggest their connection with metabolic activity.

Mitochondria have the chemical composition of a lipoprotein in which the protein part predominates. The lipoid fraction is largely phospholipid. They contain also an

[3] Maximow, 1908.
[4] Lewis, M. R., and Lewis, W. H., 1915.

appreciable quantity of ribonucleotides, and various enzymes and the vitamins A and C.[5] By virtue of hydrolytic and oxidizing enzymes they support the metabolic processes of the cell, especially in relation to the accumulation of fats and glycogen. Benda, Meves and Duesberg regard them as the cytoplasmic basis of heredity and ascribe to them an important rôle in histogenesis. Wallin [5a] regards them as symbiotic bacteria. Rods and granules described as mitochondria were probably actually bacteria.[5b]

FIG. 11.—INTRACELLULAR NETWORK, OR TROPHOSPONGIUM, WITHIN A PURKINJE CELL OF THE CEREBELLUM OF STRIX FLAMMEA.

Golgi's stain. (Golgi.)

Golgi Apparatus.—The *internal reticular apparatus of Golgi*, in "fixed" material, occurs typically in the form of a network (Golgi net) closely adjacent to or encircling the nucleus (Fig. 12). In the living cell stained with methylene blue the "Golgi apparatus" appears generally in the form of "a series of chromophilic vesicles each of which may encircle a colorless chromophobe." [6] The chromophobic portion is regarded as the "developing product." These Golgi vesicles (bodies), following fixation with osmic acid, may become modified through collapse and fusion into a reticular structure. Like mitochondria, Golgi bodies readily reduce osmic acid and assume a dark brown color. The Golgi apparatus is generally believed to be associated with the metabolic activity of the cell, especially with the secretory process and with the elaboration of fats and proteins. Claims have been advanced that the trophospongium of Holmgren (canalicular apparatus, Fig. 11) represents the negative image, in the form of empty canals, of the Golgi apparatus.[6a] The Golgi vesicles have also been identified with the "vacuome" of Parat, and the Golgi bodies (granules) with mitochondria. Recent evidence favors the conclusion of morphologic and genetic independence among Golgi apparatus, vacuome, trophospongium, mitochondria and chromidia.

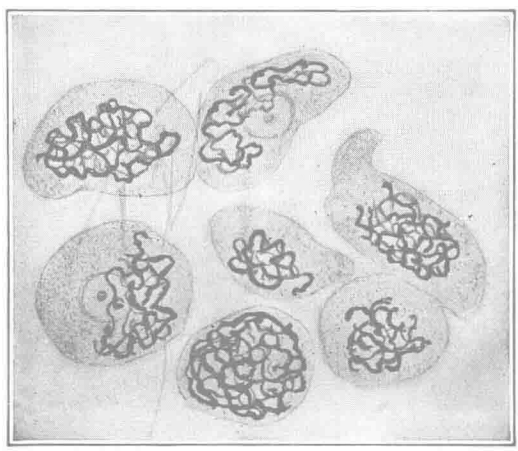

FIG. 12.—DECIDUAL CELLS OF HUMAN PLACENTA AT TERM.
Note the internal reticular apparatus of Golgi. (Vecchi.)

Tonofibrils.—The term tonofibrils ("inofibrils," Tello, Cajal) was introduced by M. Heidenhain to designate certain "supporting fibrils" in epithelial cells, very strikingly represented in the relatively wide and coarse intercellular bridges and their intracellular approaches in the prickle cell layer of the stratified squamous epithelium of human skin

[5] de Robertis, Nowinski and Saez, 1949; [5a] Wallin, 1927; [5b] Miller, 1937; [6] Whorley, 1944; [6a] Beams, 1931.

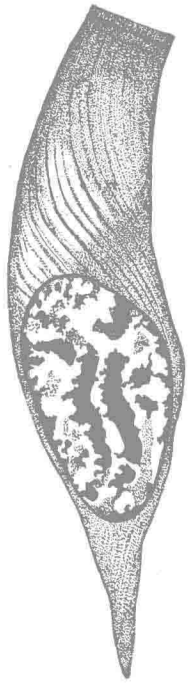

FIG. 13.—TONOFIBRILS IN EPITHELIAL CELL OF INTESTINE OF FROG. ×2300.

(Redrawn from M. Heidenhain.)

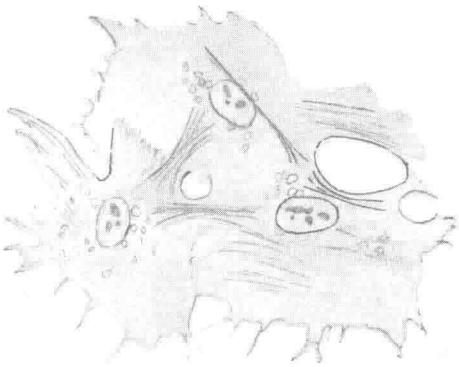

FIG. 14.—TONOFIBRILS IN EPITHELIAL CELLS OF 48-HOUR GROWTH FROM AMNION OF 5-DAY CHICK EMBRYO.

Mallory's stain. (Redrawn from M. Lewis.)

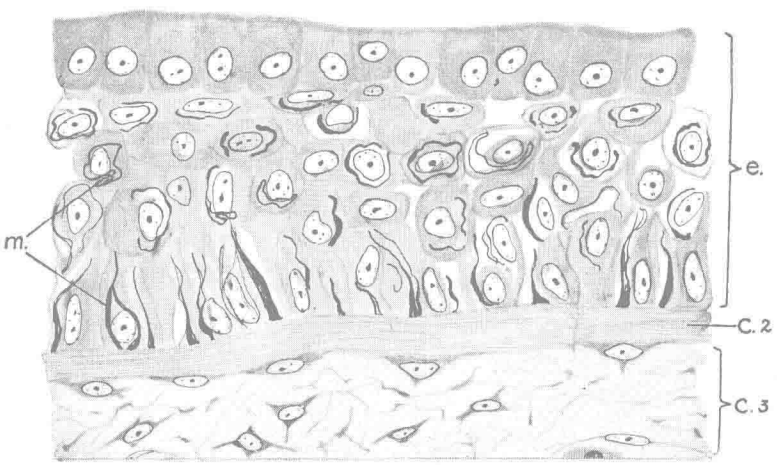

FIG. 15.—VERTICAL SECTION OF SKIN OF HIND LIMB OF FROG TADPOLE, SHOWING TYPICAL TONOFIBRILS (*m.*) IN THE BASAL CELL LAYER OF EPIDERMIS (*e.*). ×600. (Speidel.)

(Fig. 38). Such fibrils are widely present in epithelial cells under conditions requiring a certain degree of protoplasmic rigidity to prevent excessive deformation against factors of strain and pressure. They are most prominently disclosed with the iron hematoxylin staining technic. Good examples of tonofibrils are shown in the columnar cells lining the intestine of the frog (Fig. 13) and the squamous cells of the amnion of the chick (Fig. 14). They appear conspicuously also in the columnar cells of the basal layer of the epidermis in human skin (Fig. 276) where they simulate a striated or denticulated border. These coarse perpendicular basal fibers are apparently identical with those of the skin of certain frog tadpoles (Fig. 15), originally described by Eberth (1866) and since then variously interpreted as supporting elements,[7] mitochondria[8] and connective tissue processes.[9]

The concept of tonofibrils has been erroneously extended to include also the initial fibrils of fibroblasts,[10] in their coarser form identical with the fibroglia fibers of Mallory,[11] the primitive fibrils of leiomyoblasts and those of spongioblasts. These specific original fibrils of connective tissue cells, smooth muscle cells and neuroglia cells stain equally well with iron hematoxylin, but can be readily discriminated from true tonofibrils on the basis of a differential staining reaction in special technics and on the basis of their genetic relation to definitive reticulum fibrils, myofibrils and glia fibers, respectively. The very similar fibers ("rootlets") of certain ciliated cells (Fig. 16) are apparently analogous with tonofibrils, but have in addition to their function of providing rigidity to the cell as a whole also that of serving as a support for the lashing cilia. Furthermore, their mode of origin is very different from that of tonofibrils; they arise as intracellular sprouts from the basal bodies to which the cilia are attached. Columnar cells with nonmotile cilia, as in the case of the epididymis, are provided with tonofibrils identical with those of nonciliated cells. Bensley[12] makes the interesting suggestion that tonofibrils are irreversible products of a fundamental fibrous constituent of protoplasm which he designates "plasmosin."

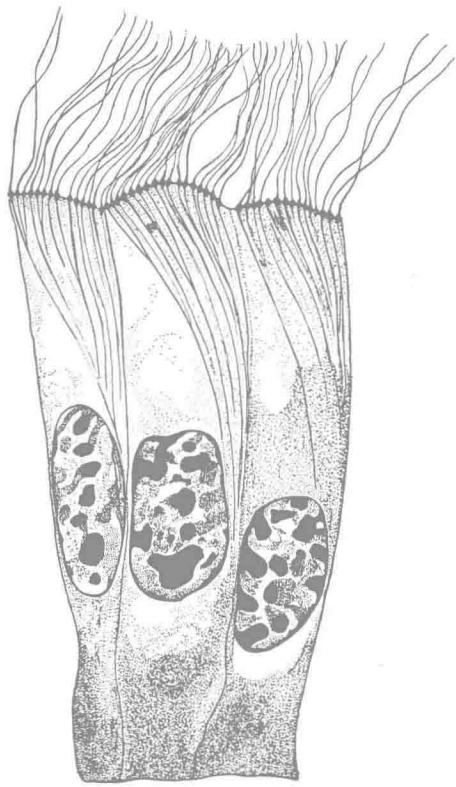

FIG. 16.—THREE CILIATED CELLS FROM THE BILE DUCT OF THE SNAIL, HELIX HORTENSIS.

The cells have a single row of basal granules, to which both cilia and rootlets are attached. ×2300. (M. Heidenhain.)

[7] Studnička, 1908.
[8] Saguchi, 1913.
[9] Weed, 1934.
[10] Maximow, 1929.
[11] Mallory, 1904.
[12] Bensley, R. R., 1938.