NATIONAL ACADEMY OF SCIENCES

FRANZ SCHRADER

1891—1962

A Biographical Memoir by

KENNETH W. COOPER

Any opinions expressed in this memoir are those of the author(s) and do not necessarily reflect the views of the National Academy of Sciences.

Franz Schrader

FRANZ SCHRADER

March 11, 1891–March 22, 1962

BY KENNETH W. COOPER

THE ONLY CHILD of Franz Schrader and Hedwig Dorothea Rohde, Schrader received his early schooling in the cloister of the magnificent Magdeburg Cathedral and the Magdeburger Bürgerschule. In 1901 he came to the United States with his mother, who was divorced from his father, and her second husband, Friedrich Wille, a prosperous specialist in mining enterprises. The family lived on Staten Island (the borough of Richmond, New York City), where Schrader attended grammar and high school. Left to his own devices, on that still unspoiled island he continued the natural history pursuits that had so delighted him on vacations with his father in the Harz Mountains. That zest for fieldwork, and especially for the natural history of insects and fish, never abated; it gave a unique and significant stamp to Schrader's cytological research.

Schrader attended Columbia University: first its School of Mines (1910–1912), at his stepfather's urging; then, yielding

Reprinted from *Dictionary of Scientific Biography*, Vol. 18, Supp. II, pp. 795–99, New York: Charles Scribner's Sons, entitled "Schrader, Franz [Otto Johann Wolfgang]."

to his own interests, Columbia College, from which he graduated (B.S., 1914). Following college and two summers (1915, 1916) as assistant in the Bureau of Fisheries at Woods Hole, Massachusetts, Schrader served in Minnesota as supervisor of fisheries for the U.S. Bureau of Fisheries (1916–1917). There he carried out investigations on the feeding behavior of mussels and on parasites of fish. In 1917 he returned to Columbia as assistant in zoology, completing his doctoral degree in 1919 under the preeminent cytologist Edmund Beecher Wilson. His dissertation, published in 1920, was a landmark contribution, for it proved for the first time that sex may be determined by haploidy or diploidy of a zygote; that fertilized females can produce male progeny parthenogenetically; and that these males, unlike their sisters, are fatherless, for their single set of chromosomes comes only from their mother.

After receiving his doctorate, Schrader was appointed chief pathologist of the U.S. Bureau of Fisheries in Washington, D.C., where he applied his cytological skills to an analysis of nuclear changes in oocytes that accompany the loss of fecundity of penned pike-perch. Though all went well in that post, he resigned in 1920—a pivotal year. That year Schrader accepted appointment as biological associate at Bryn Mawr College, and on 1 November he married Sally Peris Hughes, doctoral student under Wilson and lecturer at Barnard College of Columbia University, whose skills and interests in cytology and natural history matched his own.

At Bryn Mawr, Schrader's research was largely devoted to chromosomal problems of sex determination, an outcome of which was the comprehensive treatise *Die Geschlechtschromosomen* (1928). Remarkably, he found species of coccids that provided possible evolutionary intermediates between ordinary diploid species with sex chromosomes and haplo-diploid parthenogenetic species. In these coccids, one set of chromosomes of the diploid male undergoes heteropycnosis, leading, he surmised, to inactivity and ultimately to effective haploidy of the nominally diploid male. Schrader pointed out that all of one haploid set in these cases may be viewed as a compound X chromosome (an X chromosome consisting of more than one element), and all of the other set as a compound Y. On this basis a hypothesis for the evolutionary origins of haplo-diploid parthenogenesis was formulated (Schrader and Hughes-Schrader, 1931), a hypothesis that is still in the forefront though mistakenly attributed by some to M. J. D. White (1954).

In 1930, as had both Wilson and Thomas Hunt Morgan before him, Schrader left Bryn Mawr to become professor in the department of zoology at Columbia University, assuming the post vacated by Wilson at retirement. Again like Wilson, Schrader was named Da Costa professor (1949) in recognition of the world renown he had attained in chromosomal cytology. During his twenty-nine years at Columbia, Schrader served twice as executive officer (chairman) of the department of zoology (1937–1940, 1946–1949), as member of the National Research Council Fellowship Committee (1939–1943), as an editor of the Columbia Biological Series (1930–1962), as one of the founding editors of *Chromosoma* (1939–1962) and of *Journal of Biophysical and Biochemical Cytology* (later *Journal of Cell Biology*, 1954–1961), as member of the editorial boards of *Journal of Morphology* (1932–1935) and *Biological Bulletin* (1939–1954, 1959–1962), and as trustee of the Marine Biological Laboratory at Woods Hole (1934–1951). He was elected vice president of the American Association for the Advancement of Science and chairman of the Section of Zoological Sciences (1947), president of the American Society of Zoologists (1952), and member of the National Academy of Sciences (1951) and of the American Academy of Arts and Sciences (1953).

The man who gained these distinctions was of cosmopolitan outlook and aristocratic mien. Sensitive, perceptive, intuitive, with a penchant for fine foods and wines, game fishing, Near Eastern rugs, art, classical music, literature, pre-Columbian archaeology, and travel, he had exceptional social grace and was a delightful host. His research and the trips to the tropics it entailed were pursued as most satisfying pleasures. Critical, dispassionate in judgment, with a vast range of learning, regarding continuity with the past as a necessity, and, like Wilson, keenly interested in the diversity of chromosomal behavior, Schrader's publications were never trivial or given to polemics. Like his book *Mitosis*, they stand apart with their clear, engaging, and individual style, with full consideration of the findings and ideas of his forerunners.

From the age of twenty-four Schrader was intermittently troubled by a weakened heart. Nevertheless he made many field trips with his wife to Central America for specially sought species. Those out-of-the-way organisms made his (and Sally Hughes-Schrader's) work unique, and so it remains today. The 122 different species upon which he published over the years, representing four phyla and some 64 genera, nearly all so different from the common grist of cytological research, added greatly to what is known of the diversity of chromosomal behavior in somatic and meiotic mitoses.

Schrader's research at Columbia may arbitrarily be viewed as comprising two periods of emphasis: 1932–1953, interrelations of spindles and chromosomes, and—overlapping the former—1945–1961, the diversity of meiotic systems, comparative cytochemical studies, and evolutionary considerations of DNA content of nuclei among related species and genera, all of which he interrelated.

The regular occurrence of very strange yet functional spindles at meiotic mitoses of some coccids he had investigated (monopolar spindles in *Pseudococcus*, tubular spindles within which chromosomes are aligned in single file in *Protortonia*), as well as the remarkable compound spindles discovered by Hughes-Schrader, diverted Schrader from problems of sex determination to an extensive research and review of spindles and the relations between chromosomes and spindles. One outcome of that preoccupation was his widely influential book *Mitosis* (1944; 2nd ed., 1953), which placed what was known of these subjects under searching analysis and offered new directions for research on chromosomal movements.

In 1930 it was generally believed that mitotic spindles are real entities, of short half-life, that originate independently of chromosomes yet are necessary for their movements. Since spindles of healthy, living cells appear nearly optically homogeneous, the fibrous structure that appears within spindles when cells become moribund, or are fixed, was widely regarded as artifactual, especially by physiologists. However, on the basis of his study of the consistency of paths taken by the fibrous components of spindles in fixed cells (1932), and on the results of his carefully controlled centrifugation experiments with living cells (1934), Schrader concluded that spindles in living cells do indeed have a fibrous structure, albeit an invisible one. In bipolar spindles he described these fibrous arrays as consisting of(1) those running from a spindle pole to each chromosome or chromatid, namely, chromosomal fibers or half-spindle components; (2) continuous fiber systems from pole to pole; and, in some organisms (3) interzonal fibers of quite different nature connecting the ends of separating chromatids at anaphase. Final proof of the validity of Schrader's conclusions came with Shinya Inoué's remarkable time-lapse motion pictures of cells undergoing consecutive mitoses, taken by means of Inoué's vast improvement of polarization optics. In these now classical films, first widely shown to audiences in 1949, the strikingly birefringent groups of chromosomal and continous "fibers" stand out for all to see.

Before Schrader's studies of mitosis, most took for granted that the relation of spindles to chromosomes is fundamentally the same throughout eukaryotic organisms, and that spindles play the determining role in mitosis. However, both Schrader and Hughes-Schrader had described clear instances in which it is the chromosome that determines development of the spindle. Furthermore, Schrader had shown in *Pseudococcus* that the state of a chromosome can be critical in the formation of a spindle. In Schrader's view, nonchromosomal spindle initiators and chromosomes are clearly interactive and may show various degrees of predominance at certain developmental stages and in certain cells.

Schrader (1935) contrasted those spindle "attachments" located at a fixed point on a chromosome, or localized kinetochores of complex morphology and common to most organisms, with holokinetic (or "diffuse") kinetochores first discovered in homopterous and heteropterous bugs. The diffuse kinetochore is of no known special morphology, the chromosome appearing to have spindle fibers normal to its entire poleward surfaces. These two sorts of kinetochores appear to be mutually exclusive, for all chromosomes of an organism's complement in a given cell have either localized or diffuse kinetochores. The properties that Schrader described imply that all, or nearly all, fragments of holokinetic chromosomes, unlike all but one of those of a chromosome having a localized kinetochore, should be capable of spindle fiber association and undergoing mitosis. That holokinetic chromosomes do indeed have that property was first proved by Hughes-Schrader and Hans Ris (1941).

The discoveries and their interpretation by Schrader are now regarded as expressions of fundamental properties of chromosomes in relation to spindles. Chromosomal "spindle fibers" have been shown to have their physical basis in ultramicroscopic microtubules, along with associated molecules, which in some cells appear to be formed first in fibrous arrays at kinetochores, and in others at future spindle poles or centrosomes. The distinctions between holokinetic and localized kinetochores are borne out by electron microscopy, but the evolutionary relationship between the two remains a Gordian knot. Finally, as Schrader predicted, the main advances in the resolution of these problems are now being made physicochemically.

Unlike the seminal contributions made by Schrader to sex determination, mitosis, and chromosome structure, his other studies have not been so readily assimilated or assimilable. Cyril D. Darlington's "precocity theory" (1932) was the prevalent cytogenetic theory, an eclectic one ingeniously constructed but not from wide-ranging comparative cytology. It imposed rules of behavior upon chromosomes, a behavior guaranteed to conform to classical genetics, which is based on few kinds of organisms. If chromosomal behavior could not be fitted to the "rules," it was ignored. Despite those cardinal inadequacies, in Schrader's time Darlington's theory dominated cytological work on meiosis, and Darlington's following among geneticists and cytologists was immense.

A chain of relations is required under Darlington's theory for segregation at meiosis, with failure at any link automatically resulting in random assortment of chromosomes. That chain is as follows: precocious onset of prophase $\subset$ synapsis $\subset$ crossing-over (chiasma formation) $\subset$ conjunction as bivalents ⊂ segregation. From his very early work (1923) to nearly his last (1960), Schrader had found unassailable cases in many diverse organisms in which segregation occurs despite failure of synapsis in some, of chiasmata in others, and of bivalent formation in still others. What is more, molecular geneticists proved that the first meiotic prophase is not "precocious," as Darlington's theory requires, for chromosomal DNA is doubled before synapsis; the theory in its original form has thus collapsed. However, its former adherents now hold crossingover, which they equate with chiasmata, to be the sine qua non of conjunction and segregation, so most of Schrader's demonstrations of the remarkable diversity of meiotic phenomena among some forty organisms remain unassimilated by current cytogenetic theory, and accordingly are ignored by most.

Schrader's 1945–1960 studies of meiosis in what he called the "harlequin lobe" of the testes of twenty-one tropical or semitropical pentatomid bugs bear importantly on the complexity of meiosis. In that special lobe in each species, there occurs a species- or genus-specific, fantastic distortion of meiosis, wholly unlike the regular meioses in cells of the other testicular lobes. In all of these species highly aneuploid spermatozoa result that no longer can have an ordinary gametic function at fertilization. In some, only the sex chromosomes undergo their customary meiotic maneuvers and segregate. Autosomal behavior is exceptional in all, variously but regularly—according to species—involving combinations of asynapsis, desynapsis, chain formation, clumping, lateral displacement on the spindle, non-random segregation, and so on. Differentiation of the harlequin lobe in related species has evidently brought about different uncouplings of events of normal meiosis that are both numerous and complex, and regular in their consequences.

The harlequin lobe phenomena therefore are hightly significant, for, side by side, they present an aberrant meiosis and the normal meiosis from which it was derived.

Schrader believed that theoretical resolution of these and other problems would require painstaking comparative physicochemical investigation of the astonishing variety of cytological conformities and nonconformities. Accordingly he welcomed T. Caspersson's introduction of cytochemical tests quantifiable by photometry. With Cecile Leuchtenberger (1946–1956) and others, Schrader carried out a variety of photometric studies on DNA content of cells in relation to quantities of RNA and protein, on infertility in man and in dwarf bulls, on development of nebenkern and acrosome, and on apparent exceptions to DNA constancy.

Of this series, several studies of pentatomid bugs by Schrader and Hughes-Schrader (1956,1958) are specially notable. A study of six species of *Thyanta* showed that five species, like the majority of pentatomids, have six pairs of autosomes; the sixth species, *T. calceata*, however, has twelve pairs. Remarkably, all six species have "a surprising uniformity in nuclear content of DNA." This unexpected state of affairs is accounted for by assuming that pentatomid chromosomes are polytenic, and that a longitudinal, equal separation of strands of each autosome doubles the number of autosomes without increasing the total amount of DNA per nucleus. Somewhat more complicated, but similar, relations among ten species of *Banasa* are also interpreted in terms of polyteny and "chromatid autonomy"—attributes that are suggested to have played important roles in chromosomal evolution.

The notion of polyteny of mitotic chromosomes of course flies in the face of the widespread belief that chromatids of all mitotically competent chromosomes are composed of but one bineme of DNA. The explanation given by the

Schraders to these and still other cases is not the only possible one, but the chief basis today for rejecting their hypothesis lies in the fact that it is counter to widespread belief. That dogma, however, is not based on widespread investigation; rather, it depends upon analyses of chromosomes of a very limited range of organisms. In any case, the findings for *Thyanta* and *Banasa* are of such potential significance regarding both chromosome structure and evolution that it is to be hoped that these cases will be reinvestigated with molecular methods.

At retirement as Da Costa professor emeritus in 1958, Schrader was invited to Duke University as visiting professor and Hargitt Fellow, privileges he gladly accepted and much enjoyed. His last research (1960–1961) was published from Duke's laboratories, continuing with characteristic gratification his exploration of harlequin lobe meioses as well as an experimental study of the properties of holokinetic chromosomes and their fragmentation products at meiosis. In 1961 the editors and publisher of *Chromosoma* presented him with a Festschrift. He died in the following year of renal neoplasia, and Sally Hughes-Schrader—whose last research paper was published in 1983 (at age eighty-eight)—died in 1984. They were a remarkable pair of outstanding cytologist-naturalists.

SELECTED BIBLIOGRAPHY

I. ORIGINAL WORKS. A list of Schrader's publications is in *Journal of Cell Biology*, **16**, no. 3 (1963), xvi–xix, to which must be added a posthumously published article, translated into German by W. E. Ankle: "Edmond Beecher Wilson, 1856–1939," in *Geschichte der Mikroskopie, Leben and Werk grösser Forscher.* 1. *Biologie* (Frankfurt am Main, 1963).

Those cited in the text are "Sex Determination in the White-Fly (*Trialeurodes vaporariorum*)," in *Journal of Morphology*, **34** (1920), 267–305; "A Study of the Chromosomes in Three Species of *Pseudococcus*," in *Archiv für Zellforschung*, **17** (1923), 45–62; "Haploidy in Metazoa," in *Quarterly Review of Biology*, **6** (1931), 411–38, with Sally Hughes-Schrader; *Die Geschlechtschromosomen* (Berlin, 1928); "Recent Hypothesis on the Structure of Spindles in the Light of Certain Observations in Hemiptera," in *Zeitschrift für wissenschaftliche Zoologie*, **142** (1932), 520–39; "On the Reality of Spindle Fibers," in *Biological Bulletin*, **67** (1934), 519–33; *Mitosis: The Movements of Chromosomes in Cell Division* (New York, 1944; 2nd ed., 1953); "Polyploidy and Fragmentation in the Chromosomal Evolution of Various Species of *Thyanta* (Hemiptera)," in *Chromosoma*, **7** (1956), 469–96, with Sally Hughes-Schrader; "Polyteny as a Factor in the Chromosomal Evolution of the Pentatomini (Hemiptera)," ibid., **8** (1956), 135–51, with Sally Hughes-Schrader; "Chromatid Autonomy in *Banasa* (Hemiptera: Pentatomidae),"ibid., **9** (1958), 195–215, with Sally Hughes-Schrader; "Cytological and Evolutionary Implications of Aberrant Chromosome Behavior in the Harlequin Lobe of Some Pentatomidae (Heteroptera)," ibid., **11** (1960), 103–28; "Evolutionary Aspects of Aberrant Meiosis in Some Pentatominae (Heteroptera)," in *Evolution*, **14** (1960), 498–508.

American Men of Science, III–VI (New York, 1921–1938), VII–IX (Lancaster, Pa., 1944–1955), and X (Tempe, Ariz., 1960), lists memberships not cited here or in the 1963 account (below). Schrader was starred in the fifth (1933) through seventh editions as among the 150 most eminent zoologists. He strongly objected to starring, and the practice was dropped with the eighth edition. See his "Stars in the Biographical Directory of American Men of Science," in *Science*, **85** (1937), 360.

Insight into Schrader's values, attitudes, and personality may

be gained from his "Edmund Beecher Wilson—Scientist 1856–1939," in *Columbia University Quarterly* (1939), 218–24, which, unlike his posthumous article of 1963, is addressed to a general audience.

II. SECONDARY LITERATURE. On Schrader's life and work, see Kenneth W. Cooper, "Franz Schrader, 1891–1962," in *Journal of Cell Biology*, **16** no. 3 (1963), ix–xv; and Donald E. Lancefield, "Franz Schrader," in *Biological Bulletin*, **125** (1963), 9–10. There is much of interest in Kenneth R. Manning, *Black Apollo of Science; The Life of Ernest Everett Just* (New York, 1983); the episodes and anecdotes relating to Schrader (which are indexed) came directly from Sally Hughes-Schrader or were verified by her. Schrader's "scientific pedigree" is diagrammed by A. H. Sturtevant in *A History of Genetics* (New York, 1965).

Citations in the text to authors other than Schrader are Cyril D. Darlington, *Recent Advances in Cytology* (London, 1932; 2nd ed., 1932; repr. 1965); Sally Hughes-Schrader, "Chromosomal Segregational Mechanisms in Ant-Lions (Myrmeleontidae, Neuroptera)," in *Chromosoma*, **88** (1983), 256–64, and "The Diffuse Spindle Attachment of Coccids, Verified by the Mitotic Behavior of Induced Chromosome Fragments," in *Journal of Experimental Zoology*, **87** (1941), 429–56, with Hans Ris; Shinya Inoué, "Studies of the Structure of the Mitotic Spindle in Living Cells with an Improved Polarization Microscope" (Ph.D. diss., Princeton University, 1951); for reproduction of frames from his motion picture, see Inoué's "Polarization Optical Studies of the Mitotic Spindle. I. The Demonstration of Spindle Fibers in Living Cells," in *Chromosoma*, **5** (1953), 487–500; M. J. D. White, *Animal Cytology and Evolution*, 2nd ed. (Cambridge, 1954). Festschrift articles appeared in *Chromosoma*, 12, no. 1 (1961) and were privately presented as a bound volume entitled *Franz Schrader sum 70. Geburtstag gewidmete Arbeiten. . . .*