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RICHARD BENEDICT GOLDSCHMIDT

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A Biographical Memoir by

CURT STERN

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RICHARD GOLDSCHMIDT left not only a published record of nearly sixty years of scientific activities but also a full autobiography and a detailed sketch of his life written in fulfillment of the traditional request of the National Academy of Sciences. In addition, he preserved many letters which he had received from colleagues all over the world and deposited them in the archives of the Library of the University of California at Berkeley. It would be possible to reconstruct a large part of the development of the biological sciences in the twentieth century on the basis of Goldschmidt's publications and their interaction with his contemporaries. It would also be possible to explore in depth the personality of the man as it was formed through the impact of his time. These may be worth-while tasks for future historians. The present Memoir can present only a selection out of the multitude of his activities.

Richard Goldschmidt was born on April 12, 1878, in Frankfurt am Main, Germany. He died in Berkeley, California, on April 24, 1958. His parents came from respected, prosperous local families and the circle of his relatives included an unusually large number of well-known scientists, bankers, and philanthro-

The final form of this Memoir owes much to the critical comments of F. Baltzer, E. Caspari, E. Hadorn, H. Nachtsheim, Leonie Piternick, J. Seiler, and Evelyn Stern. Th. Bullock and R. B. Clark provided evaluations of Goldschmidt's early work on the nervous system of Ascaris, and the late F. Schrader on some of Goldschmidt's cytological investigations.

pists. In his own words, he grew up in "a typical German bourgeois family, comfortable but strict and even parsimonious in spite of cooks, nursemaids and French governesses." The city itself had a proud and distinguished history and provided an atmosphere of rich interest in all cultural pursuits. Simultaneously it was democratic in spirit. There he attended the Gymnasium with its curriculum of nine years of Latin, French, and mathematics and six years of Greek as the nucleus of education. The young boy was a voracious reader: world literature, Goethe, prehistory, archaeology, and comparative linguistics were the major areas. When he was thirteen years old he began to see himself as a future naturalist and world traveler and, three years later, the center of his interest permanently became biology. At seventeen he could read rather fluently French, English, Italian, Latin, and Greek and made abundant use of these abilities. He also tried to read the works of philosophers from Spinoza to Nietzsche, but confesses that he did not succeed in understanding them then or later.

When he entered Heidelberg University he enrolled at his parents' request as a medical student. Among his "glorious teachers" were such historical figures as Bütschli, the zoologist, Gegenbaur, the comparative anatomist, and Kossel, the biochemist. After two years of study he passed his premedical examinations and then went to Munich. At this point he abandoned further medical training and became a student of zoology under Richard Hertwig, with minors in botany, physiology, and paleontology. At the age of twenty-one he completed his first paper, a detailed account of developmental features in a tapeworm, the result of a chance finding during course work. Shortly he returned to Heidelberg where he became laboratory assistant to Bütschli, his beloved teacher and later lifelong friend. Under him he worked out his Ph.D. thesis on maturation, fertilization, and early development of the trematode Polystomum.

For a year the progress of Goldschmidt's zoological research was interrupted by the compulsory period of training in the German Army. When he returned to civilian life he followed an invitation from Richard Hertwig to join his staff at Munich, remaining there until 1914.

The first seven years of this period show Goldschmidt as the intense worker which he remained throughout his life. However, in contrast to his later periods he had not yet found a great central problem for his studies. Instead he tried his hand—and brain—at histology and neurology, cytology and protozoology, embryology and a monographic treatment of the anatomy of the "Amphioxides stages" of the lancelets. This was no mere dabbling. Although some of his publications at this time were but short reports on random findings made during his brief visits to the Mediterranean marine laboratories of Naples, Villefranche, Banyuls, and Rovigno, many were detailed accounts of elaborate studies. The most impressive of these is the sequence of papers on the nervous system of the parasitic roundworm Ascaris. It was Bütschli who suggested to Goldschmidt the study of the histology of the nematodes and particularly their nervous system. Goldschmidt discovered that in Ascaris this system is composed of a fixed, relatively small number of cells, 162 in the male and 160 in the female. He set himself the task of establishing the topography and the interrelations of every one of these cells, by making dissections and reconstructions from microtome sections. Altogether between 1903 and 1910 more than 350 printed pages were given to the results, accompanied by numerous text figures and nearly 20 plates, all drawn by the author. One cannot but admire the patience, the persistence, and the thoroughness with which these observations were made and put on paper. Some of the illustrations give fine details of cytologic and histologic nature; others, on folded charts of up to 65 × 37 cm, depict the paths of nerve fibres in a manner resembling the intricate system of a railroad switchyard. These studies find no equal in our knowledge of the nervous system of any other invertebrates. Unfortunately, they have borne no fruit as a basis for physiological investigations. For one reason, Goldschmidt's description of the interconnections of the nerve cells does not provide a picture of the probable routes of conduction of impulses between the sensory and motor elements; in any case, the parasitic nature of Ascaris did not seem favorable to experimental work. It is not known either how many of Goldschmidt's findings would stand up to a reinvestigation. While they were in the process of publication, they found support in the work of Martini, who confirmed and expanded Goldschmidt's discovery of cell constancy of various organs in nematodes. On the other hand, a special study of the nervous system of Ascaris by Deineka came in part to very different results. Goldschmidt responded vigorously to Deineka's publication and its defense by Dogiel, Deineka's teacher, accusing the St. Petersburg authors of having stained indiscriminately all kinds of tissues and then having regarded them all as parts of the nervous system. It is the belief of modern surveyors of the literature that Goldschmidt was probably much closer to the truth than his adversaries, but only new original studies can decide the issue. It may be added that the Ascaris work gave Goldschmidt occasion to make histological findings beyond those reported here, to participate in the discussions of the validity of Cajal's neurone theory, and to apply Koltzoff's principle of the necessity of cellular fibrils as a skeletal basis for the morphology of nonspherical cells.

The series of papers on the Amphioxides cover very different ground. Perhaps still under the influence of the comparative anatomists of his student days, Goldschmidt asked to be entrusted with the material of acrania which the German Deep Sea Expedition of 1898-1899 had collected in southern oceans. In 1905 he submitted the results of his work in a monograph of nearly 100 quarto pages and 10 plates of illustrations. One half of the work gives the details of the anatomy and histology of his forms, the other half a thorough analysis of the development of Amphioxus and the phylogenetic implications of the findings on Amphioxides. Among his various specific discoveries Goldschmidt himself ranked highly those of the solenocytes in an excretory organ of the animal, strangely enough unaware that this important cellular feature had already been described some years earlier by Goodrich who had found it in the kidney tubules of living specimens. Nevertheless, Goldschmidt's independent recognition of the annelid-type nature of the excretory organs, made on specimens which had not been too well fixed when they were collected, is testimony both to his powers of observation and to his powers of interpretation.

The 1905 monograph discusses carefully the question whether the Amphioxides really represents an independent, more primitive, or neotenic group of acrania than Amphioxus or whether they are developmental stages of Amphioxus itself. Goldschmidt originally decided in favor of taxonomic independence but, soon afterwards, on the basis of a new find recognized that his material belonged to Amphioxus. Until 1909 he added new observations on the Amphioxides forms. In 1933, after a brief stay at the Bermuda Biological Station, he returned once more to them.

While the work on Ascaris and Amphioxus was a late fruit of nineteenth-century interests, the third main area of young Goldschmidt's studies belonged directly to his time. The great discoveries of the last decades of the past century on chromosomes, mitosis, maturation, and fertilization had also made apparent the existence of many unsolved fundamental problems. Many of the outstanding biologists therefore were active in cell research and Goldschmidt joined their ranks. Two aspects attracted his attention, the chromidial apparatus of protozoan and metazoan cells and the problems of meiosis. In 1902 Richard Hertwig had published an interpretation of his observations on the presence of numerous granules in the cytoplasm of Actinospherium and other protozoa. Since these granules stained similarly to the nuclei, he assumed that they were nuclear equivalents, arising from well-formed nuclei, in some cases by breakdown, in others by being extruded from intact nuclei. In their turn, the chromidia, as the granules were called, supposedly could give rise to well-formed nuclei. Goldschmidt studied chromidial elements in the flagellated amoeba Mastigella, in the tissue cells of Ascaris, and in the so-called yolk nucleus, a cytoplasmatic element of the egg cells of spiders and other animals. He believed that he could trace the extrusion of chromidia from the nucleus, observed variations in the extent of the chromidial apparatus in relation to the functional state of cells, and devised a comprehensive theory to account for his own and a variety of other findings.

The chromatic material of all cells was assumed to consist of two kinds: that concerned with the metabolic functions and that concerned with the reproductive functions, trophochromatin and idiochromatin. We now know that the chromidial apparatus was a concept which encompassed in a single term a great many essentially different kinds of cytoplasmatic elements such as mitochondria and Golgi bodies and, in some protozoan cases, even intracellular parasites. Nevertheless, the similarity of the concept with modern knowledge of the derivation of cytoplasmatic RNA from the DNA of the nucleus is not just an analogy. The recent insights were foreshadowed by the work of Goldschmidt and a host of followers. Goldschmidt himself watched with keen interest the cytochemical and fine-structural investigations of the 1940s and 1950s. With his last Ph.D. student, T. P. Lin, he described in 1947 the Feulgen staining properties of the end parts of the Ascaris chromosomes which are, as is well known, left behind in the cytoplasm during the mitoses of the future somatic cells of the embryo.

Goldschmidt's doctoral dissertation had dealt with oögenesis and other cytological phenomena in the trematode Polystomum. In order to broaden his observations he soon turned to other trematodes: *Zoogonus mirus* (1905) and *Dicrocoelium lanceatum* (1908). In Zoogonus, he saw a most remarkable phenomenon, the reduction of the diploid chromosome number to the haploid in a single division by simple migration of one half of the chromosomes to one pole of the spindle and of the other half to the other pole. None of the elaborate chromosomal maneuvers which occur in the meiotic prophases of other organisms were seen. The term "Primärtypus" of reduction was coined for the newly discovered process, which corresponded completely to Weismann's prediction of chromosome reduction. Dicrocoelium was studied in the hope of encountering the primary type in this form also, but to his disappointment Goldschmidt found its oögenesis to be of the standard type.

The Zoogonus paper led to a dramatic sequence of events which may be reported in the words of a letter to the author (March 25, 1960) by the late Franz Schrader:

"The Zoogonus case was at one time very close to me because, as you may not remember, after Goldschmidt I was the next man to claim that meiotic reduction may sometimes occur without a preceding series of pairing maneuvers. So far as Goldschmidt was concerned, his arguments concerning Zoogonus represented one of those intellectual premonitions of which he had so many. . . . One must not forget that when Goldschmidt, in 1905, claimed to have a case of 'Primärtypus,' the cytologists and geneticists had barely succeeded in establishing the regularity of the meiotic process; any one who tried to upset the applecart again was regarded as nothing less than a fool or a criminal.

Hence Goldschmidt's conclusions were opposed by all the powers that ruled the roost, among them the Schreiners and Grégoire.

"It was almost fatal to make a little mistake therefore, and G. [Goldschmidt] did make such a mistake; he miscounted the chromosome number of Zoogonus.

"But the Schreiners, who proceeded to annihilate him, made an even bigger error in their counts and, for the rest, were so prejudiced that their analysis of the meiotic prophase doesn't mean much.

"Grégoire finally established the right chromosome number, but he too was so biased that his view of the synapsis period is anything but final.

"When, in 1911, Wassermann began to reexamine Zoogonus, he concluded that Grégoire had been correct about the chromosome number but that there is something funny in the prophase that Grégoire had misinterpreted. But Wassermann never really cleared up the case which therefore still stands in abeyance."

It remains to be added that Goldschmidt had made his original slides available first by request to the Schreiners and then on his own initiative to Grégoire so that the divergent findings were based on the same material, in some instance on the same individual cells. In their criticism of Goldschmidt the Schreiners had attempted to remain within bounds but Goldschmidt's reply exceeded, in sharpness, aggressiveness, and denunciation, perhaps all other scientific controversies at a time which was rich in personal invective. It must be admitted, however, that the allegation that he was unable to distinguish 10 from 26 chromosomes not only deeply hurt Goldschmidt personally but also endangered greatly his future career as a young scientist. His relation to Grégoire remained on a different level. When the latter wrote to him of his own interpretation Goldschmidt answered that, after renewed examination of the slides, he had to stand by his original views. However, spontaneously he once more sent Grégoire his material with the authorization to publish the divergent results. Grégoire in his paper acknowledged these facts with the following sentence: "C'était mettre le comble à l'amabilité et au desintéressement scientifique."

The year 1910 terminated the first period of Goldschmidt's biological work. However, a somewhat later paper belonging to his studies in genetics will be reported here, since it resembles the Zoogonus episode in committing a serious mistake.

In 1911 de Vries published the results of his investigations on the hybrids of *Oenothera biennis* and *O. muricata,* results which, in Goldschmidt's words, belonged to the most peculiar phenomena uncovered by hybridization studies and which caused the greatest difficulties for a deeper understanding. It is not necessary here to describe de Vries's discoveries. Suffice it to say that Goldschmidt conceived an explanation of them which was as ingenious as unexpected. He assumed that in these species crosses the maternal nucleus of the fertilized egg cell degenerates and that development proceeds solely on the basis of the paternal nucleus. This assumption of "merogony" was subject to test and Goldschmidt proceeded to furnish it. At his request Renner, his younger colleague in the Department of Botany, repeated de Vries's crosses and provided the necessary stages for the cytological study made by Goldschmidt. The examination seemed to bear out his theory completely. He adduced various observations in its favor, the most decisive of which was the finding of the haploid chromosome number 7 in the cells of early hybrid embryos in contrast to the diploid number 14 in normal embryos. In spite of his pleasure in proving his theory correct Goldschmidt must have felt that the evidence which he provided was less conclusive than he had persuaded himself to believe, for he asked Renner to study the cytology anew. A year later Renner demonstrated, and Goldschmidt agreed, that grievously incorrect observations had been made, that the hybrids had 14 chromosomes like the normals and not 7, and that there was no indication of merogony.

In a draft of his autobiography, Goldschmidt refers to his Oenothera work as the single instance of which he had reason to be ashamed. "There is an excuse: at that time I was so overworked that I should not have written anything, had I been wise. But as I was not wise I had to suffer for years, when I realized what I had done." In 1916 he attempted to show the possibility that the hypothesis of merogony in slightly changed form had still a chance of being correct. Soon, however, the solution of the Oenothera riddle came from a very different approach, primarily thanks to Renner who had entered the field on the stimulus provided by Goldschmidt. In the printed list of the latter's "Publications 1900-1954" the two merogony papers cannot be found.

When one looks back at Goldschmidt's accomplishments between 1900 and 1910 one finds that the young scholar had achieved a highly prominent place in his field. He had enriched zoological knowledge by many discoveries based on an astonishing amount of hard and detailed work and had provided stimulating hypotheses and theories in various biological areas. Although he had made some serious mistakes and his position was not unequivocal, his influence was felt widely. Moreover, at the age of twenty-nine he had founded the *Archiv für Zellforschung,* which under his editorship instantly became a most important, if not the most important, international center for publications in cytology. He had also written a pioneering textbook of genetics, first to appear in 1911, which constituted a brilliant, highly original achievement. In Hertwig's institute he had been promoted stepwise to the Associate Professorship, had given lecture courses and supervised laboratory instruction, and had become the leader of a school of advanced students from all over the world.

It was during this decade that Goldschmidt was married to Else Kühnlein. Their two children, Ruth and Hans, were born in 1907 and 1908 respectively. These happy personal events found their echo in the publication of two small popular volumes, one on the protozoa and one on reproduction in the animal kingdom. The royalties for these books paid for the expenses connected with the birth of the children. Ruth later became a physician, Hans an engineer.

It was natural for an ambitious young biologist of the new century not to be satisfied permanently with purely descriptive work. In 1909, therefore, he turned to genetics, "influenced considerably by the logical and dissecting presentation of this then novel field" as given in Johannsen's *Elemente der exakten Erblichkeitslehre,* published in that year. The choice of his own experimental material was suggested by a study of the Swiss entomologist Standfuss's experiments on moths carried out mostly before the rise of genetics. Goldschmidt selected two problems, one in evolutionary genetics, the other in the area of sex determination. The first made use of the nun-moth *Lymantria monacha,* which furnishes one of the classic examples of so-called industrial melanism, the spread in historic times of melanic phenotypes particularly in areas of large-scale industrial activity. In the course of six breeding seasons Goldschmidt studied the genetic situation which distinguishes melanic from nonmelanic forms. After extrinsic delays the results were published in 1921. Goldschmidt not only gave the Mendelian analysis but discussed in astonishing depth its evolutionary implications. By applying the mathematics of the Hardy-Weinberg law (then still unnamed and hardly recognized in its importance) he showed that mutation pressure alone was unable to account for the observed increase of melanism unless demonstrably impossibly high mutation rates were assumed. He concluded that in industrial regions unknown physiological advantages were correlated with the possession of melanism. That the selective advantage of melanism consists in the protective coloration of the phenotype, as has been shown in recent years, was too naïve an explanation for the thinking of the somewhat disillusioned evolutionists of the times. The paper on the nun-moth aroused little attention, undoubtedly because it was greatly ahead of its time and because its author did not pursue the topic much further. It is a testimony to the agility of Goldschmidt's mind that this paper shows him as a pioneer in population genetics, by using a method which was original and yet not close to his own way of thinking.

The problem of sex determination was an object of much study in Hertwig's laboratory. There it proceeded mostly on the basis of non-Mendelian approaches. Goldschmidt decided to analyze it by means of crosses of different species or races, led by a statement of Standfuss's that abnormal sex types frequently appear in such hybrids. He tried a variety of forms, among them the gypsy moth *Lymantria dispar.* In crosses of a European with a Japanese race he obtained in F_1 normal males but instead of typical females, sex intergrades. Goldschmidt later called it "an unbelievable piece of luck" that he happened to have had available two races which would give this result although a great many other racial hybrids of Lymantria consist of the normal sexes only. One may disagree with this opinion. Goldschmidt's restless large-scale activities were bound to provide him with new discoveries and his mind was eager and ready to make the most of them. Indeed, he immediately realized the importance of the result, repeated the crosses on a much larger scale with more geographic varieties, and recognized that the variable results obtained required that many different sexually determined races must exist in Japan. "But the decisive point was that, walking home a dark night the two miles from the lab, I suddenly understood [in 1911] the amazing genetical situation, which was outside the accepted Mendelian tenets. I had found what is today called the balance theory of sex determination."

He had even found more than that. After ten years of describing one mendelizing gene after the other, in many plants and animals, biologists not yet stimulated by the just initiated work of the Drosophila group were in the process of becoming bored with these findings. Goldschmidt himself from the start of his genetic work was anxious to progress beyond the exploration of the Mendelian mechanisms and hoped to accomplish this by combining Mendelian with developmental physiological investigations. When he began raising Lymantria he saw that the caterpillars of different races had different markings and that certain hybrid larvae at first were light like the light parent and then stepwise became dark like the dark parent. This phenomenon, to which the purely descriptive term of change of dominance applied, called for an explanation in terms of developmental events. The flash of insight which came to the thirty-three-year-old man in 1911 combined *Beobachtung und Reflexion* on sex aberrant adults and color types of caterpillars in a general theory of genic action. For many years the flame then lighted was to burn bright and passionately in Goldschmidt's mind and to illuminate the thinking of a generation of biologists.

The early Mendelians had recognized the genic constitution of organisms and the Drosophila workers had uncovered in detail the chromosomal mechanism of heredity. These great discoveries were of classical character, solidly based on a multitude of well-established facts. By themselves, however, they would not have been sufficient to place genetics in the central position within biology which it was to assume. Beyond the "static" analysis of gene transmission an insight was needed into the dynamic role of genes in cellular physiology, biochemistry, and development. Goldschmidt recognized this aspect and outlined in brilliant generalizations a physiological theory of genetics. Necessarily the prophetic nature of this achievement —romantic in the sense of Ostwald's classification of great scientists and their discoveries—transcended its factual basis. It was the audacity of the theoretician unimpeded by the still scanty data which gave a new focus to biological thought.

Before describing in some detail the essentials of the Lymantria work and the deductions derived from it, external events in Goldschmidt's life need to be related. In 1911 the Kaiser Wilhelm Gesellschaft for the promotion of science was founded in Germany and began to organize its institutes, which were to become superlative centers of research. Boveri was offered the directorship of the Institut für Biologie and it was he who with extraordinary insight selected as leaders of its departments four men, all but one still in their thirties, and two of them destined to win Nobel Prizes: Spemann, Hartmann, Warburg, and Goldschmidt. On January 1, 1914, Goldschmidt was appointed a member of the institute then being built in Berlin-Dahlem. At the same time he was awarded a traveling fellowship in order to go to Japan and look for new races of Lymantria. In Tokyo, as guest of the Imperial University just before the outbreak of World War I, he bred the forms which he had collected, and was able to send the living material back to Germany where Seiler, his former student in Munich and now first assistant in Dahlem, carried the cultures through the tumultuous years until Goldschmidt's return, which was greatly delayed. When Goldschmidt arrived in San Francisco on his homeward journey from Japan, he found that the British blockade made his further travel to Germany impossible. After two months in the Zoology Department of the University of California he proceeded east to become a guest in Harrison's laboratory at Yale University for a period of years "during which I learned to love and admire my great host." Breeding work was done during summers at Harvard's Bussey Institution and at Woods Hole. His family was permitted to leave Germany and joined him late in 1915. Then, early in 1918, like many other Germans, he was interned in a civilian prisoner camp in Georgia and not released until after the war was ended. In later years Goldschmidt would entertain his guests by vivid and good-humored accounts of his sojourn in a local jail, the transfer to the state prison, and his solitary march the length of lower Manhattan to Pennsylvania Station, handcuffed under guard of two soldiers with loaded guns!

Before leaving Munich, Goldschmidt had given some accounts of his Lymantria work on sex determination. He published additional preliminary papers on the same topic in American journals throughout the war years. In 1917 he wrote two book manuscripts in which he formulated in detail his new insights and generalized them broadly. When he finally took up work in the Kaiser Wilhelm Institut he quickly brought these up to date. In 1920 there appeared the *Mechanismus und Physiologie der Geschlechtsbestimmung,* a book which gave not only his own theories on the physiology of sex determination but also a comprehensive account of the accomplishments of the preceding twenty years on the mechanisms; the *Quantitative Grundlage von Vererbung und Artbildung;* and the first of the documentary "Untersuchungen über Intersexualität," an article of 199 pages. This was to be followed by five more papers under the same heading, the final one dated 1934.

The impact of the two books and of the supporting material was great, both in Germany and abroad. For Germans the years of the war, the defeat, the revolution, and the not-yet-ended inflation constituted a deep cleft which separated two eras. The desire for something more permanent than the catastrophic course of history made scientific achievements objects of consolation and hope. Within the field of biology the main sources of elation were Goldschmidt's syntheses and Morgan's *Material Basis of Inheritance,* soon made available in a German translation by Nachtsheim, another former student of Goldschmidt's.

The aberrant sexual types which Goldschmidt had produced in Lymantria crosses were at first considered under the term "gynandromorphism," a designation which was then used to describe a variety of abnormal forms in which female and male traits occurred side by side in the same individual. Soon, however, Goldschmidt recognized that his gynandromorphs differed from other gynandromorphic insects. Most of these were specimens in which the male and female parts had different genetic constitutions, such as having one X-chromosome in the cells of one part and two X-chromosomes in the other. Contrary to this situation, all of the cells of the Lymantria intergrades were genetically alike. In 1915 Goldschmidt coined the term "intersex" for them. The crosses in which the intersexes were produced showed that two genetic elements were involved, a maternally inherited female tendency F, and an X chromosomally inherited male tendency M, thus giving a normal female the formula FM and a normal male FMM. This scheme, according to which sex is determined by the relative "strength" of F and M—one M being less effective than F and two M's more effective—had been proposed also by Morgan, adjusted to the somewhat different situation regarding sex determination in flies as compared to moths.

In most organisms, where one meets with the normal sexes only, the scheme was not subject to test. In Lymantria the genetic analysis showed that different races had F's and M's of different effectiveness. Within each race the sex factors were so balanced that the relations $1M<F$ equals female and $2M>F$

equals male always were upheld, but hybrid combinations of F's and M's from different races could lead to FM intersexes whenever a "weak" F could not sufficiently overbalance a "strong" M, or to FMM intersexes whenever a strong F could partly outweigh two weak M's. Depending on the relative strength of F and M in hybrids between different races one could obtain slight, intermediate, or extreme intersexuality, including complete sex reversal. The experimental proof for these relations preceded by years Bridges's famous discovery of triploid intersexes in Drosophila. There, the quantities of the constant F and M factors can be read off the numbers of chromosomes of different sex forms and a direct demonstration can be provided that increasing quantity expresses itself in increased strength of the sex determiners. Goldschmidt himself had interpreted the racially different strengths of the Lymantria sex factors in terms of different quantities of F or M genic molecules.

It was surprising that the imbalances of the sex factors in the intersexes of Lymantria did not lead to intermediate development between male and female for the sex-determined or sex-controlled parts of the specimens. Rather, the intersexes are mosaics of male and female differentiated tissues. More surprising still, there seemed to exist two radically different kinds of intersexes. The quantitative balance theory of sex determination would lead one to expect that whether a given imbalance was on the basis of an FM or FMM genotype should make no difference, since it was not the *number* of M factors in the X-chromosomes but the relative effective strengths of the two sex antagonists which counted. Yet, the morphology of intersexual FM types appeared to differ in some basic way from that of FMM ones. Influenced by his observations on the changing color intensity of hybrid caterpillars, Goldschmidt modeled his thoughts on intersexuality into the "time law" theory. The sexually mosaic nature of intersexes and the occurrence of two different types or series was explained by the assumption that development of an intersex, from fertilization on, begins under the influence of one of the two sex factors and, at a turning point, changes over to development under the influence of the opposite sex factor. The spatially mosaic nature of intersexes he considered as the morphologic consequence of a mosaicism of sex tendencies in time, female FM intersexes having started as females and then switched to maleness, and male FMM intersexes having gone through the opposite sequence.

The theory of the time law led to a long series of morphologic and developmental investigations by Goldschmidt and his students and to searching critical analyses by other authors, among whom Kosminsky in Leningrad, Seiler in Zurich, and Baltzer in Bern were outstanding. Theoretically, "a sexual mosaic" could be produced by an alteration of determination in time or by simultaneous but alternative determination of different cells. The latter possibility is realized in the intersexes of the moth Solenobia, as has been proven by Seiler. The painstaking, fact-finding work of this investigator, which led him to abandon the time law, stands in fascinating contrast to Goldschmidt's all-embracing theoretical convictions.

In the later 1940s and subsequently, Goldschmidt and Seiler had repeated literary exchanges concerning the interpretation of the facts in Solenobia. Goldschmidt was unwilling to concede that Seiler's observations were at variance with the demands of the time law. Similarly, he had attempted earlier to fit into his original concepts some specific findings by Kosminsky on Lymantria which were not easy to understand in terms of the time law.

It seems not possible today to gain a final view of the Lymantria situation. In contrast to the single, albeit widely variable type of intersexes in Solenobia, in Lymantria a major difficulty is presented by the occurrence of the two above-mentioned kinds of intersexes, male and female. In reality there are even more kinds, since female intersexuality in which sex genes of the Japanese Gifu race are involved and certain intergrades obtained by Kosminsky differ morphologically from all other types of female intersexuality and in their coarse mosaicism resemble typical male intersexuality. The phenomenon of Gifu intersexuality remained basically ununderstood by Goldschmidt, and even the morphology of male intersexuality had aspects not immediately derivable from his theory. Perhaps the two, or more, different kinds of intersexes in Lymantria are less different in their development than has been assumed for so many decades; this is an important area for renewed study. That the existence of two developmentally opposite types of intersexuality is actually contrary to Goldschmidt's own tenets was mentioned above. This was early pointed out by F. Lenz but not considered worthy of comment by Goldschmidt. The endeavors of other authors to devise different interpretations than his own were dissected mercilessly. With respect to a specific critique he concluded: "This attempt, which only resulted in a poorer version of my own ideas, has confirmed my conviction that there just does not exist any other explanation than the one found by me" (translation). His adversary's reaction to this was understandable: *Roma locuta est*—Rome has spoken.

Goldschmidt's general theory of genic determination of development was based on his interpretation of the action of the sex factors. All genes, he postulated, are enzymes and different alleles of specific genes are different quantities of a specific enzyme. The function of these gene-enzymes in development is a typically chemical one: to produce "hormones" of differentiation, in quantities which are proportional to the quantities of the genes themselves. Development, then, is based on the tuned, harmonious chemical reaction system of the totality of genes: "The mass law of reaction velocities is one of the basic laws of genetics." He illustrated his theory with schemes of curves, in which the abscissa represents time of development and the ordinate the amount of gene product. To account for the time law of intersexuality he fitted the M and F curves so as to cross each other at the appropriate assumed turning points. He applied the theory to a variety of phenomena observed by himself and others in different organisms—the patterns of lepidopteran wings and their temperature dependence, the polymorphism of natural populations and the head shape of Daphnia—and derived a theory of evolution which was based on selection of different multiple alleles causing different reaction velocities. He recognized that any quantitative shift in one gene would be physiologically feasible only if other genes and the reactions dependent on them were shifted correspondingly so as to produce a new physiological balance. This, he pointed out, accounted for the observation that geographic races, in contrast to local mutants, differ from one another by numerous traits, in Lymantria as well as in birds and mammals. If one disregards the specific interpretation of allelism as variation in gene quantity Goldschmidt's views of evolution are seen to be very similar to those of the later Neo-Darwinians.

Incessantly, Goldschmidt elaborated his general views, defended them against criticism, and emphasized their significance. If Darwin had his protecting bulldog, Huxley, and his prophet, Haeckel, Goldschmidt was his own bulldog and prophet. In 1927 appeared his book *Physiologische Theorie der Vererbung,* which tried many new forms of curves to account for the development of the Lymantria sex types and of caterpillar coloration, for dosage effects, deficiencies, multiple factors, mutation, and other genic phenomena in Drosophila and in general. It was a brillant performance, but psychologically made partially ineffective by harsh attacks on the Drosophila geneticists whose discoveries he praised highly but whose refusal to accept a quantitative theory of allelism and mutation and to go beyond "the narrowest interpretation of the factor theory" he disdained. Ten years later, one further presentation appeared, in English, *Physiological Genetics.* This book not only furnished another outline of Goldschmidt's dynamic developmental views but was actually a comprehensive review and critical analysis of all known important facts on genic action. As such it served for many years as a basic text in this area of genetics. An important change in the author's viewpoint from earlier years concerned the nature of the gene. He abandoned the idea of alleles being different quantities of the same molecule in favor of looking at a chromosome as a single gigantic macromolecule in which local "steric changes [account for] deviations from wild type which may be described as mutations, even as point mutations, though no actual wild-type allelomorph and therefore no gene exists." We shall return to this new concept.

Earlier than *Physiological Genetics,* Goldschmidt had written a monograph, *Die sexuellen Zwischenstufen* (1931), a remarkably complete survey of the great variety of intersexuality in the whole animal kingdom. Although more than thirty years have passed, during which new material has accumulated and some of Goldschmidt's interpretations have had to be abandoned because of later work, it is still a very useful book.

Twice in the 1920s Goldschmidt had again traveled to the Far East to collect additional material of Lymantria. For two years he was professor at the Imperial University in Tokyo where he continued his large-scale breeding work. Otherwise the Dahlem Institut served as an ideal place for research with its ample resources and the freedom of its staff from any other obligations than "to lay ostrich eggs," as Baltzer once wrote in a poem sent on the occasion of Goldschmidt's fiftieth birthday. Apart from intersexuality, geographic variation as a general phenomenon formed the core of Goldschmidt's activity during those years. From 1924 to 1933 appeared the six voluminous "Untersuchungen zur Genetik der geographischen Variation." Here the sex races, the differential characters of the life cycle—length of larval development, number of larval instars, nature of diapause, growth and size, color and marking of larvae and moths, cell-, egg-, and chromosome sizes—were all analyzed with respect to their genetics, physiology, and ecologic-geographical distribution. Goldschmidt particularly emphasized the adaptive nature of many racial traits in the sense that length of diapause, for instance, has to be related to the seasonal cycle of the respective geographic region. The significance of this work has been characterized by Mayr in his *Animal Species and Evolution* (1963; p. 298):

"The present generation of evolutionists can hardly appreciate the enormous impact of the demonstration by Schmidt (1918) for the fish Zoarces, by Goldschmidt (1912-1932) for the gypsy moth (*Lymantria dispar*) and by Sumner (1915-1930) for the deer mouse Peromyscus that the slight differences between geographic races have a genetic basis."

In 1934, after twenty-five years of work on Lymantria, Goldschmidt published a final comprehensive monograph and regarded his analysis "as finished as far as my own person is concerned." The facts which he had found and the views he had formulated would continue to play important roles in his future research.

The study of geographic variability had originally been initiated with the thought that its genetic analysis would provide a key to the problems of speciation. When, however, all the material had been assembled, Goldschmidt announced that his views had changed fundamentally. The many races of

Lymantria dispar, he emphasized, still belong to one single species. The small mutations of the Neo-Darwinians would explain geographic diversity within a species but, he argued, could not serve as bridges over the fundamental gap which separates one species from another. This skeptical view, first pronounced at the Sixth International Congress of Genetics in Ithaca (1932), was gradually replaced by a positive theory which would account for speciation and even the sudden origin of much greater newness in evolution. Goldschmidt invoked the occurrence of "macromutations," causing fundamental changes in the structure of mutated individuals and thus abruptly leading across the unbridgeable gaps. He recognized that from the point of view of the old species the macromutants would appear to be monsters, but he showed that some of these might be "hopeful monsters" which had an evolutionary future. When he was appointed Silliman Lecturer at Yale University, he decided to formulate a comprehensive treatment of his concepts of evolution and chose as a topic *The Material Basis of Evolution* (1940). The first half of the book is given to microevolution, the origin of intraspecific diversity. Its conclusion is: "Subspecies are actually, therefore, neither incipient species nor models of the origin of species. They are more or less diversified blind alleys within the species." He thus was led to the concept of macroevolution which dominates the second half of the book. The brilliant main part of this section is entitled "Evolution and the Potentialities of Development." Here it is demonstrated, by reference to experimental changes in development, to hormonal effects resulting in vertebrate metamorphoses, to the alternation of larval and adult forms in insects, to the diversity of the sexes in the same species, and many other examples, that "the developmental system of a species is capable of being changed suddenly so that a new type may emerge without slow accumulation of new steps." It is further shown that mutations exist which affect early development and thus are liable to have large consequences. From these facts it is concluded that true evolution, macroevolution, can be and actually is based on genetic changes which are in effect unlike those of micromutations. By these changes development is recast in a fundamentally new pattern, that of new species.

In this fascinating book the knowledge of a lifetime of zoological experience, genetic experimentation, and all-embracing reading in biology is assembled in order to support its thesis. Goldschmidt knew well that his theory was contrary to the imposing structure of the New Systematics in which the work of two decades by leading investigators on theoretical and experimental population genetics as well as taxonomy had culminated. It was no surprise to him that his theses were rejected by the great majority of Neo-Darwinian evolutionists. Furthermore, his subsidiary assumption that the required macromutations were "systemic mutations," by which he understood basic repatternings of chromosomal macromolecules, was an easy target for criticism. The concept of the unified action of the "chromosome-as-a-whole" did not appear acceptable. Actually, as we shall see, the concept originated in part independent of evolutionary considerations and was not really essential to them. Developmentally it was conceivable that a macro-effect of a genic change could be the result of some micro-changes in the chromosome as well as of the hypothetical macro-changes. Notwithstanding the fact that the evidence and the doctrine of the Neo-Darwinians have withstood the impact of Goldschmidt's erudition and interpretative initiative, *The Material Basis of Evolution* contains elements which may well enter future thoughts on evolution. It is significant that two years after the author's death a reprint of the book, which had been out of print, has made it available again.

Long before the Silliman lectures appeared, the course of world events had once more deeply affected Goldschmidt's personal fate. The Nazi revolution ultimately forced him to leave Germany. For a few years he still worked quietly in the Kaiser Wilhelm Institut, which under Hartmann and von Wettstein remained an island of decency in distressing surroundings. In 1936 he accepted a professorship in the Department of Zoology of the University of California at Berkeley. "This turned out to be one of the most happy events of my life," he wrote later, "crowned by my becoming an American citizen in 1942." The happiness had to be bought at a high price. The Goldschmidt of pre-Hitler days was one of the imposing figures of German intellectual life; the Goldschmidt of the United States between the wars was one of the large number of professors whose prestige was limited. What weighed heavier, his status as a scientist was much in doubt among many of his colleagues. The attacks against their opinions which he had waged for so long and their critical attitude to his own pronouncements did not provide a background for ready acceptance except where the person, not the scientist, was involved. And it did not make matters easier when the embittered, psychologically and physically heartsick man chose the time of his arrival in the country of Morgan's Theory of the Gene to announce in a funereal voice: "The theory of the gene is—dead!"

This statement was the outcome of fully justified doubts, mainly arising from the phenomenon of position effect, the fact that the effect of a gene in many cases is influenced by its chromosomal neighbors. Goldschmidt felt that the concept of materially and physiologically separate genic elements in the chromosome was in need of revision. He rejected the old "beads on a string" analogy and tried to replace it by a concept which considered chromosomes as single super-macromolecules in which changes at any site would affect the action of the whole. In a way Goldschmidt's theory of evolution as affected by his older concepts of the genes as enzymes and of the quantitative nature of differences among alleles had prepared him for his new views. If ordinary mutations would not alter the nature of the gene enzymes but only change their quantity, it seemed difficult to him to believe that such mutations could result in the large-scale repatterning of development which he regarded as necessary for macroevolution. By discarding the idea of the individually separate genes of formal genetics, he abandoned at the same time his own idea of genes as separate enzymes. The concept of the genic nature of the chromosome-as-a-whole permitted both localized minor changes available for microevolution and over-all repatterning of the chromosome necessary for macroevolution.

For many years he found no willing ears, but gradually the climate of opinion changed. His own probings into the gene concept met with those of others, e.g., Barbara McClintock, E. B. Lewis, and later the microbial geneticists. It was a sign of the times that in 1950 he was invited by the Genetics Society of America to give the main address at the Jubilee Meeting in celebration of fifty years of genetics. In the following year he was asked to open the Cold Spring Harbor Symposium on Chromosomes and Genes. When the Ninth International Congress of Genetics was organized in Italy, he was elected President. He took the occasion of the presidential address to discuss "Different Philosophies of Genetics," his own "physiological or dynamic" and the "statistical or static," with one of his main unnamed targets, R. A. Fisher, as Vice-President, smilingly sharing the rostrum.

Already before the work on Lymantria was terminated, Goldschmidt began to experiment with Drosophila. From 1934 on, this organism was his exclusive tool. He began by studying in genetically wild-type individuals the effect of larval and pupal heat treatments on the phenotype of the adult, and discovered that he could produce a great variety of abnormalities resembling those produced under normal conditions by mutant genes. The induced changes were not heritable. He and his students in Berkeley, and workers in many other laboratories, have deepened our understanding of these "phenocopies," his suggestive term which has gained wide usage. Two experimental papers in this area, by Goldschmidt and Piternick, appeared shortly before his death. Other Drosophila studies were concerned with homoeotic mutants, with complex, poorly understood mutation phenomena, with sex determination, and with a plethora of other items. Much of this activity centered on the problems of evolution. The homoeotic mutants served to demonstrate that fundamental morphological changes can be the outcome of genetic changes in single loci or groups of loci. If antennae or wings can become leglike, or if the two forelegs of Drosophila can fuse to form an unpaired structure resembling the labium of the Orthopterans, are these not models for macroevolutionary events? A different area was explored in the laborious inquiries into presumed mass-mutational or "dependent, successive, and conjugated spontaneous mutation" phenomena, which extended over more than a decade. Here was an experimental, even if not fully convincing, attempt to prove the existence of repatternings of chromosomes by means of deficiencies, inversions, and translocations as a basis of evolutionarily significant mutations. Some of these works were documented in voluminous publications so crowded with details that they were read carefully by few only, but at least one, the monograph by Goldschmidt, Hannah, and Piternick on podoptera, a leglike replacement of the wing region, has found an important place in Lerner's considerations of *Genetic Homoeostasis*.

After the Congress in Italy Goldschmidt suffered a severe heart attack. When he was able to travel back to Berkeley he was confined to his home for several months. This gave the seventy-six-year-old man the opportunity to compose *Theoretical Genetics,* a closely reasoned book of 563 pages! It is an amazing work, to use an adjective of which he was fond. "Theoretical Genetics comprises the problems connected with the following questions: (1) What is the nature of the genetic material? (2) How does the genetic material act in controlling specific development? (3) How do the nature and action of the genetic material account for evolution?" The treatment of these topics is highly personal. Goldschmidt repeats, revises, and expands the pronouncements of decades and relishes showing how he had been right before. With an unbelievable grasp of the literature he expounds, criticizes, and warns of erroneous narrowness. Some of the then newest discoveries are dealt with, such as those of Visconti and Delbrück, Pauling and Cori, Watson and Crick. If the book is one-sided, and if large parts of it do not stand the test of time, it is still an achievement which hardly anyone else could have matched. Its merit greatly surpasses its limitations. Many parts remain highly relevant to current work, others are valuable in giving insight into the ever-questioning and constructive thinking of a remarkable scientist.

The range of Goldschmidt's biological activities was much wider than can be described in a limited memoir. A few further aspects will at least be listed. During his sojourn in Ross Harrison's laboratory Goldschmidt did pioneer work in tissue culture, being able to follow spermatogenesis of the Cecropia moth in vitro. Later, in collaboration with Katsuki, he made a comprehensive analysis of a case of inherited gynandromorphism in the silkworm. Other work dealt with the structure of salivary gland chromosomes in Drosophila, maternal effects in inheritance, and heterochromatin. In human genetics Goldschmidt described a fascinating case of multiple race crossings on the Bonin Islands and, in a curiously naïve and highly revealing paper, a pedigree of personality traits in the "M Family," obviously his own. To these activities should be added his critical reviews of unusual types of sex determination, evolutionary genetics, and mimetic polymorphism.

His influence as a teacher and lecturer would deserve a special section. In his university functions in the early Munich period and in Berkeley, he was clear and critical, deeply conscientious, and sympathetic to the students, with highest standards for himself and without dogmatism. He had an important personal influence on the development of genetics in Japan, as Komai testified in a historical survey. Many of his students became outstanding investigators themselves. Before scientific and general audiences on most continents he was a much admired speaker. His textbook of genetics, which appeared in five editions from 1911 to 1928, was a masterpiece, full of new thoughts, broad, and didactically skillful. His several popular science books were translated into many languages. "This my work in helping to educate the masses is very dear to my heart especially in view of the havoc wrought by the journalistic popularizers of science." In Germany he was active and prominent in many committees and societies and his editorial work was unusually comprehensive. Once he wrote an article on "Research and Politics" (1949) which was reprinted in Portuguese, German, and French. A book on his travel in outlying areas of pre-World War II Japan was composed during his second, long stay in that country.

Of the many external distinctions which came Goldschmidt's way the honorary doctoral degrees from Kiel (1928), Madrid (1935), and Berlin (1953) and foreign and honorary memberships in many academies and learned societies may be mentioned. He was nearly seventy years old when he was elected to membership in the National Academy of Sciences in 1947.

The springs from which the stream of Goldschmidt's activities was fed were manifold. Our motives are complex and often unknown to ourselves and to others. Goldschmidt was a naturalist who enjoyed the phenomena of life. Although his main activities were in the laboratory, he spent repeated periods at marine stations, visited the coral reefs of the South Seas, and watched the glowworms in the caves of New Zealand. If his theoretical work often seemed to lack a sufficient basis of factual contributions, a general judgment that he was primarily a theoretician can easily be shown to be incomplete. The many plates and drawings of morphological detail, the hundreds of tables of experimental data are evidence of a biologist's realism. If, in spite of this great amount of specific work, the foundations of his hypotheses frequently were not established solidly, it was due to the breadth of his interests and the width of his generalizations, which no single individual could anchor securely. Positive and negative attributes were curiously mixed in this great scientist. The sweep and penetration of his theoretical insights, the manifoldness of his objects of study, the courage to abandon seemingly established notions, including some of his own, stood side by side with the lack of rigor with which he could use imperfect observations when they fitted into his deductions, or sometimes disregard perfect ones when they failed to do so.

He served Nature but he also tried to dominate her. He relished the mastery over mere facts which his quick mind and his astonishing memory seemed to make possible. As a young man he aspired to prominence in the world of science, and as an adult, when he had attained it he carried it with deep conviction. Yet in spite of his assured bearing it is likely that he felt insecure. His oversensitivity to or, sometimes, his brushing away of criticism, his exaggerated literary reactions to it, his principle not to solicit comments on his writings before they went to press, and particularly the absolute tone of many of his dicta are signs of hidden doubts. It would, however, be very wrong to judge the man only from his technical writings and his often forbidding appearance in the laboratory. He gained lasting friendships based on mutual loyalty of many men such as the zoologists Bütschli, Richard Hertwig, Methodi Popoff, Ross Harrison, the painter Henrik Moor, the conductors Karl Muck and Ernst Kunwald, and his technician-in-chief Michael Aigner. When he had to leave the Kaiser Wilhelm Institut sadness and tears were on the faces of most, from the cleaning lady to his colleagues. At the end of his last lecture in Berkeley before retirement, his students in a general class surprised him with the gift of an ancient Chinese figure, an unheard-of act in the large, necessarily rather impersonal university. In his nontechnical publications there is evidence of fairness, of devotion, and of humor, witness his *Ascaris, eine Einführung in die Wissenschaft vom Leben* (1922), which has been enjoyed by tens of thousands of readers in its original version and in translations into five different languages. Witness also the touching letter of the seventy-six-year-old Goldschmidt to the ninety-four-year-old Karl Jordan, the lively *Portraits from Memory* (1956) in which he sketches his recollections of zoologists and the atmosphere of German universities in their classical period, and his sensitive obituaries and biographical memoirs on Bütschli, Popoff, Kofoid, Federley, and others. He was warm and solicitous to the young people around him. He could keep separate his disagreement in matters of science from appreciation of the opponent as an individual. He was a relaxed and in a deep sense charming host in his and Mrs. Goldschmidt's treasure-filled home in which their guests experienced a unity of beauty and humanity. His interests were not exhausted by intense occupation with his work. From youth to late middle age he was active and excelled in various sports. He played the violin and viola and once wrote: "Music is still to me what religion is to the believer." He became an expert in objects of art, particularly those of the Far East. With the pleasure of an amateur and connoisseur he collected all through his life select pieces of pottery, statues, prints, and paintings.

The first sentence of Goldschmidt's autobiography reads as follows: "I come from an old German-Jewish family." Many times in the book he returns to the experiences of anti-Semitism to which he had been subjected, as a child in the streets of Frankfurt, at the hands of teachers in school, and in the withholding of an officer's commission at the end of his military service, events which preceded by decades the disaster which forced him to leave Hitler's Germany. The facts and consequences of his background had an important part in the shaping of his personality.

To his associates the emphasis on his Jewish origin in the autobiography was a surprise. Only very rarely had he spoken of it. There is no mention of the fact in his outline for the National Academy. His mode of life was anything but parochial. His wife came from Protestant ancestors and his children grew up in an atmosphere which led them in their turn to choose non-Jewish spouses. His earlier identification with German patriotism had been strong. Nobody could forget his description of that November night in 1918 when the factory whistles in Georgia carried to the German prisoners' camp the announcement of the end of the war and sobbing rose from the barracks where the men mourned the defeat of the fatherland.

The part which an individual's work plays in the development of his science varies greatly. There are the unique persons, whose often single achievements are the towering, long-persisting landmarks on the road of history. There are the many modest workers who contribute their few bricks or their bits of mortar to the unlimited edifice of knowledge. There are those whose discoveries and insights remain unnoticed in their lifetime and even—who knows—forever. There are those who march in the forefront of their contemporaries, leading the way in making new finds, warning of barren deserts, promising lands of fulfillment. And there are those who erect the scaffold on which others reach the spaces where they can fit their parts into the yet imaginary construction. The scaffold is abandoned some day and it disappears while the building stands. Goldschmidt partook of the traits of many of these men: contributor of permanent parts, some very large; preceptor and critic of his era; designer of frameworks for the future.

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KEY TO ABBREVIATIONS

Am. Naturalist = American Naturalist
Arch. Entw. Mech. = Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen
Arch. Protkd. = Archiv für Protistenkunde
Arch. Zellfg. = Archiv für Zellforschung
Biol. Bull. = Biological Bulletin
Biol. Centrbl. = Biol. Zentrbl. = Biologisches Zentralblatt
J. Exp. Zool. = Journal of Experimental Zoology
J. Heredity = Journal of Heredity
Münch. Med. Wochschr. = Münchener Medizinische Wochenschrift
Naturwiss. = Die Naturwissenschaften
Proc. Nat. Acad. Sci. = Proceedings of the National Academy of Sciences
Quart. Rev. Biol. = Quarterly Review of Biology
Sci. Monthly = Scientific Monthly
Sitzungsber. Ges. Morph. Physiol. = Sitzungsberichte der Gesellschaft für Morphologie und Physiologie
Univ. California Publ. Zool. = University of California Publications in Zoology
Z. indukt. Abstl. = Zeitschrift für induktive Abstammungs- und Vererbungslehre
Z. wiss. Zool. = Zeitschrift für wissenschaftliche Zoologie
Zool. Anz. = Zoologischer Anzeiger
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