

Memories of Professor Hans Spemann's Department of Zoology at the University of Freiburg, 1920-1932

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Professor Spemann came to Freiburg in the spring of 1919, as the Chairman of the Zoological Institute of the University. It had been founded in 1867 by his famous predecessor, August Weismann, and flourished under him. But lately it had declined. Under Spemann's leadership it became the center of experimental embryology in Germany. Spemann had established his reputation as the chairman of the Department of experimental embryology at the Kaiser Wilhelm (now Max Planck) Institute for Biology in Berlin-Dahlem, and its co-director, with the botanist C. Correns, 1915-1918.

I arrived in Freiburg in the spring of 1920; I had been a student of zoology at the University of Heidelberg for two semesters. The Director of the Zoological Institute, Prof. Curt Herbst, had admitted me to an advanced seminar in experimental embryology. I became fascinated with the relatively new branch of biology and saw my future in doing experiments on embryos, but I was not interested in the experimental work he and his students did at that time.

In the spring of 1919 a friend and I had spent a vacation visiting Freiburg and hiking in the nearby Black Forest, which reminded me of the *Riesengebirge* (Giant Mountains) in Silesia, where I had grown up. I was enchanted by the medieval spirit of Freiburg, which the center of the city had preserved. Its narrow winding streets were lined by small rivulets (*Bächele* in the local dialect). In the center of the town, the large cathedral square (*Münsterplatz*) is flanked by Renaissance, Baroque and modern buildings. The large gothic cathedral (*Münster*) is one the most beautiful in Germany, decorated with sculptures altar paintings and stained glass windows by famous artists.

The environs of Freiburg are unique. To the west extends the Rhine Valley. At its center, visible from the city, rises, like an island, the *Kaiserstuhl* (Emperor's Chair), a hillside of volcanic

rocks, strewn with prosperous villages, each surrounded by large vineyards.

We hiked for days in the Black Forest and climbed its highest peak, the *Feldberg*, which rises above timberline. Clearly, this region was much better for hiking and skiing than the hills near Heidelberg. When I found out that Professor Spemann had moved to Freiburg, my mind was made up that I would transfer to that University. I stayed there from 1920 to 1925, with the exception of one winter semester in Munich. In the spring of 1925 I received the Ph.D. I spent the years 1926-1928 at the Kaiser Wilhelm Institute for Biology in Berlin-Dahlem, where Professor Otto Mangold, Spemann's oldest and favorite student, had become his successor, as the chairman of the Division of Experimental Embryology. In 1928 I returned to Freiburg as an instructor and stayed there until the fall of 1932, when I received a Rockefeller Fellowship to spend a year in Dr. F.R. Lillie's laboratory in Chicago.

In 1920 the Zoological Institute in Freiburg was a modest two-storey building that dated back to the 1880s. In the meantime, a large auditorium and a building that housed Weismann's large collection of preserved specimens and microscope slides had been added. The first floor of the main building was occupied by the office of Spemann, the other staff members, a library and a "reprint room". Its walls were stacked with the large collection of Spemann's reprints, which were available to all of us. On the second floor was a room with tables for students who worked on their Ph.D. theses (the Doktoranden) and two large rooms for the introductory and the advanced laboratory courses (the *Kleine* and the *Grosse Praktikum*).

The Department was completely dominated by experimental embryology. Besides Spemann, there was Otto Mangold, who had a position equivalent to that on an Assistant Professor. He

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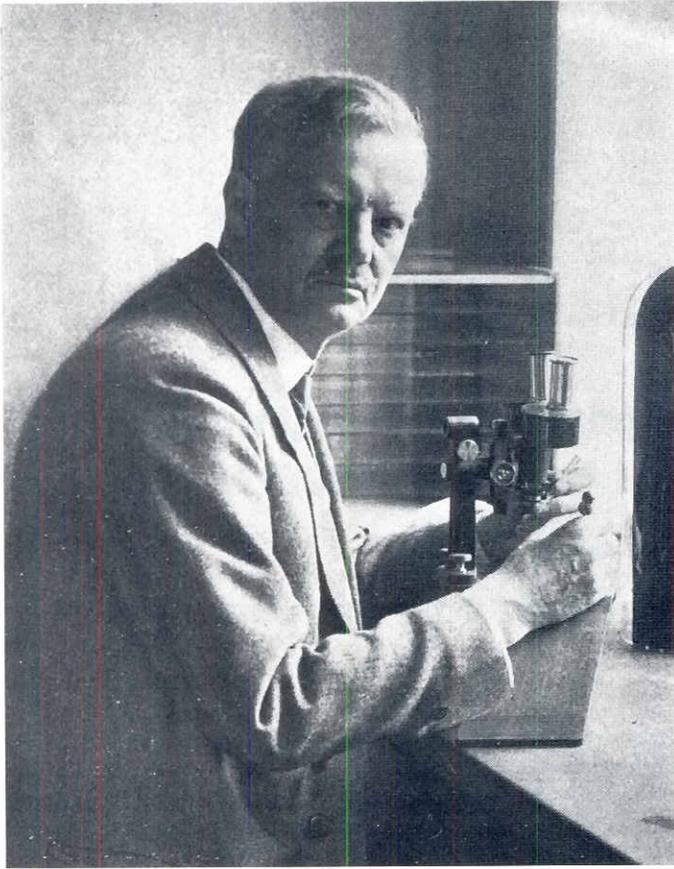


Fig. 1. Hans Spemann (1869-1941). Photograph courtesy of Prof. Klaus Sander.

followed in the footsteps of his mentor and did some creditable work. Professor F. Baltzer, like Spemann a student of the famous cyto-geneticist Th. Boveri, taught genetics. I took his two-semester course and learned a great deal. He left already in 1921 to become the chairman of the Department of Zoology at the University of his home town Bern in Switzerland. He was not replaced by another geneticist. Dr. B. Geinitz, an entomologist, was recruited by Spemann temporarily for experimental embryological work, but he returned to his specialty and later founded a Honey Bee Institute. In addition, there were two insignificant lecturers, whose courses I did not take. In 1924, Dr. F. Süffert joined the Department. His field was the study of adaptative coloration in butterflies and moths. He was an excellent scientist with original ideas, and a good teacher. We became friends, particularly after my return to Freiburg in 1928. I think that this specialization in the department was not unique. Research in most science departments in Germany was concentrated on the research interests of the chairman. Only the Institute of Prof. Alfred Kühn in Goettingen was known for its diversity. I spent a few months during the winter of 1925-1926 in his laboratory. I did experiments on color vision in fish, a project in which several students of his had preceded me. He himself and his associate Henke worked at that time on the determination of the color patterns of the scales on the wings of butterflies and moths.

We attended lecture and laboratory courses in our minor fields (mine were botany and geology) and philosophy, but most of our time was spent in the *Grosse Praktikum*, an all-day laboratory course, in which we studied individually, at our own tempo, representatives of all phyla, from protozoa to mammals, using preserved specimens and microscope slides. On several mornings each week, the instructor gave us directions, and also references to books and articles that were available in a bookshelf in the laboratory. After 2-3 years of the *Grosse Praktikum*, we were ready to start our Ph.D. thesis. There were no examinations in either lecture or laboratory courses. We were responsible for our own progress in scientific proficiency.

The atmosphere in the Institute was relaxed. Spemann was not the stern *Herr Geheimrat* as he is sometimes pictured. He was tall, slender, dignified. He spoke with a slight Swabian accent. He had a subtle sense of humor. When a colleague in a review article mentioned that an American investigator had transplanted the upper blastoporal lip of a gastrula long before Spemann and that he should get credit for the organizer, Spemann wrote: "One can make a discovery without intending it, but not without noticing it". When after a lecture on birds a student asked whether birds are lighter than air, he said: "Yes, that is why they cling so tightly to branches". In meetings and seminars he could be very critical, but his criticism was often softened by a touch of humor.

Spemann came from an affluent family. His father owned a well-known publishing house in Stuttgart. He lived in a spacious house in a suburb on a hillside, with a view of the forested foothills of the Black Forest. In the vestibule there were life-size copies of Albrecht Dürer's four apostles, in his rooms many sculptures and paintings; in his study, one wall was filled with works of Goethe and Goetheana. I remember an assembly of illustrious guests, among them Dr. Harrison of Yale, on the big veranda, on the occasion of Spemann's 60th birthday in 1929. Earlier that day, W. Vogt, co-editor, with Spemann, of *W. Roux' Archiv*, had presented him with a *Festschrift* of five volumes of this journal. Of course, the Springer Verlag, which published *Roux' Archiv*, had to raise the subscription price very considerably. Afterwards, it had to promise irate subscribers that it would never raise the subscription price again.

One came closest to knowing Spemann when the faculty and *Doktoranden* met in the afternoon at the tea hours in the reprint room. There were lively discussions of ongoing research, discoveries by others in our field, evolution, philosophical themes. Spemann was not convinced that natural selection could explain all complex adaptations. Süffert tried to convert him, but he was not successful. One may wonder why the work day was interrupted in the afternoon for tea. Nowadays such gatherings in some departments would take place at lunch. But in those days the routine was different, one had the main meal at mid-day. Spemann went home at around one o'clock for dinner, took a rest and returned around three p.m. He then worked until around seven p.m., and some of us worked longer hours. When we went home, we had just a snack of cold cuts.

Life in the department was animated by guests from abroad. F. Lehmann and O. Schotté from Switzerland worked there for several years. R.G. Harrison was a frequent summer guest. He spoke German and had a German wife. He liked to spend his vacations in Switzerland. One summer he wrote an article in the

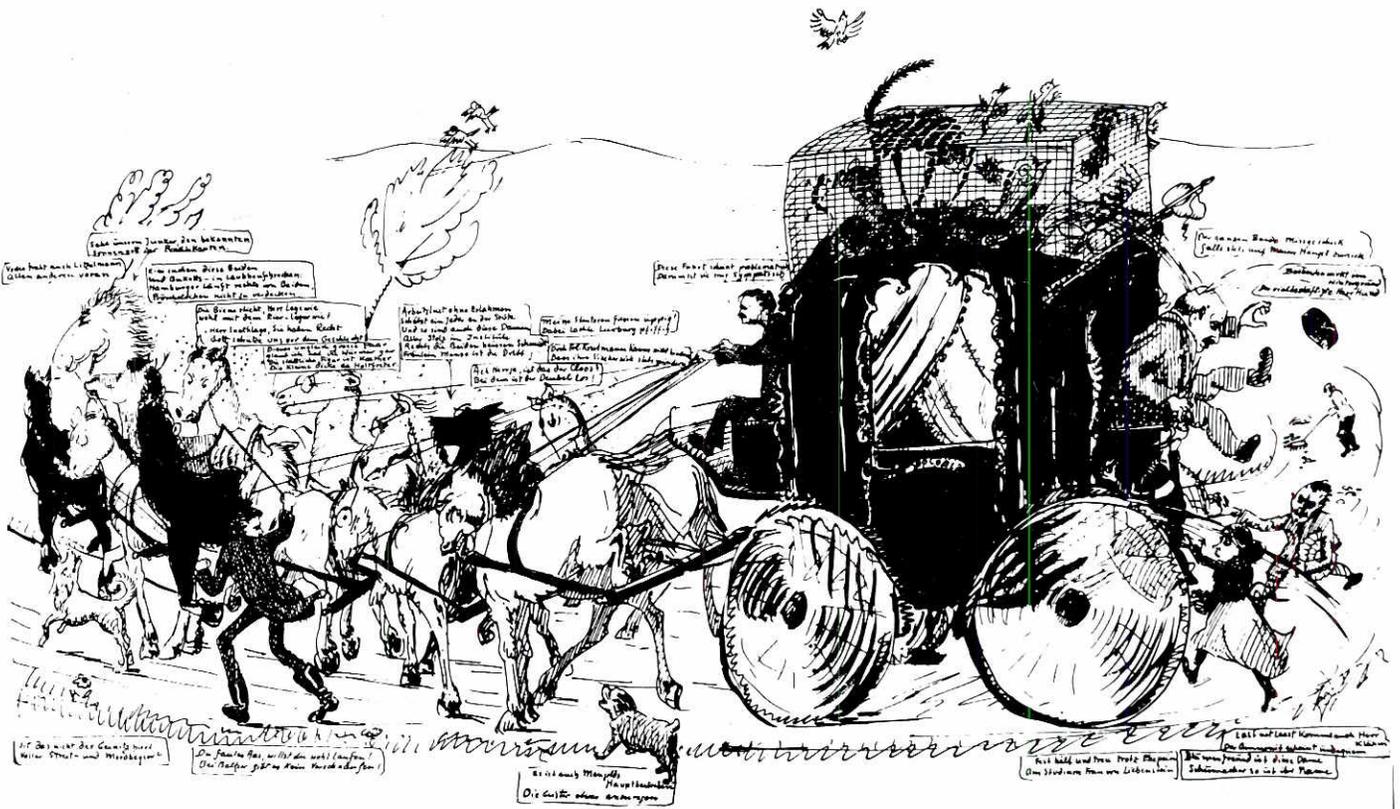


Fig. 2. "Die Institutskutsche", satirical drawing by Johannes Holtfreter in 1925 representing the people working in Spemann's institute at the time. The horses represent the students, among them Hilde Pröschoidt, Johannes Holtfreter and Viktor Hamburger; the dogs are Bruno Geinitz and Otto Mangold, while the horse servant is Fritz Baltzer. Spemann himself drives the stagecoach. Behind the stagecoach, the technical staff. Photograph courtesy of Prof. Klaus Sander.

reprint room. He was very close to Spemann. Runnstroem from Sweden, Woerdeman and Bijtel from Holland, E.G. Hall and S. Detwiler from the USA, T. Sato from Japan, G. Schmidt from Russia and others spent weeks or months in the Institute.

At the end of the summer semester, there was an outing to a country place, at which everyone in the Department participated, including the secretaries and the much respected custodian (*Diener*), Herr Johann Mayer and his family. He had served every chairman since A. Weismann. One of his duties was to assist Spemann in the lecture course. He took care of the lecture material and changed the wall charts during the lecture, the precursors of slides. (A fellow student and I did the charts of gastrulation).

Hilde Proescholdt and Johannes Holtfreter had also joined the Department in the spring of 1920. We were assigned adjacent tables, and I befriended both of them. Hilde was a vibrant, highly intelligent young woman who shared my interests in nature, art and philosophy. We took many week-end outings together. She was somewhat older and more advanced than Hannes and I, and started her Ph.D. project already in the spring of 1921. She had to transplant the upper lip of the blastopore of a salamander gastrula to the belly region. It became famous later as the organizer experiment. I still remember the excitement of Spemann and all of us, one morning in May 1921, when she showed us the first induced secondary embryo. She married Otto Mangold later that year, and they moved to Berlin-

Dahlem, where Mangold became Spemann's successor at the Kaiser-Wilhelm Institute for Biology. She was not destined to enjoy her success. She died of severe burns after an accident at her home in 1924, the year in which the Spemann-Mangold article on the organizer appeared in *W. Roux' Archiv*. I have paid a tribute to her in an article, "Hilde Mangold, co-discoverer of the organizer" in the *Journal of the History of Biology*, 17, 1-11, 1984.

Hannes Holtfreter and I remained life-long friends until his death in 1992. He became the most imaginative and most productive experimental embryologist of his generation.

Spemann's ingenuity in designing experiments was matched by his craftsmanship in inventing the tools for executing them. He told us that inventing the instruments, the glass needles, hair loops, micropipettes and other gave him as much satisfaction as doing the experiments. His manual skill was remarkable, indeed. Before the breeding season and our experiments began, at the end of March, we were taught how to prepare these tools. Occasionally, Spemann looked over our shoulders; he insisted that they be not just adequate but perfect.

When the salamander females gathered in the ponds, they were brought to the laboratory, where they spent a few weeks in aquaria. They laid single eggs, each folded neatly in a leaf of a water plant. For operations on early embryos, round glass dishes had been provided with a wax bottom. The embryo was prepared by removing the jelly membranes and the vitelline mem-

brane. It was then very soft and delicate and had to be handled very gently. It was placed in a small groove at the center of the wax bottom. The operations were done with glass needles that were drawn out to a very fine point. For a transplantation experiment, two embryos of the same stage were placed side by side. A tiny hole was cut in the host embryo at the site of implantation. Then the transplant was cut out of the donor and transferred to the host in a micropipette. It was fitted in the hole and held in place by a glass bridge. After an hour or two it was healed in, and the bridge was removed. The embryo was then lifted out of the groove and turned over with a hair loop. Steady hands were required because the operations were done under a low-power binocular microscope which magnified our movements. And we had to do hundreds of experiments, because the mortality was very high, in the absence of a balanced salt solution and with no protection against bacterial infection. It took at least two breeding seasons to complete an experiment.

After three years of study, I was ready for work on my Ph.D. thesis. During the years of preparation for this critical moment, Spemann had instilled in all of us an understanding of the intricacies of embryonic development as a sequence of complex interactions between the various parts of the embryo, and thus a great respect for the living embryo which integrates all these interactions. On the other hand, he gave us confidence that our minds could penetrate this complex interplay of forces by way of the well thought-out analytical experiment. I think that we were then not fully aware of the limitations of our endeavors. We had at our disposal only two methods: extirpation and transplantation. The scope of the latter had been broadened by Spemann's introduction of heteroplastic and xenoplastic transplantation. In

retrospect it seems remarkable how much information was obtained by these modest resources.

Spemann did me a great favor by the choice of a topic for my Ph.D. thesis. While most of his *Doktoranden* worked on early embryos and problems closely related to his own interest in determination, induction and regulation, he suggested to me a project in neuroembryology, which was then a modest side-branch of experimental embryology, initiated by Dr. R.G. Harrison of Yale University. I think his idea was to introduce me to a field of research independent of his own. This would later facilitate my academic career. I was to settle a dubious claim by a colleague, B. Duerken: that the normal development of the legs of frog larvae depends on a normal supply of innervation. He had extirpated the right eye of very young larvae; he found, as expected, a hypoplasia of the left midbrain and observed more or less severe abnormalities of the hind limbs in a high percentage of cases. He had then hypothesized that the midbrain deficiency would result in further deficiencies of the central nervous system, all the way down to the lumbar spinal cord and to the innervation of the legs. My results of many hundreds of eye extirpations were somewhat equivocal, and I designed my first original experiment: the production of nerveless legs by the extirpation of the lumbar spinal cord before nerve outgrowth had begun. The legs were normal in every respect, though the muscles became atrophic. Hence, Duerken's hypothesis was disproved. This launched my life-long career in experimental neuroembryology. Thus Spemann, who had discovered the origin of the nervous system as the result of induction by the subjacent mesoderm, had unwittingly opened the door to a deeper understanding of its further development.