the mixed and deep layers is readily obtainable as:

$$\frac{N^*_m/N_m}{N^*_d/N_d} = \frac{K+\lambda+k_{d-m}}{K+k_{d-m}}$$
(7)

Goldberg and Arrhenius (17) have computed a value of  $10^{-4}$  yr<sup>-1</sup> for K. Since this refers to both the soluble and particulate forms of silicon, a reduction by a factor of 2 of the rate of introduction of silicon based on an induction of Rex and Goldberg (13) that up to 50 percent of the silicon enters the oceans in solid phases, gives a more realistic figure of  $5 \times 10^{-5}$  for K. Since K is many orders of magnitudes smaller than other exchange coefficients, uncertainty in K does not affect our model calculations.

A plot of the ratio of the specific activities of Si<sup>32</sup> in the mixed and deep layers, calculated from Eq. 7, versus  $1/k_{a-m}$  is shown in Fig. 3. It is quite clear from the graph that this potentially measurable ratio is a quite sensitive indicator of the rate of mixing of deep waters into the mixed layer. It is of interest to note that this ratio is independent of the production rate of Si<sup>32</sup>. In the same figure, the expected specific activity of Si<sup>32</sup> in the mixed layer  $(\lambda N^*_m/N_m)$ , obtained by solving Eqs. 3 and 7, is plotted, taking for  $R^*$  a value of  $1.7 \times 10^{-4}$  atom/cm<sup>2</sup>/per second. The average silicic acid contents of deep and mixed layers are taken as 120 and 15 micromoles per liter, respectively.

The observed specific activity of 19.6 disintegrations per minute, per kilogram of Si, represents principally a value for the mixed layer, inasmuch as the sponges were retrieved from coastal waters of depths under 100 meters. This corresponds to an average mixing time (that is,  $1/k_{d-m}$ ) of more than 1500 years on the basis of the discussed model.

The quantitative significance of a photosynthesizing siliceous organism in the soluble silicon cycle in the sea can be readily seen by solving Eq. 5 for the biological removal constant B:

$$B = \frac{N_d}{N_m} (K + k_{d-m}) + (K - k_{m-d})$$
(8)

By taking a ratio of 49.6 for the volumes of deep to mixed layers (16), a value of 397 for Na/Nm is found. It is apparent that the second term is trivial compared with the first and can be neglected; furthermore, since K is small compared with  $k_{d-m}$ ,

$$B \approx 397 \ k_{d-m} \tag{9}$$

For likely values of  $k_{a-m}$ , say between  $2 \times 10^{-3}$  and  $5 \times 10^{-4}$  yr<sup>-1</sup>, values of B range between 0.8 and 0.2-that is, the silicon is removed from the mixed layer to deep layers or sediments due to biological activity in mean periods of 1 to 5 years.

In addition to studies of mixing times in the oceans, there are other obvious applications of this isotope as a tracer for studying problems in earth sciences: (i) the rates of accumulation of rapidly growing sediments containing large amounts of biogenous or hydrogenous siliceous phases; (ii) the individual characteristics of water masses within oceans with respect to mixing; (iii) the silicon cycle in the continental hydrosphere; (iv) changes in cosmic ray intensity with time during the last few thousand years; (v) ages of the polar ice caps.

## **References and Notes**

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## Ross Granville Harrison, Experimental Embryologist

Ross Granville Harrison, born in Germantown, Pa., on 13 January 1870, died 30 September 1959. In his 89 years of life he encompassed an era of science in which he found absorbing interest. His early schooling was in Germantown and then in Baltimore. When he entered Johns Hopkins Uni-

versity it was as an undecided undergraduate who was interested in gaining as much general knowledge as possible. He spent many hours browsing in the library. Later he had his own library facilities, and to the end of his intellectual life he enjoyed browsing in literature at a specialist's level.

Harrison's father was an engineer and was called upon to carry out many major engineering projects abroad. One of these was the construction of Russian railways, in the course of which he had to map part of the trans-Siberian railway in order to determine the characteristics of the railbed over this vast and then uncharted land. Ross' son, Richard Edes Harrison, is the recognized leader in modern cartography.

During Harrison's early childhood his mother died and his care devolved upon an aunt. This probably developed in him an early realization of his individuality. He felt early that he was the master of his own destiny. He realized that his father was abroad because of his business and professional problems, so he had no feeling of neglect.

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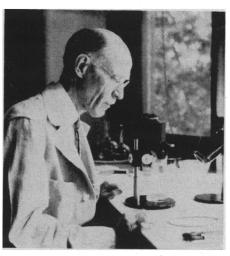
He may not have wished it so, but he accepted the situation without question. During this period he was known as one who walked alone, for he thought nothing of starting out on a 20-mile hike and later of touring most of Maryland and Pennsylvania on a bicycle.

His standing at Hopkins and his interest in biology led him to choose his graduate work in biology, with W. K. Brooks as his teacher. His experience during that period brought him in touch with E. G. Conklin, T. H. Morgan, D. H. Tennent, and others of Brooks' students. His reverence for Brooks was unspoken but real. Brooks' picture hung in his laboratory, and the stories which he told of Brooks, while whimsical, were always related with exceptional respect.

Harrison received his Ph.D. at Hopkins in 1894; his thesis was on the embryological origin of the rays of the fins of teleost fishes. This morphological study was to lead him to study of the paired fins and, later, to his classical work on asymmetry. In the fall of 1894 he went to Bryn Mawr as an instructor and lecturer in morphology. After a year in Germany (1895-96) he returned to Hopkins, as a member of the department of anatomy in the medical school. This was the time when the medical school at Hopkins was becoming the prototype of modern medical schools, with Welsh, Osler, Kelly, Halsted, and Martin on its staff. Mall headed the department of anatomy, with Harrison, Warren Lewis, Lewellys Barker, and Florence Sabin. It was a stellar group.

After several years of teaching, Harrison returned to Germany and earned his M.D. at the University of Bonn in 1899. On his first trip to Germany he had met Ida Lange, whom he married in 1896. From this time on, even as the family grew, all went to Germany each summer. Some of the crossings were strenuous, but during the summers of work and relaxation many of Harrison's acquaintanceships grew into lasting friendships. Of these, I will mention only a few: Sedgwick, Martin, and Bateson in England; M. Nussbaum, Driesch, and Spemann in Germany; Guiseppe Levi in Italy; and Przibram in Austria. These associations, together with his friendship for Anton Dohrn of Naples, were to prove valuable relationships.

When he left Hopkins in 1907 to become Bronson professor of com-



Ross Granville Harrison

parative anatomy at Yale, Harrison was at the beginning of a career which lasted far beyond his academic retirement. When he came to Yale he had President Hadley's promise that a new and really modern laboratory should be built for the university department of zoology. Temporarily Harrison's activities were housed in the old Sheffield mansion, which had been adapted for laboratory use. In it were housed all the ancient facilities and many of the past faculty members, such as Sidney Smith and A. E. Verrill, who were still active, although Smith was almost blind. In an adjacent wing the departments of physiological chemistry, established by Russel H. Chittenden and then headed by Lafayette B. Mendel (with F. P. Underhill), and bacteriology, headed by Leo Rettger, were housed. Chittenden was director of the Sheffield Scientific School and nominally had charge of the departmental appointments which Harrison might wish to make. Wesley R. Coe was the only other active member of the zoology department when Harrison took over.

Within a relatively short time Harrison recruited a staff consisting of L. L. Woodruff and A. Petrunkevitch which. with Coe and himself, was able to carry on the work as it was then scheduled at 1 Hillhouse Avenue. He was fortunate in his choice of men. Coe proved to be of the greatest assistance both in planning the new department which Harrison envisaged and in carrying through the necessary readjustments. Woodruff was brought to Yale from Williams, where he had established a reputation as a stimulating undergraduate teacher. This reputation was upheld during his life at Yale,

and thousands of Yale men secured a scholarly and inclusive introduction to biology through his "Biology 10." The department, in the more than a decade since he relinquished the course, has progressed numerically from Biology 10 to Biology 11 without being able to increase the content or improve the scholarly approach. Petrunkevitch was brought to Yale from Indiana University. He had fled from Russia to Germany, where he studied under the great Weismann. He has since come to be the world's greatest arachnologist. Harrison had good men with him, and they were then, and throughout his career, loyal to him. His attainment warranted their respect, and his treatment of them commanded their loyalty.

But this was not Harrison's only contribution. He demanded of the administration that the science departments be made university departments, and the demand was met. There was for him no division of the academic from the scientific, for do not both together constitute knowledge of the world in which we live? He was more modern in his viewpoint than he thought.

As new branches of zoology appeared he added specialists to the staff: E. C. MacDowell in genetics, Renald Spaeth in the physiology of smooth muscle, Henry Laurens in special sense physiology, B. W. Kunkel in modern morphology, and T. S. Painter in cytology. These men added to the teaching and research potentials of the new Osborn Laboratory, which now was a reality.

Harrison, after securing a laboratory for zoology, insisted that botany be added in an adjoining wing, where it is still located, the facilities of both departments being thus made accessible to students in a real biological sense. Completion of the Osborn laboratories required two years during which Harrison had made daily inspections of construction and had met constantly with the architect to discuss revisions and remodeling to meet changing needs. He planned at least 20 years in advance of his time.

Harrison's training of students was founded on F. P. Mall's system, known to the Osborn students as the "sink-orswim" method. The student did his own planning; his choice of fields was his own. Acceptance or rejection of the method was up to the student himself. Harrison was patient with all of his students as he watched for latent talents to manifest themselves. He recognized that not all could attain the brilliance of an S. R. Detwiler or the mature deliberative thinking of an F. H. Swett. There were quite a few who could not survive the sink-or-swim method but resigned themselves to coddling, which even in Harrison's day was more prevalent than it should have been.

At the time of his retirement he could have said in retrospect that he had created biological experimental science at Yale. He had so advanced the standard of the institution that, where it had once produced only an occasional graduate student in anatomy and zoology, it now was recognized throughout the world as a source of leading anatomists and zoologists. Many from abroad came to study with Harrison.

Scientifically this period was truly a high point for biology. It marked Harrison's solution of the neuron outgrowth riddle which, in its influence on biological thinking, has had value equal to that of Einstein's theory of relativity, Galileo's telescope, or Planck's quantum theory in other fields. His adaptation to animal material of Sach's culture methods, modified according to the needs of the cells to be studied, focused all biological science upon the possibility of eliminating influencing organismic reactions.

Tissue culture had its origin in the discovery of a method which could be crucial in determining the correctness of the neuron theories. One theory claimed outgrowth from the central nervous system (His, Cajal), while the other claimed that the nerves existed in predetermined paths (Hensen). Harrison proved the correctness of the outgrowth theory. His method was simple. He took cells from the central nervous system (spinal cord) and placed them in hanging drops of lymph fluid withdrawn from the lymph heart of the frog. The neuron grew from the central cell body. This marked a turn in the philosophical import of the study of the part isolated from the whole.

It was thus that tissue culture got its start, and the possibilities which can be attained by it have not yet been exhausted. Practical applications are numerous. The method first applied by Alexis Carrel to the study of connective tissues has been followed by many others—Earl, Paul, Fell, and Enders—to the point where it is of primary consideration in certain elementary views of disease.

Harrison attacked the problem of asymmetry with the same critical keenness, unhampered by the restrictions that had accompanied our earlier attempts to study *situs inversus*. By using the limb or the ear, both of which normally show the asymmetry of the side upon which they develop, he was able to devise experiments through which their laterality could be controlled and the rules under which they operate could be described.

The limb shows a gradual determination, with a fixity of its three axes at different times. One of these is established before the limb has become superficially apparent while the others come slightly later in development.

These studies impressed Harrison with the similarity between the formation of a crystal lattice and that of an organic complex, since the spaced (in time) appearance of the axes simulated many of the chemical conditions found. He attempted to secure more unifying data by working with Astbury in studying frozen-dried preparations for their x-ray diffraction pattern at different axial stages. This study, unfortunately, proved inconclusive.

Harrison was a gentle man who

could readily admit mistakes in judgment. He stated, and frequently, "Each day is a day of discrimination, a period of judgment which must be passed on acquaintances, friends and colleagues. I hope that I have answered objectively and critically without being swayed by my personal feelings."

In the era of biology which included Morgan, Conklin, Wilson, Parker, Lillie, and Child, Harrison stood out as an individualist who pursued his research while doing other important things. As a department administrator he handled all affairs with a minimum of red tape. As managing editor of the Journal of Experimental Zoology he set the standards of scientific excellence which he demanded of all contributors. After his retirement he entered the field of administration as chairman of the National Research Council, where he was admired for his complete objectivity. He handled, during World War II, the increasing responsibilities for the national government with which the National Academy and the National Research Council were faced. His decisions, supported by Frank B. Jewett, president of the National Academy, formed the basis of some of our national policy in the critical days of atomic development.

Harrison was a perfectionist, and those of us who knew him best knew that his very human tendency to procrastinate was due to his weighing of all possible relevant evidence. As many of his admirers have stated, his passing marks the end of an era characterized by the dominance of a willingness to serve others, to judge fairly and without prejudice, and above all to seek both the truth and an accurate expression of its meaning.

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