In memoriam: Hermann Hartwig, 1910–2012

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Antler biology mourns the loss of its nestor, whose work laid the foundations for our current understanding of the developmental biology of antler growth and regeneration. After a long life in science, Professor Dr. Hermann Hartwig passed away on 9 September 2012 at the age of 102.

Hermann Hartwig was born on 1 January 1910 in Bielefeld. He attended school at his hometown and in 1929 qualified for university entrance. Subsequently, he was admitted to the University of Greifswald, where he studied zoology, botany, and geology for his first two semesters. He then continued his studies at the University of Göttingen, where he worked in the laboratory of Alfred Kühn. Hartwig's doctoral dissertation concerned the effect of temperature on the thyroid gland of larval fire salamanders and their development. His oral doctoral exam took place on 6 May 1935. The thesis was published in 1936 (*Roux' Arch Entwicklungsmech Org* **134**, 562–587) and Hermann Hartwig's doctoral diploma therefore dates from that year.

After his oral exam, Hermann Hartwig moved to the University of Freiburg where, funded by the Rockefeller Foundation, he worked in the University's Chemical Laboratory that was headed by F. Gottwalt Fischer. Fischer collaborated closely with the director of the Zoological Institute at the University of Freiburg, Hans Spemann (Nobel laureate of 1935), on the chemical nature of the inductive agents operating during early amphibian development. Hartwig's work was focused on oxidation/reduction activities and oxygen consumption in amphibian embryos. He received a friendly welcome into Spemann's group and the contact with Spemann, like that with his teacher Kühn, had a decisive impact on his scientific thinking. Hermann Hartwig's scientific worldview was that of an experimental zoologist, and his

firm belief was that the right way to solve a scientific question was to design and perform the appropriate experiment.

In 1937, Hermann Hartwig moved to Cologne University to take up a position as assistant lecturer at the Zoological Institute. Here, he cooperated mainly with his friend Eckhard Rotmann, a former graduate student of Spemann. Together, they worked on neoteny in newts. During this period, Hartwig also studied the local action of thyroxine in amphibian metamorphosis. He was the first to demonstrate that local metamorphic effects could be triggered by implantation of thyroxine-soaked agar beads.

All further plans for an academic career became futile with the outbreak of World War II. Hermann Hartwig served first as an infantryman and later as member of a bacteriological lab of the Army Medical Service. After the war, he returned into a heavily destroyed Cologne. His foremost activities during the early postwar period were to participate in rebuilding the Zoological Institute and in restarting teaching activities. In 1951, he earned his habilitation and thereafter became a "Dozent" and later a professor. He lectured mainly in the fields of animal embryology and developmental biology, but also in ethology. In the latter field, he was strongly influenced by the works of Konrad Lorenz.

In the early 1960s, Hermann Hartwig started with the work for which he became famous, namely the developmental biology of pedicle and first antler growth in deer. His experiments, which used the classical techniques of tissue deletion and transplantation, were performed on roe deer fawns that Hartwig kept in his private garden, cared for by him and his family.

In a first series of experiments, Hartwig demonstrated that autologous transplantation of the skin overlying the prospective pedicle site of the frontal bone to the thigh region did not result in ectopic antler growth. It was further shown that replacement of the skin from the prospective pedicle site with skin growing in from surrounding scalp areas did not prevent

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orthotopic pedicle and antler growth. In contrast, removal of the periosteum from the prospective pedicle site inhibited pedicle and antler growth. This indicated that in deer, the periosteum of the prospective pedicle site, not the skin, is responsible for the initiation of cranial appendage growth. In a second series of experiments, the periosteum from the prospective pedicle site was grafted to other areas of the frontal or parietal bones, which caused ectopic pedicle and antler growth from these locations. Finally, he demonstrated that autologous transplantation of the periosteum from the prospective pedicle site to the metacarpal region likewise induced ectopic antler growth. The bony structures that formed at the metacarpus were short and abnormally shaped, but covered with typical velvet skin during growth and replaced in synchrony with the antler growing from the unoperated site. Hartwig's seminal paper on these experiments was published, with J. Schrudde as coauthor, in the *Zeitschrift für Jagdwissenschaft* (20, 1974, 1–13).

Hermann Hartwig's discovery of what is now known as the "antlerogenic periosteum" and its decisive role for pedicle (and first antler) formation constitutes a milestone in the history of antler science and opened up a whole new field of research. The first to continue this line of investigation was R. J. Goss, who confirmed and extended Hartwig's findings in a second species, the fallow deer. Further studies then addressed the specific properties of the antlerogenic periosteum in more detail. These studies led to the currently held view that the formation of pedicles and primary antlers is dependent on stem/progenitor cells located in the cambium layer of the antlerogenic periosteum, and that annual antler regeneration depends on the activation of stem/progenitor cells in the pedicle periosteum, derived from those of the antlerogenic periosteum.

Upon retirement, Hartwig discontinued his experimental studies, but retained a keen interest in all questions related to antler growth and morphogenesis. Following the dictum "pathologia physiologiam illustrat," he intensified his long-standing interest in antler malformations in an attempt to achieve a better understanding of normal antler growth by studying specific abnormalities. His occupation with abnormal antlers resulted in some very thoughtful analyses of antler anomalies in roe deer. Given the focus of his scientific interests, it does not come as a surprise that Hermann Hartwig's two last scientific papers, published at age 79 (*Z Jagdwiss* 35, 1989, 130–136 and 184–191), concerned questions of pedicle and antler growth. After discontinuing his own research activities, he followed the progress in antler research with great interest for more than another 20 years.

His former undergraduate and graduate students will remember Hermann Hartwig as an exceptional academic teacher. He was known for his attention to precision in exposition,

both in his lectures and his writings. He also expected precision from his students, and frequently his remarks and corrections on a draft paper were much longer than the draft itself. He was convinced that the search for the right word was always a worthwhile enterprise, and often referred to Mark Twain's sentence that "the difference between the almost right word and the right word is really a large matter—it is the difference between the lightning bug and the lightning." Hermann Hartwig was thus certainly not the "easiest" tutor that one could choose; however, he was always a very engaged one with a strong interest in promoting the intellectual advancement and scientific progress of his students. With many of them, he established a life-long contact, and he followed their careers with great interest and sympathy.

A pervading theme of Hermann Hartwig's life was his love for nature and animals. He kept dachshunds for a long time, his four-legged companion accompanying him each day to work in the University. Throughout his life, Hermann Hartwig was also a devoted student of animal behavior. Thus, then already in his nineties, he could proudly demonstrate to visitors a wild mouse from his garden that he had trained with great patience to climb up the rainwater pipe, proceed through the open living-room window, and take a sunflower seed from his hand before returning into the garden. Since his youth, Hartwig had also been a hunter for whom hunting was a way to come into close contact with nature and to attain a better understanding of wild animals and their behavior.

Herrmann Hartwig was a person of great composure and a very modest man, who never strived for public appreciation and thoroughly disliked all fuss about his person. He lived a secluded life, mostly staying in contact with his friends and colleagues by exchange of letters. His mastery in writing made it a great pleasure to receive a letter from him, either written in his neat and clear handwriting or typed on his old mechanical typewriter, as he never personally entered the computer age. Those forming the "inner circle" enjoyed being invited to visit him at his home and to relish his great hospitality. These afternoon meetings with like-minded people followed an unchanged course over decades and were mostly but not exclusively devoted to the discussion of biological topics of mutual interest. You could give Hermann Hartwig a great pleasure by bringing along an interesting biological specimen, like a malformed antler or an anomalous dentition, or by being accompanied by your dog. On these occasions, he also demonstrated his great talents as a narrator. He was full of anecdotes from his long life and presented them with his typical dry wit. Hermann Hartwig not only leaves an important scientific legacy, but will also be remembered as an upright and sympathetic academic teacher and colleague, and a true professor in the literal meaning of the word.