Obituary Emeritus Prof. Dr. Stephen E. Williams

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It was with great sadness that we learned of the death of our esteemed colleague and good friend Emeritus Prof. Dr. Stephen E. Williams. He passed away on 3 April 2024 at the age of 81. We extend our deepest sympathy to his entire family. His loss also leaves a gap in science that is difficult to fill. His pioneering experiments in the research of the sundew family, in particular the world-famous Venus flytrap, have enriched biology since the 1970s with numerous, much-cited publications. With his excellent skills of observation and keen intellect, he was always able to add surprising details to the scientific knowledge about the "most wonderful plant in the world" according to Charles Darwin.

Stephen Williams with daughter Emily. Photo by Emily Tilley.

I well remember the ICPS World Conference in Tokyo, where my wife Irmgard and I first met Steve in 2002. Unusual structures of a newly described sundew had aroused his interest and he wanted to study them more closely. He approached me during a lecture break to enquire about plant samples from our greenhouse in Germany. Steve offered to examine them with a scanning electron microscope at Lebanon Valley College (Pennsylvania, USA), where he taught biology as a professor. Irmgard and I were delighted and once in conversation we quickly discovered a strong mutual interest in rapid capture motions in the sundew family. At the turn of the century, it was still rare to find such a competent discussion partner on functional morphology.

I was amazed by his detailed knowledge of the role of electrical action potentials, which trigger movement in plants in a comparable way to nerves in animals. In pioneering scientific work, Steve had experimentally examined their function in sundews and the Venus flytrap. As early as 1972, he published the paper "Receptor Potentials and Action Potentials in *Drosera* Tentacles" in Planta with his colleague and good friend Barbara Pickard. In 1982, he attracted great attention when the renowned Science magazine published his research on the closure of the Venus flytrap, conducted with Alan Bennett, in the paper "Leaf Closure in the Venus Flytrap. An Acid Growth Response". Science even dedicated the front page to him. The list of his publications is too long to mention here. However, I will go into more detail about Steve's last projects, which were very close to his heart and in which Irmgard and I had the pleasure and honor of being involved.

In 2002 in Tokyo, Steve, obviously also very pleased, enquired about our experiments with fast catapult mechanisms in sundews. He told us that he had already written to the Australian naturalist Rica Erickson in the 1970s to ask her about rapid tentacle movements in the Australian hotspot of the genus. To no avail, the author of the book "Plants of Prey" (1968) about Australian carnivorous plants was unable to provide any information. Steve knew that the snap traps of *Aldrovanda* and *Dionaea* had evolved from sticky traps. He was convinced that, because of the close relationship, there could be a fast mechanism somewhere in the sundews, which are usually described as quite slow. Now video recordings from our greenhouse showed him exactly such a fast trapping mechanism, as he had long postulated, in an Australian *Drosera*. Even faster than in *Dionaea*. Steve's hypothesis could thus be scientifically confirmed after three decades. Since this discussion at the Tokyo National Museum of Nature and Science, which was so gratifying for both of us, we have remained in friendly contact.

Even after his retirement in 2014, Steve's focus was on the "most wonderful plant in the world". For many colleagues, *Dionaea* was already considered well researched, but Steve still found details that triggered his scientific curiosity. In 2016, he asked by email if we could observe ants in *Dionaea* traps. He couldn't get the book "The Most Wonderful Plant in the World" by Frank Morton Jones (1923) out of his head. The behavior of ants in open snap traps described there aroused his suspicion of an as yet unrecognized phenomenon. This suspicion turned out to be true, but unfortunately for the moment our ants refused to cooperate. Steve also wondered why the famous wildlife filmmaker David Attenborough was able to show a cultivated *Dionaea* with thick drops of nectar being sipped by a fly on the BBC in 1993. During his extensive field tests in 1977 at the Green Swamp, North Carolina, together with Thomas Lichtner, the traps of 152 plants examined and documented with photos were dry, i.e. without visible nectar production. Moreover, flies as prey were major exceptions there. Whenever such contradictions aroused Steve's researcher's curiosity, he never stopped trying to resolve them in a scientifically correct way through research and sophisticated experiments.

So, we scoured the literature and the internet together. Steve had invited me to join his "Private University Consortium" on the ResearchGate science platform years earlier, which made it easier to read relevant papers that Steve, as a passionate teacher, regularly recommended as homework. In addition, Irmgard and I filmed and documented in the greenhouse and garden what and how much of it our numerous Venus flytraps captured. Steve needed the data to compare prey capture in culture with his field studies at the natural site in North Carolina. The results of this close and harmonious collaboration were impressive and we were very pleased when our joint paper "Prey Capture by *Dionaea muscipula*. A Review of Scientific Literature with Supplementary Original Research" was published.

In the meantime, Steve experimented with different wildlife cameras and various lenses for close-ups. He sent me the footage for editing or to create comparative collages for planned technical articles. With his brother, Richard Williams, he developed a stable mount that made it possible to film the ground beneath the cameras. For what purpose? Of course, for long-term recordings of wild growing *Dionaea*. His plan was to document an entire annual cycle in this way. This had to be well prepared.

In the spring of 2019, it came as a complete surprise when little ants decided to build their nest in our garden right next to a group of Venus flytraps. They kept running through numerous snap traps … without triggering them. But why? Steve had wanted just such a set three years earlier for new experiments. When I emailed him photos and suggestions for a series of experiments that could be

carried out immediately, he was delighted. Could we finally solve Frank Morton Jones' "ant puzzle" by this coincidence?

We photographed, filmed and documented the prey of all the plants for a month, with Steve carefully checking that everything was scientifically correct. We counted on a precise schedule how many ants passed through the traps without triggering them. There were many, an average of 520 passages per day. That was enough for a decent statistic. Each day we analyzed the new data and were delighted to see how the ants solved Jones' puzzle more and more clearly. The plant revealed a strategy to save energy by allowing unprofitable small ants to pass unharmed along a scent trail at the upper edge of the trap. Plenty of material for our joint paper "*Dionaea* Traps Selectively Allow Small Animals to Escape" for the December 2019 issue of CPN as well as a film documentary of the same name. A comparison showed how amazingly effective the mechanism found is: only 0.04% of the passing ants were caught. The risk of a hospital patient dying from a treatment error in Germany is 0.1%, which is 2.5 times higher. Steve was really pleased to see that Jones' "ant puzzle" could be solved so clearly.

Then Steve's last big project made progress. In 2019, he contacted Bill Scholl in Florida, who owns a plot of land with wild growing *Dionaea*. Steve and Bill knew each other from some CP-events and he was planning to install three time-lapse cameras there with his brother Richard and his daughter-in-law. Unfortunately, Covid intervened. The planned trip was canceled. So, Steve sent a first camera with the special mounts by post. Bill Scholl managed to get such remarkable shots that he ended up with three cameras, which he monitored regularly. One camera ran continuously from May 2020 to January 2024.

Steve regularly sent me the footage via OneDrive for editing. This project was very close to his heart. He followed the editing of the raw material with excitement. Once again, it was a very harmonious collaboration and we were both really happy when the single shots taken during rain and storms, including a hurricane and controlled fires, gradually developed into an almost smooth, informative time-lapse during editing.

Then the bad news began. Since March 2023, the project has been on hold for a while due to hospitalization and a cure. Thankfully, Steve's daughter Emily kept in touch with us when her father was temporarily unable to do so. I was finally able to show Steve the finished timelapse film in May 2023 and he delightedly gave the green light to upload it to YouTube under the title "Monitoring Venus Flytraps. Amazing 1-Year Timelapse." It was to be Steve's last big project. In one of his last emails, Steve wrote: "Siggi, … I am still alive but not doing so well these days. I wish I had more time for Carnivorous plants." And typical of Steve: "I think that the article linked at the end of the message below will interest you."

In April 2024, an email arrived from his daughter Emily with the sad news of his passing. Dear Steve, we all miss you so much. Rest in Peace.

I would like to take this opportunity to pass on to Steve's family and friends the spontaneous condolences received from a number of scientific colleagues who knew him and appreciated his expertise. Dr. Jan Schlauer (University of Tübingen) mentioned: "Very sad news, indeed. Stephen was one of the first investigators to describe the closing movement of the Venus flytrap as an acid growth process at a time when it was widely considered a "simple" turgor loss response like in the pulvini of Mimosa."

Dr. Simon Poppinga (Scientific director of the Botanical Garden of the TU Darmstadt) wrote: "Even though I was unfortunately never able to meet Stephen in person, we were still "digitally closely connected" over the last few years. I fondly remember his many, sometimes very long and

detailed emails in which he reported on largely unknown peculiarities of Venus flytraps and sundews. For example, he put their trap leaves into the so-called Scholander bomb to determine their water potentials. He also determined the stiffness of the epidermises of the Venus flytrap trap leaf qualitatively and by hand, by treating them in the open and closed states with a punch roller. I was fascinated by his profound comments and recommendations of current literature. He was always an astute reader and critic, and answering his questions about my own publications satisfactorily was always both a pleasure and an excitement for me. It is a pity that Stephen is no longer with us."

And Dr. Andreas Fleischmann (Curator of vascular plants Botanische Staatssammlung Munich), whose words I would like to quote in conclusion: "I will always remember having met Stephen Williams at the ICPS Conference 2006 in Frostburg, where I enjoyed chatting with him about carnivorous plants. The pioneer in carnivorous plant action potential research was a very kind, helpful and cheerful colleague - I will miss the scientific carnivorous plant correspondence I had with him in the past years. Rest in peace, Stephen."

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