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Justin Schmidt's originality

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Abstract

The research career of Justin O. Schmidt (1947–2023) is reviewed and assessed. The pioneering nature of his research lay in treating the defensive means and tactics of aculeate hymenoptera and some arachnids as features of their overall anti-predator strategies. He devised methods for comparing the effects of hymenopteran venoms and stings that challenged the assumed correlation between venom potency and the pain that it induces.

Keywords

Dasymutilla, defensive tactics, honey bee, Hymenoptera, *Pogonomyrmex*, sting, venom

Introduction

Justin Orvel Schmidt (1947–2023) was an American entomologist, the main focus of whose long and fruitful life in science was stinging insects (Hymenoptera: Aculeata) and how venom figured in their lives. He was born in Wisconsin, USA into a middle-class family. During most of his life he lived in the USA, while traveling widely and studying stinging insects in the field in all habitable continents. Our purpose here is to characterize Schmidt's research program and how it stands apart from all others. In this we have relied on some of his writings (especially his 2016 book "The Sting of the Wild" and an unpublished 2020 autobiographical essay), some of what others have written about him (Binford et al. 2023; Cane et al. 2023) and our long personal association with him.

Becoming a Chemical Ecologist

Schmidt (Fig. 1) was born on 23 March 1947 and spent his formative years in Pennsylvania, USA. Like many children, he was drawn to natural history from a very early age. Unlike most, he persisted throughout his life in a powerful fascination with nature and its creatures and a desire to make sense of their workings.

He was first introduced to stinging insects as a child when he accepted a challenge from other boys to throw a stone at a nest of the large social wasp *Dolichovespula maculata*. For this he was punished by the wasps. During his primary and secondary schooling he showed a keen interest in many fields of natural science, of which chemistry came to take precedence. He received his BS in Chemistry in 1969 at Pennsylvania State University and then enrolled in a PhD program in the same area at the University of British Columbia. However, as a student at UBC two factors prompted a major change in direction. First, the working environment of a professional chemist -- white lab coats in a room smelling of solvents – was distasteful to him. Second, he had a long-standing affinity with insects and the outdoor activities of natural history. The critical point may have come when his wife, Deborah, remarked to him one day that by temperament he was a biologist, not a chemist. Accordingly, he downgraded his Chemistry degree to an MSc (1972). This presented a dilemma, as Debbie had yet to complete her degree. Justin made use of the interval by enrolling in the College of Education to obtain his teaching certificate for high school science. While he never taught high school, he considered the training worthwhile in developing the skills in making public presentations that were later to become a large part of his activity.

Upon completion of their degrees at UBC, the Schmidts moved across the continent for graduate study at the University of Georgia (UGa). It was a natural development for Justin to combine his expertise in chemistry with his developing strength in natural history to focus on chemical ecology. His major professor, Murray S. Blum (1929–2015) (Fig. 2), was a pioneering figure in the chemical interactions of insects with their environment and with each other. Also advantageous was the presence in UGa's Department of Entomology of Robert S. Matthews, a specialist in insect behavior, and Henry R. Hermann, the leading expert on the hymenopteran venom apparatus. As outlined below, it was as a student at UGa that Schmidt framed the research program in arthropod venoms and envenomation that would be his main occupation for the rest of his life. It should be noted that during this period Debbie succumbed to a rare and very aggressive form of cancer.

Schmidt met his second wife, Patricia, in Arizona. In some ways they were a very good match, as she shared many of his scientific interests and collaborated well with him in field work. However, a stable, harmonious marriage requires more than that, and after some years they parted company. A few years later he recruited a promising student from China, Shen Li, to study in the USA and aid in his research. It is a well-known rule that "nothing propinks like propinquity", and in time she became his third wife, remaining with him to the end of his life.

Figure 1. Justin O. Schmidt early in his post-doctoral career. Source: Archive of the International Union for the Study of Social Insects.

An innovative research program

Stings and venom were a matter of comment already in classical antiquity. In the 2nd century BC, for example, Nicander of Colophon (1953) presented an extensive list of stings and their remedies. Similarly, two centuries later Pliny the Elder (1855) listed many supposed antidotes to various stings. However. this remained the extent of writings on the topic until much later. Later centuries saw an increasingly exact understanding of such aspects as the composition of venoms and their effects on human health (e.g. Piek 1986). In addition, there gradually emerged more or less isolated studies of various biological aspects of venoms.

Accordingly, there was already a substantial literature on the venoms of Hymenoptera and other arthropods when Schmidt entered the field in the mid-1970s, although with a predominant medical/pharmacological focus. Almost entirely missing from the literature was research from the animal's point of view, and the few studies taking such a biological viewpoint can best be described as scattered or isolated. The larger question remained "What roles do venom play in the lives of those who synthesize and deploy them?"

Justin Schmidt's originality lies precisely in addressing this question with respect to a wide array of creatures, especially aculeate Hymenoptera. As he later expressed it with respect to his experience in Georgia (Schmidt 2020), "I had finally found

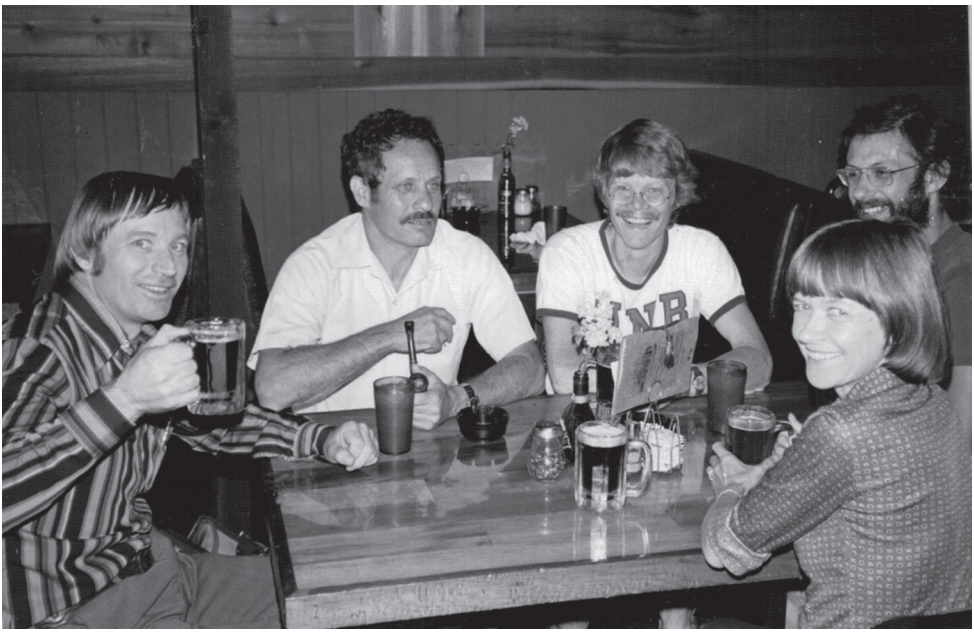

Figure 2. Murray S. Blum and associates circa 1980. Left to right: Post-doc David J.C. Fletcher, Blum, Schmidt, Mrs Pauline Fletcher, Post-doc Clive G. Jones. Source: Archive of the International Union for the Study of Social Insects.

what I wanted to do in life. That was, study defensive behaviors and venoms of ants, wasps, and bees, and how they enabled the evolution of sociality in the Hymenoptera."

We can depict the components of Schmidt's research program in a two-dimensional graph, in which each dimension represents a group of thematically-associated problems (Fig. 3). On the x-axis are some of the main means by which arthropods defend themselves and – in the case of social insects – their colonies against predators and other natural enemies. On the y-axis are aspects of venom studies. While the whole of Schmidt's research ranged over much of this graph, its core lies at the interface between the two axes, the effects of stinging on the adversary.

The two dimensions are already apparent in Schmidt's (1977) PhD thesis. Titled "Defensive strategies of wasps and ants: *Dasymutilla occidentalis* and *Pogonomyrmex badius*", it comprised three chapters. The first analyzed the full repertory of physical and behavioral defensive features of the solitary wasp *D. occidentalis* that make it all but invulnerable to most classes of potential predators, although not to all of them. The other two treated the biochemical, pharmacological and toxicological features of the venom of the harvester ant *P. badius*, all within the context of the life of the colony. While working on *P. badius*, he also collected and studied several other members of the genus toward understanding how and why their venoms varied. This arose from the question of why their stings were so painful and the venom so very toxic. It was a natural progression from there to extend attention to a broad array of aculeate Hymenoptera, with some attention to arachnids.

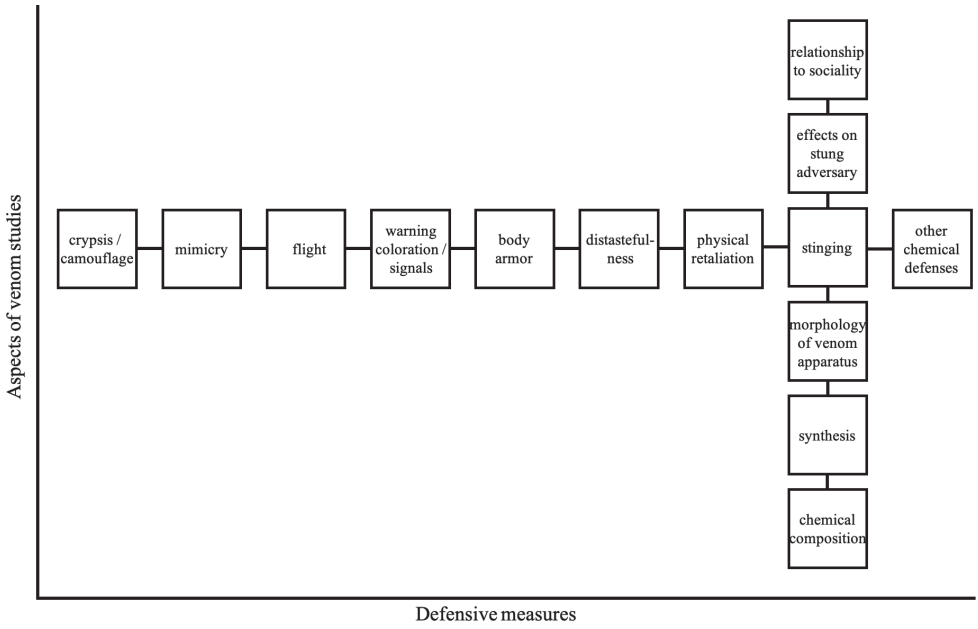

Figure 3. Diagrammatic representation of the scope of J.O Schmidt's research program. Further explanation in text. Graph by Nova Y. Starr.

His decades of investigations of a great many additional species and the nature of their venoms has opened a new era in the biological understanding of stinging insects. He devised and implemented new ways of extracting venom, analyzing its chemical composition and comparing venom toxicity, and documented the relative pain of their stings to humans. Once again, let us emphasize that the focus of this latter was not how we humans feel about this or that sting but on what it means in the lives of those who sting. Over the decades one of us (CKS) has recorded stings (and a few sting-like bites) from more than 60 species of Hymenoptera. That is quite respectable, but Schmidt (2016: Appendix) tops it with his own list of effects from 77 species, which appears not to comprise his entire experience.

No one before had addressed the question of what tissue damage from stings has to do with the pain that they cause. Perhaps the most striking result of Schmidt's comparative studies across taxa was the conclusion that there is no particular correlation between these two aspects, all within the context of their significance in the life of the insect (Schmidt 2016, 2019). He found, for example, that they very painful stings of spider wasps (Pompilidae) have very low toxicity.

One occasionally encounters the notion of Schmidt as a strange guy who liked to be stung. This is nonsense. He very seldom deliberately induced a sting, and then only when he had no other way to find out how much it hurt and its other effects. It was all in the interest of science, and of course when he did get stung by chance he was not going to let it go to waste but took careful note of the effects.

Before Schmidt, the roles of venoms in the lives of stinging animals had seldom been treated in any but a perfunctory manner, and the effects of venom on the stung

had remained a pharmacological question. Part of Schmidt's radical departure was to separate three kinds of sting effects in the affected animal -- pain, tissue damage, and immobilization, especially the first two – and to ask how and why these should vary among venomous animals. His most striking result was that there is at most a very weak correlation among the different effects. While some insects (e.g. harvester ants, *Pogonomyrmex* spp.) have very painful stings that are at once highly toxic, some others (e.g. spider wasps, Pompilidae) deliver very painful stings that quickly immobilize their prey but are of only slight toxicity. This led to the conception of stings as a deception or false alarm, and selection pressure on some predators (e.g. skunks on soil-nesting social wasps and bees) to disregard the pain.

Taking this separation of effects a step further, a part of his biochemical research consisted in identifying venom components that cause pain and those that cause tissue damage (Schmidt 2016: Ch. 5).

In trying to understand why harvester-ant stings, for example, are so painful to humans (and presumably to most other vertebrates), Schmidt directed his attention to both proximate and ultimate causation. That is, he addressed both the question "What is it about the venom or its delivery that makes it hurt so much?" and "How is it in the ants' interest for their stings to hurt so much, or is it?"

The Amateur Scientist

Some comment on Schmidt's employment history is in order. Aside from a brief post-doctoral position in Blum's lab not long after completing his PhD, he was hardly at all employed to do the research that we describe here. Most notably, his one long-term job (1980–2005) was as a bee nutritionist at the Carl Hayden Bee Research Center of the US Department of Agriculture (USDA) in Tucson, Arizona. It bears mention that he had no experience in beekeeping aside from a very limited project in a youth group long before.

As the African honey bee, *Apis mellifera scutellata*, moved north through Central America toward the southern USA in the 1980s, his official duties came to include some attention to monitoring and managing "killer bees", while he was still paid mainly to work on such questions as characteristics of various pollens that make them attractive to the bees. Accordingly, as a venom researcher Schmidt was an amateur in the narrow sense of one who does it out of avocation, rather than gainful employment.

The conditions of his employment are very much relevant to this factor. Unlike the considerable freedom of research in academia, government labs tend to be quite restrictive in the problems that scientists may pursue. He later commented (Schmidt 2020) that "The change from an academic and intellectual environment in Georgia to a USDA environment in Tucson was an earthquake-sized cultural shock." To him, the USDA lab was little better than an intellectual wasteland and one beset by bureaucratic obstacles to serious research. These latter extended to suspicion of independent research outside of working hours. He gained some relief as an adjunct member of the

graduate faculty in Entomology at the local University of Arizona. As another major work-around, he established a substantial home lab as the Southwestern Biological Institute, in which he kept a broad array of experimental animals. In addition, he lived and worked in a spectacular part of the country, the Sonoran Desert, with a grand abundance of creatures of interest. The result of these factors is in abundant evidence in his research output. If anything, this increased in intensity after his retirement from the USDA in 2005.

It should not be supposed that Schmidt neglected the job for which he was paid. As seen in his list of publications, he was productive in projects relating to beekeeping, even if these may not figure prominently in his legacy.

The final push

After receiving a number of hints over the years that all was not well in his physical makeup, in 2013 Schmidt was unequivocally diagnosed with a relatively severe form of Parkinson's Syndrome. It affected his mental acuity hardly at all, but it gradually came to impose severe physical limitations. It was plain that he could not expect to live a great many more years. Facing the situation, he determined to give greater attention to completing his research projects, with emphasis on those already at a fairly mature stage. At the same time, he also accepted some invitations to prepare papers that could be completed relatively quickly (e.g. Schmidt and Overal 2021). As seen in the bibliography (Suppl. material 1), the last 10 years of this life saw the publication of 55 papers and "The Sting of the Wild".

The Public Intellectual

Many scientists and others with advanced degrees are quite incapable of communicating their subjects to the general public (if it even occurs to them that they should try). Schmidt was very far from being in this mold. There was a keen public interest in stinging insects and arachnids, and he was the very rare individual adept at satisfying it. He knew the subject in greater depth than anyone else, communicated well to individuals and groups in all sectors of society, projected well on television, and he was glad to go public.

Schmidt had always been a sought-after speaker at scientific gatherings, interviewed several times by the news media, and in 2015 a recipient of the prestigious Ig Nobel Prize (https://en.wikipedia.org/wiki/List_of_Ig_Nobel_Prize_winners). With the success of "The Sting of the Wild", he became yet more of a public figure and in greater demand for interviews. Most prominently, he was a featured guest on the "Jimmy Kimmel Live" television show https://spaces.hightail.com/space/rFcTAWlG1a. "The Sting of the Wild" probably did as much as all of his media appearances to promote the biological view of venoms and stinging. It is presented in an unrelenting spirit of

curiosity, even of fun, with many episodes of trial-and-error learning recounted. One virtue of the book is its frequent mention of unanswered questions. Although he never held an academic position, Schmidt was very much a teacher, as the many younger individuals that he mentored can testify (e.g. Binford et al. 2023). In pointing to areas of ignorance, he was plainly hoping to stimulate and guide others to provide answers through research.

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* Asterisks mark a selection of Schmidt's papers that we consider most significant (whether cited in this paper or not). For a complete list of his research publications, see the Suppl. material 1.

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Supplementary material 1

Publications of Justin O. Schmidt

Authors: Christopher K. Starr, Robert S. Jacobson, William L. Overal

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