

Linzer biol. Beitr.	55/2	495-622	29.12.2023
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## Hannes F. Paulus - a versatile biologist celebrates his 80th birthday<sup>1</sup>

Hannes F. PAULUS

**Abstract:** On the occasion of his 80th birthday on October 17, 2023, Hannes F. Paulus compiles details of his scientific career. His paths to entomology are described as a schoolboy, during his school days in Mainz and during his biology studies in Mainz and Vienna. His encounters with Prof. Friedrich Schaller in Vienna and later with Prof. Günther Osche in Freiburg shaped his further scientific career. Beginning with his doctoral thesis on the eyes of collembolans, he expanded his research in Freiburg into the evolution of arthropod eyes. This eventually led him back to Vienna as a full professor, succeeding Schaller. Here he finally started a family and married Urte Paulus, who is herself versatile, creative and internationally successful. Two children, now grown up, are one result. Further research focused on the pollination biology of the orchid genus *Ophrys*. Here, important mechanisms of sexual deception were elucidated with the help of his colleagues. Systematics ran through his entire scientific life. He was able to describe a whole series of new species and genera of beetles and even over 40 new species in the genus *Ophrys*. All taxa newly described by Hannes Paulus are listed. He was allowed to give numerous lectures, many lectures and exercises at his universities. Excursions with students, but above all for his research, took him mainly to the Mediterranean region. His scientific work consists of many publications, several books and films. All publications are arranged according to subject area. He still has plenty of projects and plans for further work.

**Key words:** University of Freiburg, University of Vienna, Department of Evolutionary Biology, scientific opus of H. Paulus, *Ophrys*, new species list, pseudocopulation, systematic of Coleoptera, Orchidaceae, evolution of arthropod eyes, Byrrhidae, Lymexylidae, list of publications.

### Foreword

*Just a few decades ago, it was a matter of course that diversity of topics in biology was practiced and taught by university staff. The pressure exerted by ECTS (European Credit Transfer and Accumulation System) and the impact factor, as well as third-party funding, led to the gradual decline of some disciplines, particularly organismic biology and other areas of this discipline. Taxonomy, morphology, but also faunistics, floristics, the history of science and related topics require long periods of work, the creation of collections, extensive literature research and, if necessary, visits to external research institutions. Students and university staff have too little time*

<sup>1</sup> **English version of:** „Hannes F. Paulus – ein vielseitiger Biologe feiert seinen 80. Geburtstag“ [https://www.zobodat.at/publikation\\_volumes.php?id=72607](https://www.zobodat.at/publikation_volumes.php?id=72607)

*and resources available for this in times of ever-increasing knowledge growth, and the collections at Austrian universities that are required and maintained by the custodians are largely non-existent anyway. What is the solution to this plight? The focus is on topics for which no broad knowledge of species, no study of literature back to Linné, no collection facilities and therefore no disproportionate amount of time is required to produce top papers. Molecular genetics as a collective term seems to be the solution here, which also means that the flow of third-party funding and publisher-controlled impact evaluations are proceeding as desired, unfortunately at the expense of species knowledge, which should enjoy the highest priority in times of biodiversity crises.*

*These preceding lines should by no means give the impression that molecular-biological research has no importance or necessity, quite the contrary, only that a balanced training and publication track should be pursued that meets all the requirements of a modern and necessary research strategy.*

*Which brings us to our well-wisher Hannes Paulus, who is probably one of the last of his guild to have immortalized himself through the breadth of his research. Taxonomy, systematics, phylogeny, morphology, faunistics, evolutionary biology, physiology, ecology, floral biology, population genetics and DNA studies, learning behavior and signal evolution in both botany and zoology (Coleoptera, Lepidoptera, Hymenoptera, Chelicerata), didactics, provision of illustrative materials, historian of science, publisher, editor and reviewer of scientific journals and books, his range of activities is almost incomprehensible. Finally, it should be noted that Hannes also earned merits at his university through his numerous lectures, seminars and student excursions, supervision of systematic-taxonomic work, lectures, and through his association activities in the Austrian Entomological Society. It should also be noted that Hannes Paulus did not cultivate any academic arrogance and willingly shared his knowledge with interested parties. His mental and physical fitness should also enable him to pursue his hitherto unchecked scientific curiosity for many years to come, for which we wish him all the very best. Ad multos annos!*

Fritz Gusenleitner, Esther Ockermüller

## **Biography of Hannes F. Paulus**

### **My childhood**

Towards the end of the Second World War, I was born on October 17, 1943 in Berlin-Schöneberg in the midst of the turmoil of war as the son of Annemarie Paulus and Hannes Kubsch (stage name Hannes Dahlberg, born on January 11, 1921), who was missing at the time. Unbeknownst to the family, my father was interned as a political prisoner in Buchenwald concentration camp at the time, and later in Mauthausen and Ebensee. He belonged to a group that was very committed to helping numerous Jews escape from Germany during the last years of the war in order to avoid being

murdered in concentration camps. However, one day he was betrayed and classified as a political prisoner and interned in the aforementioned concentration camps. He also survived thanks to his pseudonym Dahlberg, as this meant that it was never recognized that he was half-Jewish.<sup>2</sup>

After weeks of bombing in Berlin and being buried in a cellar for days, my mother finally fled with me as a young baby from Berlin to Genthin near Magdeburg in what was then the Russian zone, later to become the GDR (Fig. 1a). When the borders of this zone threatened to be closed to the west in 1948, my mother crossed this border with me, now almost 5 years old, at night and in fog in order to reach her relatives in Koblenz.



**Fig. 1a-1b:** Left: My mother Annemerie Paulus and me in the age of 8 month; right: my father (Hannes Dahlberg) with me on 30.8.1947.

In Koblenz, I started school for the first time in 1950 at the Schenkendorf School, but was soon interrupted by a 6-month cure for pulmonary TB, after which I went back to first grade in Dienheim near Oppenheim (I was placed in a village children's home there). In the meantime, my mother had followed the state government of Rhineland-Palatinate, which had moved from Koblenz to Mainz in May 1950, as she had found a job at the Ministry of Finance. We initially lived in the Kettelersiedlung (Görresstrasse 32) on the western edge of the city. A year later, I finally went to the Eisgrubschule (elementary school) in Mainz. I then attended a humanistic grammar school in Mainz (Rabanus-Maurus-Gymnasium), but soon switched to the Gutenberg-Gymnasium, a science and modern language grammar school, where I passed my Abitur in 1966, following my scientific inclinations. These years at grammar school were very rocky for me, as I was considerably behind due to the two changes, first in English and then in French, which I was never really able to catch up

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<sup>2</sup> Some of the painful family stories in the course of the Nazi persecutions and murders in the concentration camps can be found in the book: Ruth FRIEDLÄNDER and Werner GUTER (2010): *Out of Berlin. The Friedländer and Guter Families 1933-1945*" (privately published by Drukkerij Amsterdam B.V., 454 pages) (<https://www.worldcat.org/title/out-of-berlin-the-friedlander-and-guter-families-1933-1945/oclc/679975047>).

on. So-called "honor years" were the result, which I only really mastered in the upper school.

A special event in my school days in Mainz was the first visit of Queen Elizabeth of Great Britain to Germany. On May 20, 1965, I had the pleasure of joining Queen Elizabeth II on the Rhine boat from Koblenz to Kaub and Bacharach with my school class from Gutenberg-Gymnasium in Mainz. During this trip, the Queen also came up to us and exchanged a few words with me, among others, as I was standing directly opposite her. I had to think about this when I learned of her death on September 8, 2022, 57 years after this encounter. She died at the proud age of 96 at her castle in Scotland.

My mother continued to live in Mainz until her early death. She died in 1983 at the age of just 63 after a gross "medical error" by a doctor at Freiburg University Hospital. My mother had heart problems and was supposed to have a pacemaker implanted after a cardiac catheterization. Recognized too late, she bled to death from this catheter.

After graduating from high school, I began studying biology and philosophy at the



**Fig. 2:** Ceremonial doctorate (sponson) and graduation on May 2, 1971 in the ceremonial hall of the University of Vienna

University of Mainz in 1966 and moved to Vienna in the fall of 1968 after completing my intermediate diploma. It was here that I met Prof. Dr. Friedrich Schaller, who influenced and encouraged me on my further path in zoology. In 1971, after just 10 semesters of study<sup>3</sup>, I completed my dissertation: "On the ultrastructure of the eyes of some collembolans". The graduation ceremony took place in the university's Great Ceremonial Hall, without realizing that years later I would be the promoter and present the doctoral candidates and diploma students with their certificates (Fig. 2). My doctoral thesis itself was a scientific paper on the ultrastructures of collembolan eyes, which was to pave the way for my later university career. The topic even led to my return to Vienna in 1991 to succeed Prof. Schaller as a full professor in the Department of Zoology and to reestablish his Department of General Zoology as a

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<sup>3</sup> This was still possible at the time, as a diploma course was only introduced in Austria with the university reform of 1975. Until then, you could complete your studies with either a dissertation (Dr. phil.) or a state examination (Mag.). After that, there was the degree Mag.rer.nat. (Austria) or Dipl.Biol. (Germany). Those who had further ambitions could then do a doctorate (Dr. rer.nat.). It was not until the Bologna Declarations of 1999 that Master's and Bachelor's degree programs were introduced instead.

separate Department of Evolutionary Biology. At the time, it was the first scientific institution in this discipline at a university in Austria.

After my retirement in 2013, my successor Prof. Dr. Dr. Andreas Wanninger initially renamed my department "Integrative Zoology". However, just a few years later, my old department was renamed back to Evolutionary Biology with a Department of Integrative Zoology as part of the reorganization of the faculty.

I only got to know my father (Fig. 1b) personally many years later, together with his 3 children, my half-siblings. He had married after the end of the war, initially unaware that I already existed as his son. As a political prisoner, he had narrowly survived his time in Buchenwald and Mauthausen (Ebensee) concentration camps thanks to the just-timely liberation by the Americans. The first time I met him in Berlin in his office on Kurfürstendamm (he worked there as a director, writer and screenwriter) was unforgettable for me, especially because it was there that I first met my half-sister Sabine, whom I didn't know. She later worked as a hotel manager and is now a sales and marketing consultant. The next big encounter was a few years later, when Sabine got married and this was combined with a big family celebration at the Kubsch family home in Berlin-Dahlem. It was here that I finally met my two half-brothers Christian ("Kiki") and James Kubsch, who only found out that there was another half-brother shortly before I arrived at the house. Christian later made a career in Los Angeles as a manager for the construction of "game parks" and as a special effect's director in various major film projects (including Harry Potter films). Until his retirement, James Kubsch was a pilot for a small management company (including gold trading), whose business partners he flew around the world. He and his wife Anja lived with him in Grenzach-Wyhlen near the Swiss border near Basel until my father's death. He died on 3.3.2012 at the age of 91.

### **Some other private matters**

During my doctoral thesis in Vienna, I met my future first wife Friederike Gruber and her extended family at the College (now University) of Natural Resources and Life Sciences in Vienna. She had five siblings who worked as doctors (Helmut Gruber as a professor of anatomy and Walter Gruber as a professor of gynecology at the University of Vienna), pharmacists (Helga) and medical-technical assistants (Hertha). The youngest sister Eva worked as an artist together with her husband Klaus Pitter. Klaus Pitter is still a well-known cartoonist and illustrator today<sup>4</sup>. Friederike also wrote her "term paper" on the vertebrate brain in the zoology department at the University of Natural Resources and Applied Life Sciences. After completing my doctoral thesis in 1971, she followed me to Freiburg, where I had found my first job as a university assistant in Biology I (Zoology). While still in Vienna, she initially worked as an AHS teacher<sup>5</sup> for biology and sport. Unfortunately, she was unable to find a suitable position in Freiburg, as school bureaucratic hurdles prevented this. After teaching at private schools in Freiburg, she turned to other activities and finally worked as a

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<sup>4</sup> [https://de.wikipedia.org/wiki/Klaus\\_Pitter](https://de.wikipedia.org/wiki/Klaus_Pitter)

<sup>5</sup>AHS = Allgemeinbildende höhere Schulen mit drei Zweigen: Gymnasium, Realgymnasium und Wirtschaftskundliches Realgymnasium.

passionate potter with a large workshop ("Fabrik" in Freiburg<sup>6</sup>) until her early death<sup>7</sup>. The marriage ended in 1993 without children.



**Fig. 3:** Drawing from Klaus Pitter (Cartoonist), Wien, 1993 at my 50. Birthday: "and that was just the warm-up training".

**Fig. 4:** My family: Marko, Maria (at her matura), Urte and Hannes Paulus (Wien 17.6.2011).

My appointment in spring 1991 as Full Professor of Zoology-Evolutionary Biology at the University of Vienna was also associated with a change in my private life (Fig. 3). In 1993 I married Urte Freitag, who had secretly followed me from Freiburg to Vienna in a furniture van in 1991. This marriage produced two children: Maria (1993) and Marko (1995) (Fig. 4). Maria studied astrophysics in Glasgow (Scotland) and received her doctorate in astrophysics from the University of Munich and the Max Planck Institute in Garching in 2021. She currently works at Zeiss in Munich. Marko studied spatial planning at the Vienna University of Technology and graduated with a degree in engineering. My wife Urte Paulus continued to study spiders after completing her diploma thesis in Freiburg and Vienna. This resulted in the publication of her diploma thesis on wolf spider successions in a glacier forefield in the Zillertal Alps in 1997<sup>8</sup>. During our numerous stays in Gran Canaria<sup>9</sup>, we mainly collected wolf spiders, which were processed in the course of a diploma thesis by Martin Hepner together with material also collected by him (HEPNER & PAULUS 2009). It was even possible to describe a new species (*Alopecosa thaleri* HEPNER & PAULUS, 2007). On the island, I was fascinated by the very conspicuous mating flight behavior of the large predatory fly *Promachus latitarsatus*. I therefore had Wolfgang Moser from Vienna investigate the biology of this fly in a diploma thesis in 2004-2005.

<sup>6</sup> <https://www.fabrik-freiburg.de/keramikwerkstatt>

<sup>7</sup> On December 23, 2000, she died in a car accident at the age of just 55. The funeral took place on January 15, 2001 in Vienna's Hernals cemetery.

<sup>8</sup> PAULUS U. & PAULUS H. F. (1997): [https://www.zobodat.at/pdf/BERI\\_84\\_0227-0267.pdf](https://www.zobodat.at/pdf/BERI_84_0227-0267.pdf)

<sup>9</sup> I had inherited a small apartment in the south of the island from my aunt Hannelore Paulus (my mother's sister) after she died.

Urte stayed at home for the sake of the children, of course, but was also involved in spider, insect ("Insects for kids") and dance projects at kindergartens and schools in Vienna (especially in Mauer). From 2000, Urte Paulus devoted herself more and more to archery (longbow) and achieved the highest national and international successes (world champion, multiple European champion, multiple Austrian champion). She was the national coach for the Austrian squad and is currently a national and international coach trainer. She recently published a comprehensive work on archery (Fig. 34)<sup>10</sup>. She is also the author of various articles in archery magazines and has written poems and stories that have been published in two volumes. I myself am still an archer in my spare time. After years of intensive activity in a jazz dance group, she joined a Viennese hula dance group that cultivates the tradition of these Hawaiian dances. She even won another European Championship title with this group in Vienna in 2018<sup>11</sup>. As if that wasn't enough, she recently joined a line dance group and was awarded the title of Viennese champion in September 2023 and in December 2023 with her group the title world champion in Kreuzlingen (Svizzera).

### **My path to entomology**

Even as a young boy in Genthin near Magdeburg, I was fascinated by the cockchafers that were still common at the time, for which a neighbor had built me a "cage aviary" out of a large cardboard box with strings stretched back and forth. I could watch the balancing acts of the beetles crawling on them. Even as a schoolboy in Mainz, I continued to be fascinated by insects and other "small animals". To my mother's horror, I once brought a shoebox full of spiders into my room and hid them under my bed, where they were soon discovered. We lived in the Kettlersiedlung housing estate at Görresstrasse 32 on the western outskirts of Mainz. My most important playground was a large open space, today's Volkspark, which at the time was an overgrown former Nazi Thingplatz, with numerous bunkers and several fire-fighting pools. As children, we also played inside these bunkers and discovered all kinds of relics of the past "3rd Reich", such as officers' sabres, knives, Nazi insignia, steel helmets, even bombs and hand grenades etc. Above all, however, there were all kinds of butterflies flying around the site, and one day I was particularly fascinated by a swallowtail. I had previously put together a collection of pictures of local butterflies, published by Gütermanns Nähseide<sup>12</sup>. My first butterfly in 1955 was actually a swallowtail sitting on the ground, which I was able to capture with a jam jar (!). This was followed shortly afterwards by another interest, namely beetles, which I have continued to study to this day. Together with friends and schoolmates, we explored the near and far surroundings of Mainz. We were particularly fond of the sparse Rhine meadows near Gustavsburg, the Gonsenheim Forest and especially the Mainz sands, a post-glacial steppe relict<sup>13</sup>. This initially developed into a kind of

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<sup>10</sup> PAULUS U. (2019/2023): Das große Buch vom Bogensport. Lehrbuch für Anfänger, Hobby-, Wettkampf-, Leistungsschützen und Trainer. ISBN: 978-3-938921-65-4, 5. Auflage, 568 Seiten, farbige Fotos und Abbildungen. [https://bogenschiessen.de/bogenschiessen/de/verlag/buecher/neue\\_buecher.php](https://bogenschiessen.de/bogenschiessen/de/verlag/buecher/neue_buecher.php). An English edition is going to be published in 2024.

<sup>11</sup> <https://www.akzent.at/home/spielplan/1428/2-HULA-ONI-E---EUROPA>

<sup>12</sup> <https://de.wikipedia.org/wiki/G%C3%BCtermann>

<sup>13</sup> In the Mainzer Sand or Großer Sand nature reserve, I had to witness how the unique fauna and flora were increasingly declining, mainly due to the construction of a highway through the middle of this biologically unique area. Particularly catastrophic was the decline of the highly visible diurnal butterflies such as Zygaenidae or all species of fritillaries (PAULUS 1965, 1969). Another 20 years later, the butterfly fauna of the sands had shrunk considerably (ROSE 1988:

passion, which began with the pure "hunter-gatherer" instinct, but later changed into curiosity and a desire to know about the occurrence of species and their ecological requirements.



**Fig. 5:** My work at the Natural History Museum in Mainz was even described in the newspaper "Mainzer Allgemeine Zeitung" on August 4, 1964.

To finance the excursions and trips, I earned pocket money by setting up skittles for various skittles groups in the cellar of the then restaurant "Thomas Bräu" on Neubrunnenplatz. Among them, I was particularly fascinated by the group led by Dr. Willi Scheu<sup>14</sup>, the "karnevalist" from Mainz at the time, who had become famous as "Bajazz mit der Laterne" at the carnival sessions "Mainz wie es singt und lacht" (Mainz as it sings and laughs), which were also broadcast on television from 1955. The dentist Willi Scheu was also the outstanding solo entertainer at the evening bowling sessions. As a schoolboy, I earned DM 10 per evening plus another DM 1 for every skittle I knocked down with a throw at the "Vollen". During the vacations, I mainly worked on building sites as an unskilled laborer, at Jenaer Glas as a "TV screen cleaner" or in a timber factory as a veneer salesman. With the money I earned in this way, I was able to pay for various train journeys and accommodation in southern Carinthia (Ferlach, Waidischtal, Zell-Pfarre).

[https://www.zobodat.at/pdf/NEVA\\_9\\_0069-0088.pdf](https://www.zobodat.at/pdf/NEVA_9_0069-0088.pdf)). The beetle fauna of the sands was later edited by Manfred Niehuis, using my numerous data. Manfred Niehuis was later academic director at the Institute of Biology at the University of Koblenz-Landau.

<sup>14</sup> [https://de.wikipedia.org/wiki/Willi\\_Scheu](https://de.wikipedia.org/wiki/Willi_Scheu)



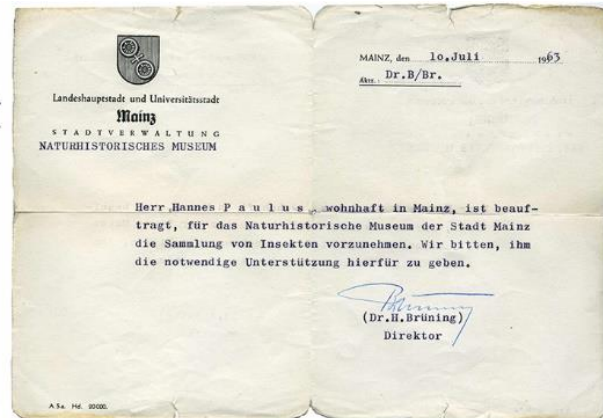
### B e s c h e i n i g u n g

Es wird hiermit bescheinigt, daß Herr Paulus als wissenschaftlicher Mitarbeiter in der Entomologischen Abteilung des Naturhistorischen Museums in Mainz tätig ist.

Mainz, 12. Okt. 1965

  
(Dr. Brüning)  
Direktor

NATURHISTORISCHES MUSEUM  
Mainz - Mitternacht



**Fig. 6a-b:** Certificates of my activities in and a permission to collect insects for the Natural History Museum in Mainz.

My encounter with Prof. Dr. Klaus Rose was formative for my more intensive study of butterflies (Fig. 59). In 1961, at the age of only 33, he had been appointed to an extraordinary professorship at the Johannes Gutenberg University of Mainz, and the following year he became a full professor and director of the Institute for General and External Economic Theory<sup>15</sup>. He was also a passionate collector of butterflies, especially blue butterflies. Together we made numerous collecting trips, including to southern Switzerland, the Altmühltal valley and, in May 1966, my first trip to the Middle East, to Lebanon, which resulted in the publication "Zur Lycaenidenfauna des Libanon" (PAULUS & ROSE 1971). A leaf-horned beetle new to science was also found there (*Tanyproctus paulusi* PETROVITZ, 1980). I had already personally handed over the animals to Rudolf Petrovitz in Vienna in 1968. It was only after his death in 1975 that a corresponding manuscript was published posthumously<sup>16</sup>. Occasional meetings with the retired animal physiologist and enthusiastic butterfly collector Prof. Dr. Wolfgang von Buddenbrock-Hettersdorf<sup>17</sup> in his apartment in Mainz were unforgettable moments for me. At the time, Buddenbrock was a famous comparative animal physiologist and was writing the last (6th) volume of his "Comparative Physiology (Blood and Heart)". He was formulating the complicated relationships of the crocodile heart, without me being able to guess at the time that such a topic would also be the subject of my lectures much later on his former chair of zoology in Vienna<sup>18</sup>. Our meetings were strictly regulated by his wife. After a good hour, we had to leave the apartment again, much to the chagrin of Wolfgang von Buddenbrock himself. He even gave me some of the butterflies he had collected in central Spain. Unfortunately, he died on April 11, 1964 at the age of almost 80.

From the end of 1962, I worked under the direction of Prof. Dr. Herbert Brüning as an hourly paid employee at the Natural History Museum in Mainz (Fig. 5, 6). There I

<sup>15</sup> [https://de.wikipedia.org/wiki/Klaus\\_Rose\\_\(economist\)](https://de.wikipedia.org/wiki/Klaus_Rose_(economist)). From an entomological point of view, Prof. Rose's speech on the occasion of his retirement in 1994, in which he linked his theories of economics with the price development of the butterfly trade, is worth mentioning ([https://www.jstor.org/stable/20714800?seq=1#page\\_scan\\_tab\\_contents](https://www.jstor.org/stable/20714800?seq=1#page_scan_tab_contents)). See also in RENKER & HENRICH (2009): S. 404-410.

<sup>16</sup> [https://www.zobodat.at/pdf/ZAOE\\_27\\_0120-0124.pdf](https://www.zobodat.at/pdf/ZAOE_27_0120-0124.pdf)

<sup>17</sup> [https://de.wikipedia.org/wiki/Wolfgang\\_von\\_Buddenbrock-Hettersdorf](https://de.wikipedia.org/wiki/Wolfgang_von_Buddenbrock-Hettersdorf)

<sup>18</sup> Prof. Buddenbrock-Hettersdorf had taken over the "Chair of Zoology" at the University of Vienna from 1942-1945 as the successor to the famous insect morphologist Hermann Weber. In this respect, I was one of his successors in this zoology chair. He had moved to the newly founded University of Mainz in 1946 and held the Chair of Zoology-Comparative Physiology. For the history of zoology in Vienna, see: [https://www.zobodat.at/pdf/VZBG\\_136\\_0001-0076.pdf](https://www.zobodat.at/pdf/VZBG_136_0001-0076.pdf)

organized the very sparse insect collection left over from the chaos of the war and set up an exhibition room for insects in the showrooms<sup>19</sup>. A large Holarctic hanging display case showed the distribution of the many species of the genus *Parnassius* (Apollo butterfly), for which missing butterflies were also purchased as exhibits. The then still legendary *Parnassius autocrator* AVINOV, 1913<sup>20</sup> from the high altitudes of the Hindu Kush in Afghanistan was represented as a paper picture from my picture collection. Prof. Brüning supported me and my scientific endeavors concerning the fauna of the Mainz region. With the official permission of the museum, I was allowed to collect insects in the surrounding area of Mainz (fig. 6).

Through the mediation of my biology school teacher Dr. Helmut Maier (Fig. 7), I was awarded the "Hörlein Prize" of the Association of German Biologists, the forerunner of the later "Jugend forscht" prizes<sup>21,22</sup>, for my intensive research into the butterfly fauna of the Mainz area and the subsequent publication of this work. As the award ceremony was held this time at the Zoological Institute of the University of Vienna by the then President of the Association, Prof. Dr. F. Schaller, this was the decisive trigger for me to decide to go to Vienna at least "for a year" (Fig. 7a, b). I only saw my biology and sports teacher again many years later at the celebration of Prof. Schaller's 90th birthday at my institute (Fig. 8).

When I moved to Vienna in 1968, my interest shifted more and more to beetles. My special interest in the beetle families Byrrhidae and Elmidae was inspired by Prof. Dr. A.W. Steffan (1933-2016) at the Department of Zoology at the University of Mainz<sup>23</sup>. Research into the larvae of the beetles arose from the study of the breeding and mating biology of the longhorn beetle *Agapanthia violacea* (now recognized as *A. intermedia*) (PAULUS 1968, 1974), of which I was able to discover and study a mass occurrence on *Knautia arvensis* along the Rheindammes opposite Mainz (PAULUS 1964).

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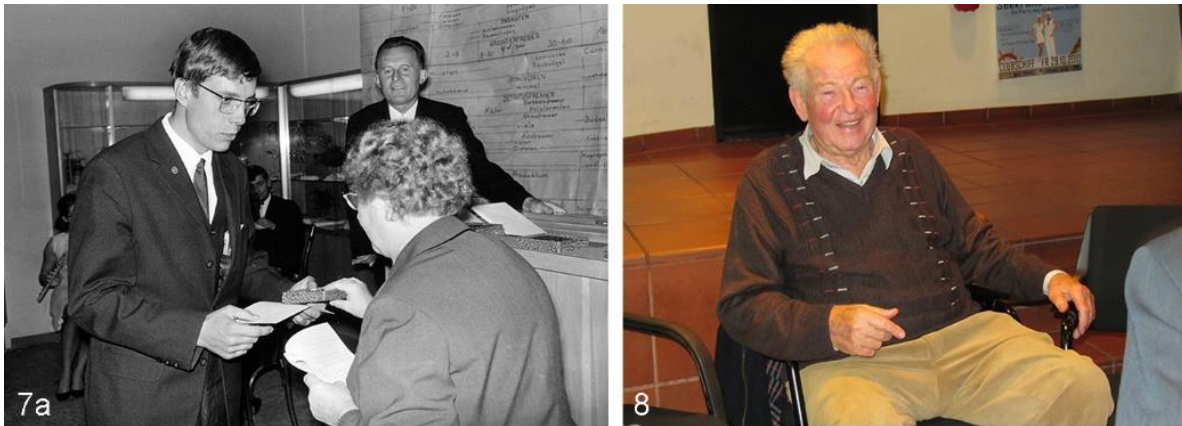
<sup>19</sup> look RENKER & HENRICH (2009)

<sup>20</sup> OMOTO K. & C. W. WYATT (1964): Die Geschichte der Entdeckung und Wiederentdeckung des *Parnassius autocrator* (The story of discover and redicover of *Parnassius autocrator*). — Kosmos, Stuttgart, Oktober 1964: 468-472.

<sup>21</sup> The association was founded in 1954 from the Society of German Natural Scientists and Physicians under the name "Association of German Biologists" (VDB). The main areas of work of the association were above all the cooperation of representatives of school and university education with representatives of research and applied subjects to rebuild biology, which had been compromised by Nazi ideology, and to assert common interests, especially in the area of "promoting young talent for all biological professions".

<sup>22</sup> The model for "Jugend forscht" came from the USA. Science Fairs already had a long tradition there and were first introduced in Germany in 1967 by the then editor-in-chief of Stern magazine, Henry Nannen (<https://www.jugend-forscht.de/stiftung-jugend-forscht-e-v/historie.html>).

<sup>23</sup> Last STEFFAN A. W. (1979): 42. family: Dryopidae. In: FREUDE H., HARDE K.W. & G.A. LOHSE (eds): Die Käfer Mitteleuropa, vol. 6. Goecke & Evers, Krefeld, pp.: 265-294. H. Paulus published a special issue of Entomologia Generalis in 2018 in memory of Prof. Dr. August Wilhem Steffan: Entomologia Generalis 37 (3/4) (Schweizerbart, Stuttgart).



7b Hörlein-Preis des Verbandes Deutscher Biologen 1966 im Rahmen "Jugend forscht" Verleihung in Wien durch Prof.Dr.Friedrich Schaller

**Fig. (7a):** Presentation of the Hörlein Prize of the Association of German Biologists in the Zoology lecture hall in the main building of the University of Vienna in 1966. In the background is the newly appointed Prof. Dr. Friedrich Schaller, then Chairman of the Association. **(7b)** Medal (front and back) of the Hörlein Prize of the Association of German Biologists, which later became "Jugend forscht".

**Fig. 8:** My former biology teacher and supporter Dr. Helmut Maier from Gutenberg-Gymnasium in Mainz on the occasion of the celebration of Prof. Schaller's 90th birthday on 2.11.2010 in Vienna. Mr. Maier was a student of Schaller during his time at the University of Mainz.

During my zoology studies in Mainz, I was inspired by the calm and competent manner of Prof. Dr. Helmut Risler (Fig. 9a), who was able to win me over to the functional morphology of insects. Among other things, he himself dealt with the question of the construction of the insect head. Several of his later prominent students wrote their dissertations on this topic with him, including friends and colleagues such as Ragnar Kinzelbach, Manfred Niehuis and Klaus Honomichel. Prof. Risler also loved excursions. For a long time, he went from Mainz to the Wutach Gorge in the southern Black Forest, to the Kaiserstuhl, the outstanding heat island in the southern Upper Rhine region, but above all to Lake Federsee: in summer for aquatic animals, in winter for birds, in spring for black grouse, in autumn, if there was nothing else, at least the various insects, spiders, birds and above all the homeotic mutation (?) of a twelve-legged stag beetle in the stucco of the eared windows of St.

Peter and St. Paul's Church in Steinhausen (Upper Swabian Baroque) (Fig. 9)<sup>24</sup>. Prof. Risler died on 19.12.1995 at the age of 81<sup>25</sup>. To honor his memory, a festive colloquium was held in Mainz in 1996, at which I was allowed to give a plenary lecture.



**Fig. 9 (left):** Prof. Dr. Helmut Risler (19.11.1914-19.12.1995), full professor of zoology, was one of my first zoology teachers at the University of Mainz (Photo: Natural History Museum Mainz/ State Collection of Natural History Rhineland-Palatinate (CC BY-NC-SA).

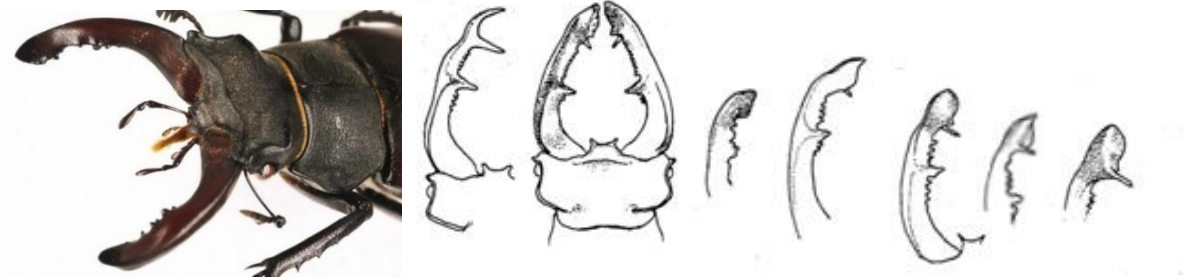
**Fig. 9 (right):** A twelve-legged stag beetle homeotic mutation (?) in the stucco of the ear windows of the St. Peter and Paulus Church of Steinhausen (Upper Swabian Baroque). [https://se-riss-federbachtal.drs.de/gemeinden/steinhausen/wallfahrtskirche-st-peter-u-paul.html#lightbox\[23518\]-37](https://se-riss-federbachtal.drs.de/gemeinden/steinhausen/wallfahrtskirche-st-peter-u-paul.html#lightbox[23518]-37). Here the artists Dominikus brothers probably only had the information in 1733 that insects have six legs, "six on each side"? This is contradicted by the fact that the other insects (housefly, hay moth) or a cross spider in the church have the correct number of legs. Homeotic genes, HOX genes, only became the rage in developmental genetics much later. Edward B. Lewis, Eric Wieschaus and Christiane Nüsslein-Volhart were awarded the Nobel Prize for this in 1995. I knew Ms. Nüsslein-Volhart from our institute in Freiburg, where she worked with Prof. Dr. Klaus Sander (1929-2015) on the genetic control of embryonic development in 1977.

Together with Prof. Dr. A.W. Steffan, I took part in several excursions from Mainz to the Rhön or the research station of the University of Giessen, the Künanzhaus on the Hoherodskopf in the Vogelsberg. There, to my surprise, I met Erich Weinreich again, whom I knew from the entomology conferences in Frankfurt as a Lucanid specialist.

<sup>24</sup> Here, the artists Dominikus brothers probably only had the information in 1733 that insects have six legs, "six on each side"? This is contradicted by the fact that the other insects (housefly, grasshopper) or a cross spider in the church have the correct number of legs. Homeotic genes, HOX genes, only became the rage in developmental genetics much later. Edward B. Lewis, Eric Wieschaus and Christiane Nüsslein-Volhart were awarded the Nobel Prize for this in 1995. I knew Ms. Nüsslein-Volhart from our institute in Freiburg, where she worked with Prof. Dr. Klaus Sander (1929-2015) on the genetic control of embryonic development in 1977.

<sup>25</sup> [https://www.zobodat.at/biografien/Risler\\_Helmut\\_Mainzer-Naturwiss-Archiv\\_34\\_0001-0008.pdf](https://www.zobodat.at/biografien/Risler_Helmut_Mainzer-Naturwiss-Archiv_34_0001-0008.pdf)

At that time, he was working on South American stag beetles, which he had depicted in incredibly beautiful drawings. Three genera from South America were named in his honor: *Erichius* MAES, 1992, *Weinreichius* LACROIX, 1978 and *Weinreichiellus* MAES, 1992<sup>2627</sup>. Erich Weinreich also discovered the conspicuous mutation "scapulodonta" in native *Lucanus cervus* males near Frankfurt, whose mandible tip is now shovel-shaped (Fig. 10)<sup>28</sup>. I myself was even able to describe this mutant from Lichtenstein Castle near Mödling near Vienna (PAULUS 1969)<sup>29</sup>.



**Fig. 10:** Conspicuous mutation "scapulodonta" in native *Lucanus cervus* males, whose mandible tip is fused in a shovel shape. (10a) Males from my collection; (10b) illustrations from Weinreich (1963: Ent. Ztschr. (Stuttgart) 73(4): 29-33) and PAULUS (1969): left left mandible normal, others right: different forms of the mutation.

[https://unmondeencouleurs.piwigo.com/index?/category/3302-cervus\\_f\\_scapulodonta\\_weinreich\\_1963](https://unmondeencouleurs.piwigo.com/index?/category/3302-cervus_f_scapulodonta_weinreich_1963)



**Fig. 11:** Prey capture behavior in the staphylinid *Stenus* from the doctoral thesis of E. Weinreich (1968).

In the Künanzhaus, he worked on the "sling-tongue mechanism" of the staphylinid genus *Stenus* as part of his doctoral thesis, which was developed as a catching apparatus with an adhesive tongue for capturing collembolans (Fig. 11)<sup>30</sup>. Years later, Oliver Betz took up the subject again at the University of Bayreuth and wrote his dissertation on *Stenus*.<sup>31</sup> He is now Professor of Zoology at the University of Tübingen.

<sup>26</sup> e. g. WEINREICH E. (1960): Revision südamerikanischer Lucanidae (Ins. Col.), II. Die Gattungen *Charagmophorus*, *Metadorcus*, *Scortizus*, *Apterodorcus*, *Beneshius*, *Sclerostomus* und *Pycnosiphorus*. — Senckenbergiana Biologica 41: 41-95.

<sup>27</sup> MAES J. M. (1992): Lista de los Lucanidae del mundo. — Rev. Nicaragua. Entomol. 22: 1-121.

<sup>28</sup> WEINREICH E. (1963): *Lucanus cervus* forma *scapulodonta*, eine auffallende Mutation unseres Hirschkäfers. — Ent. Ztschr. (Stuttgart) 73 (4): 29-33.

<sup>29</sup> [https://www.zobodat.at/pdf/ZAOE\\_21\\_0061-0062.pdf](https://www.zobodat.at/pdf/ZAOE_21_0061-0062.pdf)

<sup>30</sup> WEINREICH E. (1968): Über den Klebfangapparat der Imagines von *Stenus* LATR. (Coleoptera, Staphylinidae) mit einem Beitrag zur Kenntnis der Jugendstadien dieser Gattung. — Z. Morph. Tiere 62: 162-210.

<sup>31</sup> BETZ O. (1996) Function and evolution of the adhesion-capture apparatus of *Stenus* species (Coleoptera, Staphylinidae). — Zoomorphology 116: 15-34.

On November 1, 1963, I was present at the founding meeting of the Arbeitsgemeinschaft hessischer Koleopterologen, which took place on the occasion of the annual insect fair in Frankfurt. There were more than 20 participants, including such well-known beetle greats as Erich Weinreich (Lucanidae), Walter Heinz (Carabidae), Armin Korell (Carabidae), Otto Rebmann (Clavicornia, Apoidea) and Richard zur Strassen (especially Thysanoptera, head of the Entomology Department at the Senckenberg Museum in Frankfurt)<sup>3233</sup>.



v.l.n.r.:  
H. Buck (Murr); Hannes F. Paulus (Freiburg); Jochen Martens (Mainz); Walther Heinz (Waldmichelbach); R. Köstlin (Kornwestheim); Ernst Jünger (Wilflingen); Frau Arnold (Überlingen); davor kniend: F.-T. Krell (Bietigheim-Bissingen); Gustav Adolf Lohse (Hamburg)

**Fig. 12:** Group photo (detail) of the beetle conference in Ludwigsburg in 1984 (conference photo).

My interest in phylogenetic-systematic questions was first awakened by Prof. Dr. A.W. Steffan (see fig. 39) when he took me on as a freelancer and assistant for his studies on European hooked beetles (Elmidae) at his institute in Mainz. I was only in my 2nd semester at the time. I mainly prepared male genitalia and mouthparts of the Central European species and genera. Steffan also suggested that I could do something similar with the species of the beetle family Byrrhidae. This led to my later interest in this family. This was followed by a series of systematic studies with the description of new species and genera and the first treatment of the family in the then newly conceived, multi-volume work "Freude-Harde-Lohse: Die Käfer Mitteleuropas" ("The beetles of Central-Europe", initially 11 volumes). At the same time, I began to work more intensively on beetle larvae. I mainly worked on longhorn beetle larvae (*Rhagium*, *Agapanthia*). On a trip to Carinthia, I discovered the previously unknown larvae of the Dryopoidea family Limnichidae (PAULUS 1970) on the banks of the Drau, which had not yet been dammed at this time.

On these collecting trips to the Karawanken (Waidischthal, Loiblital) I got to know the greats of the German-speaking beetle scene at the time, who met here every year to

<sup>32</sup> [https://www.zobodat.at/pdf/Beitraege-zur-Entomologie\\_65\\_0197-0208.pdf](https://www.zobodat.at/pdf/Beitraege-zur-Entomologie_65_0197-0208.pdf)

<sup>33</sup> [http://www.flagh.de/wp-content/uploads/2021/07/IEV\\_50\\_Jahre\\_ArgeHeKol.pdf](http://www.flagh.de/wp-content/uploads/2021/07/IEV_50_Jahre_ArgeHeKol.pdf)

research the beetle fauna and Austrian beer and wine together. These were above all Heinz Freude (Munich) (1911-2007)<sup>34</sup>, Gustav Adolf Lohse (Hamburg) (1910-1994)<sup>35</sup> (Fig. 12), Klaus W. Harde (Stuttgart) (1922-1982)<sup>36</sup>, Hans Schaefflein (Straubing) (1915-1994)<sup>37</sup> or Lieutenant Colonel Otto Erich Krätschmer (Koblenz, later Mainz). I also occasionally met there with the longhorn beetle specialists from Klagenfurt Carl V. Demelt (1913-1988)<sup>38</sup> and Siegfried Steiner (1940-2013)<sup>39</sup>. Hans Schaefflein from Neutraubling in Bavaria (1915-1994) showed me how to find not only Dytiscidae but also the small Hydraenidae and Elmidae found in streams.<sup>40</sup> Together with Günther Wewalka from Vienna, he worked on the Dytiscidae for the Catalogus Faunae Austriae in 1982. I would also like to mention my encounters with Dr. Walter Braun (Pfrondorf near Tübingen) (1929-2005)<sup>41</sup> and Bronislaw Folwaczny from Bad Hersfeld (1909-1984)<sup>42</sup>, whom I met several times in Ferlach and we made several collecting trips together in the Krarawanken.

Walter Braun (1929-2005)<sup>43</sup> was initially a well-known specialist in the longhorn beetle genus *Dorcadion*, but after giving up this group he devoted himself to the genus *Otiorhynchus*. He had inherited this predilection from B. Folwaczny, who, apart from the beetles of Prussia, was particularly interested in weevils. He was best known for his book: "Verzeichnis der Käfer Preussens".<sup>44</sup> His extensive collection of weevils went to the Senckenberg Museum in Frankfurt and the Natural History Museum in Stuttgart. These acquaintances and our common interest in beetles later led me to the memorable annual beetle meetings of the Arbeitsgemeinschaft südwestdeutscher Koleopterologen, first in Ludwigsburg near Stuttgart, later in Beutelsbach, where they are still held every year. This working group was founded in 1958 by Rudolf Köstlin (1908-1987)<sup>45</sup>, Adolf Horion (1888-1977)<sup>46</sup> and K.W. Harde (1922-1982)<sup>47</sup>. The early meetings were always attended by the writer Ernst Jünger, with whom I mainly exchanged leaf-horned beetles (Fig. 12). I thought it was great

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<sup>34</sup> [https://de.wikipedia.org/wiki/Heinz\\_Freude](https://de.wikipedia.org/wiki/Heinz_Freude); [www.zobodat.at/biografien/Freude\\_Heinz\\_EntBer\\_51\\_0066-0069.pdf](http://www.zobodat.at/biografien/Freude_Heinz_EntBer_51_0066-0069.pdf)

<sup>35</sup> [https://www.zobodat.at/pdf/KOR\\_65\\_1995\\_0237-0250.pdf](https://www.zobodat.at/pdf/KOR_65_1995_0237-0250.pdf)

<sup>36</sup> JANUS H. (1983): Karl Wilhelm Harde. – Jahreshefte der Gesellschaft für Naturkunde in Württemberg 138: 289–294.

<sup>37</sup> [https://www.zobodat.at/pdf/KOR\\_65\\_1995\\_0233-0236.pdf](https://www.zobodat.at/pdf/KOR_65_1995_0233-0236.pdf)

<sup>38</sup> [https://www.zobodat.at/pdf/CAR\\_179\\_99\\_0313-0317.pdf](https://www.zobodat.at/pdf/CAR_179_99_0313-0317.pdf). His full name was Carl von Demelt-Karlstreu. As the titles of nobility had been abolished in Austria ("Adelsaufhebungsgesetz" of 10.4.1919), Carl had changed his "von" to V. His extensive collection of longhorn beetles can be found in the State Museum of Natural History in Stuttgart.

<sup>39</sup> [http://www.zobodat.at/biografien/Steiner\\_Siegfried\\_ZArbGemOesterrEnt\\_65\\_0179-0181.pdf](http://www.zobodat.at/biografien/Steiner_Siegfried_ZArbGemOesterrEnt_65_0179-0181.pdf)

<sup>40</sup> [www.zobodat.at/biografien/KOR\\_65\\_1995\\_0233-0236\\_Schaefflein\\_Hans.pdf](http://www.zobodat.at/biografien/KOR_65_1995_0233-0236_Schaefflein_Hans.pdf); Hebauer, F. (1995), In: *memoriam Hans Schaefflein. – Koleopterologische Rundschau* 65: 233–236.

<sup>41</sup> [https://www.zobodat.at/pdf/CAR\\_196\\_116\\_0265-0268.pdf](https://www.zobodat.at/pdf/CAR_196_116_0265-0268.pdf)

<sup>42</sup> [https://de.wikipedia.org/wiki/Bronislaw\\_Folwaczny](https://de.wikipedia.org/wiki/Bronislaw_Folwaczny)

<sup>43</sup> Walter Braun later had to give up his interest in *Dorcadion*, as he had developed a very strange (perhaps simply "characteristic") allergy to this genus and this genus alone. He then switched to the genus *Otiorhynchus* (Curculionidae). His extensive *Dorcadion* collection went to the Stuttgart Natural History Museum. By the way, former master Monsignor Adolf Horion also had such an allergy, but to all prepared beetles. He described this to me as "God's punishment for the blatant neglect of his ecclesiastical office", despite the honorary title of Monsignor conferred by the Pope. The Braun collections are in the Stuttgart Museum. Obituary: SCHERN H. (2006): Dr. Walter Braun zum Gedenken. - *Mitteilungen des entomologischen Vereins Stuttgart* 41: 66-68.

<sup>44</sup> FOLWACZNY B. (1979): *Verzeichnis der Käfer Preussens von Dr. Hans Bercio. Kritisch durchgesehen und ergänzt von Bronislaw Folwaczny*. Verlag Parzeller & Co., Fulda, 369 pp.

<sup>45</sup> [https://www.zobodat.at/biografien/Koestlin\\_Rudolf\\_Mitt-Ent-Ver-Stuttgart\\_22\\_1987\\_0003-0004.pdf](https://www.zobodat.at/biografien/Koestlin_Rudolf_Mitt-Ent-Ver-Stuttgart_22_1987_0003-0004.pdf)

<sup>46</sup> HORION A. (1993): *Autobiographie*. Mitt. Arb.gem. Rhein. Koleopterologen (Bonn) 3(2): 75-89

(<https://www.yumpu.com/de/document/read/13570795/eine-autobiographic-von-adolf-horion-koleopterologiede>). J. ILLIES: *Adolf Horion*. *Entomologische Blätter* 74 (3): 129-131, Krefeld;

<http://www.koleopterologie.de/arbeitsgemeinschaft/historie/biografien/gruender/horion.html>

<sup>47</sup> [https://www.zobodat.at/pdf/Mitt-Ent-Ver-Stuttgart\\_17\\_1982\\_0001-0002.pdf](https://www.zobodat.at/pdf/Mitt-Ent-Ver-Stuttgart_17_1982_0001-0002.pdf)

that at one of these meetings he gave me a signed copy of his book "Subtile Jagden - Vom Zauber der Insektenkunde" (Klett Verlag Stuttgart)<sup>48</sup>.



**Fig. 13:** Prof. Dr. Franz Huber from the Max Planck Institute of Behavioral Physiology in Seewiesen and Hannes Paulus on 7.5.2004 in Neuhaus Castle near Erlangen on the occasion of the joint 60th birthday celebration of Otto von Helversen and Hannes Paulus.

On the occasion of Prof. Dr. Ernst Josef Fittkau's retirement at 9.July 1992, I gave a testimonial lecture: "Systematics as a prerequisite for ecological field work - Larval systematics of beetles". He died on May 12, 2012, shortly before reaching the age of 85<sup>49</sup>. I particularly remember this festive event, as I sat together with various great zoologists during the evening meals and we discussed "God and the world". These included Prof. Dr. Franz Huber (Max Planck Institute of Behavioural Physiology in Seewiesen), whom I later met again and again at various conferences (Fig. 13) and we were very cordial. We last sat together on May 8, 2004 on the occasion of the joint celebration of Otto von Helversen's and my 60th birthdays at Schloss Neuhaus near Erlangen (Fig. 13). He died on April 17, 2017 at the age of 91.

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<sup>48</sup> Ernst Jünger (1895-1998) was a highly controversial but highly decorated writer who also collected beetles. His collection (FAZ: "30,000 dead beetles") can be found in the Stauffenberg'schen Forsthaus in Wilflingen (Baden-Württemberg), built in 1728, Ernst Jünger's residence from 1951-1998, since 1999 Jünger-Haus Wilflingen ([www.deutschlandfunkkultur.de/voller-buecher-und-kaefer.1013.de.html?dram:article\\_id=171674](http://www.deutschlandfunkkultur.de/voller-buecher-und-kaefer.1013.de.html?dram:article_id=171674); [www.faz.net/aktuell/feuilleton/buecher/autoren/ernst-juengers-haus-die-ordnung-der-dinge-1882718-p2.html](http://www.faz.net/aktuell/feuilleton/buecher/autoren/ernst-juengers-haus-die-ordnung-der-dinge-1882718-p2.html)). The Ernst Jünger Prize for Scientific Entomology, donated by the state of Baden-Württemberg in 1985 on the occasion of E. Jünger's 90th birthday, is named after him. Previous prize winners include Friedrich Schaller in 1998 (Vienna), Bert Hölldobler in 2010 (Arizona State University, Tempe, USA and Würzburg) and Ulrike Aspöck in 2023 (Vienna).

<sup>49</sup> [https://oekologie.badw.de/fileadmin/user\\_upload/Files/Oekologie/Geschichte-und-Nachrufe/Nachruf-Fittkau-Spixiana.pdf](https://oekologie.badw.de/fileadmin/user_upload/Files/Oekologie/Geschichte-und-Nachrufe/Nachruf-Fittkau-Spixiana.pdf)





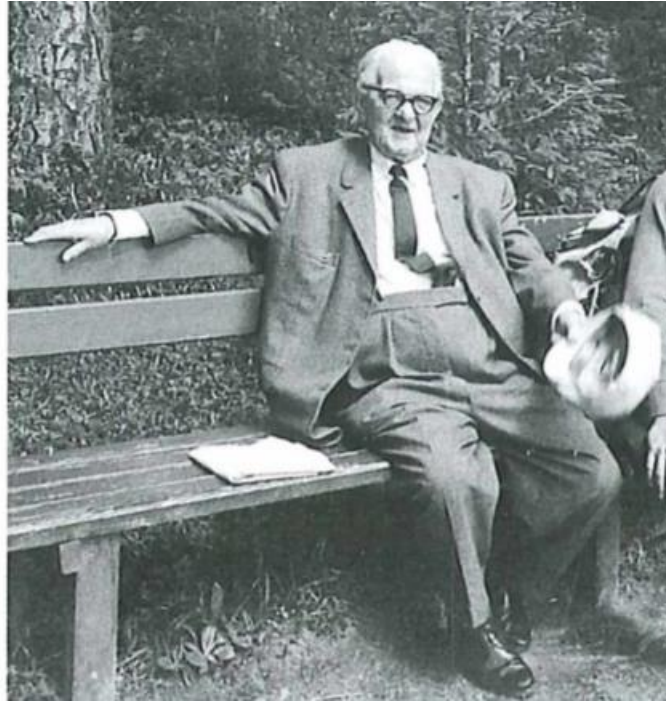
**Fig. 13:** Prof. Dr. Svante Pääbo and Urte Paulus on 3.3.2009 in Vienna on the occasion of the Darwin Year conferences.

In this same retirement session for Fittkau at 9.7.1992, the then little-known Swede Dr. Svante Pääbo also gave a lecture: “Zoological collections as molecular witnesses of past eras” and sat at the table in Munich with me and my future wife Urte and we exchanged stories about our shared fates, among other things. Like me, Svante was an illegitimate child of the then famous chemist and Nobel Prize winner Sune Bergström from the University of Lund. Like me, he grew up alone with his mother Karin Pääbo in Stockholm. It was only much later that he learned that his father led a double life and had a second family. He also learned that there was a half-brother who was born in the same year as him, 1955. It was nice to see how he and I took care of Urte back then. Svante later married the primate researcher Linda Vigilant, who also worked at the Max Planck Institute in Leipzig, while Urte and I got married in Vienna in 1993. We had both just taken up our professorships. Svante Pääbo had become Professor of General Biology at the Ludwig Maximilian University in Munich. In 1997, he moved to Leipzig to the Max Planck Institute for Evolutionary Anthropology, which he had also founded<sup>50</sup>. Since 1999, he has been one of five directors of the Department of Evolutionary Genetics, where he became famous for his investigations into the “ancient DNA” of Neanderthals, based on his earlier studies of the DNA of Egyptian mummies. To mark the Darwin Year, we invited him to speak at our conference in Vienna on March 3, 2009<sup>51</sup>. Afterwards, we all sat at the same table together with my wife Urte and Cardinal Schönborn, among others (Fig. 13). In 2022, Pääbo was even awarded the Nobel Prize for Medicine for his pioneering work on palaeogenetics.

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<sup>50</sup> <https://www.munzinger.de/search/portrait/Svante+P%C3%A4bo/0/26106.html>

<sup>51</sup> He spoke about: “The origin of man from a molecular genetic perspective”.



**Fig. 14:** Monsignor Adolf Horion (May 1971 near Innsbruck; photo: Ernst Heiss, from Klausnitzer 2013: Entomologische Nachrichten und Berichte, 57).

The priest and clergyman Monsignor Dr. h.c. Adolf Horion, who became well known for his 12 volumes of "Faunistik der Käfer Mitteleuropas". Adolf Horion lived in Überlingen at Lake Constance from 1942, where I was able to visit him several times from Freiburg until his death on May 8, 1977 at the age of 89 (Fig. 14). Because of his hearing loss, conversations with him were difficult. But he used to say, "as I can only hear a little, I do most of the talking", and then he talked "like a book" about many highly interesting things, preferably about his beetles and also about how "strange human nature" or "a sign from God" it was that he had an allergy to beetles of all things. He always signed his occasional letters to me "your old Horion".

In the course of my biology studies at the University of Mainz, I quickly came into contact with other scientifically working entomologists. Prof. Dr. Konrad Schmidt, a specialist in digger wasps, was head of electron microscopy at the time and gave me access to a joint comparative study of blue-winged wasps (Fig. 61) (SCHMIDT & PAULUS 1970).

What particularly fascinated me about Konrad Schmidt was his inexhaustible knowledge of native insects, as was demonstrated on the various zoological excursions in the Mainz area and especially on the then popular excursions to the Kaiserstuhl near Freiburg and to the Wutach Gorge in the nearby Black Forest. From Mainz I took part in a botanical excursion to Sardinia (5.4.-17.4.1968) under the direction of Prof. Dr. Hans Weber and then in a marine biology excursion to Arcachon in SW France (10.-29.9.1968). Here I had my first experience of the Mediterranean. At that time, I had no idea that Sardinia would one day become an important destination for pollination biology studies of the orchid genus *Ophrys* (PAULUS &

GACK 1995) and that a number of important scientific papers on the genus *Ophrys* would be published there.<sup>52</sup>



**Fig.15:** Prof. Dr. Jochen Martens (right) (University of Mainz, Germany); weaver's gargoyles specialist and ornithologist, here during my visit to his home on 1.7.2016 in Mainz.

In Mainz I also met Jochen Martens, who later became an ornithologist and weaver gnat specialist, and who had just started his doctoral thesis on the weaver gnat genus *Ischyropsalis* (Fig. 15). I went on a six-week collecting trip with him to the Alps, Pyrenees and Cantabrian Mountains with the Picos de Europa in northern Spain from August 15 to September 29, 1967. The main aim was to explore various caves from which a number of *Ischyropsalis* species had been described by the notorious arachnologist Carl-Friedrich Roewer<sup>53</sup>. We found almost all the species back then. In the course of the revisions by Jochen Martens, however, it turned out that several of the supposedly new species had in fact been "invented" or simply newly described based on material "transferred" from other regions to the caves of northern Spain<sup>54</sup>. At the beginning of this trip, the memorable 1st meeting of German-speaking arachnologists took place at Weisssee in the Stubach Valley from August 15-22, 1967. We were only a few participants, among them Albert Ausobsky (Bischofshofen, weavers)<sup>55</sup>, Karl Hermann Harms (Tübingen, later Rheinstetten, wolf spiders), Jürgen

<sup>52</sup> Among others, the doctoral thesis of Johannes Stökl, from which a number of results of our scientific investigations of the fusca group emerged (STÖKL J., PAULUS H. F., DAFNI A., SCHULZ C., FRANCKE W. & M. AYASSE (2005): "Pollinator attracting odour signals in sexually deceptive orchids of the *Ophrys fusca* group", *Plant Systematics and Evolution* 254 (1-2): 105-120. In Sardinia I also discovered the first cases of *Ophrys* pollination with bumblebees (*Bombus vestalis*): *Ophrys chestermanii* and *O. normanii*. J. Stökl now works as a private lecturer at the Institute for Evolutionary Ecology at the University of Bayreuth, after having turned down a professorship in Hohenheim.

<sup>53</sup> C. F. Roewer (1881-1963) was a doctoral student and assistant to Ernst Haeckel in Jena and, as a specialist in weavers and spiders, director of the Übersee-Museum in Bremen from 1933-1945.

<sup>54</sup> HELVERSEN O. von & J. MARTENS (1972) Unrichtige Fundort-Angaben in der Arachniden-Sammlung Roewer. – *Senckenbergiana biologica* 53 (1/2): 109-123.

<sup>55</sup> [https://www.zobodat.at/pdf/HdN\\_FS\\_80\\_0012-0015.pdf](https://www.zobodat.at/pdf/HdN_FS_80_0012-0015.pdf)

Gruber (Vienna, weavers)<sup>56</sup>, Vladimir Šilhavý (Starec near Trebic/CSSR, weavers)<sup>57</sup>, Jochen Martens<sup>58</sup> and I (then Mainz) as well as Otto von Helversen (then Freiburg, wolf spiders) (fig. 16) and Dagmar Uhrig (then Munich, grasshoppers), the later Dagmar von Helversen. On the way back, we also visited Konrad Thaler (Innsbruck, spiders)<sup>59</sup>, who was unable to come to this meeting. The next arachnologists' meeting did not take place until 10.6.-13.6.1971, this time in Rauristal. I then met Otto von Helversen and his wife Dagmar on our return journey in Freiburg, but above all a few years later in Freiburg when I took up an assistant position with Prof. Dr. Günther Osche<sup>60</sup> (Fig. 22). In the meantime, he was a doctoral student of the well-known cyberneticist, sensory physiologist and behavioral researcher Bernhard Hassenstein (1933-2016)<sup>61</sup> (Fig. 22, 92). I had a long-standing friendship with the von Helversen couple<sup>62</sup>. I am godfather to their eldest son Thomas. We went on many excursions together, including an almost 3-month trip to northern Colombia (Sta. Martha) (Fig. 26, 61). After that, further excursions took us to the French western Alps, northern Spain, Greece and central Italy. After his appointment to the University of Erlangen, they lived in the moated castle of the noble Crailsheim family in Adelsdorf-Neuhaus near Erlangen. I often visited him and Dagmar there and we made all sorts of plans, some of which were quite obscure. We tried to counter the impact factor epidemic in scientific publications, which was just beginning at the time, by planning to found two new journals: "Acta Polemica et Corrigenda" (following the already existing journal "Journal of Irreproducible Results", founded in 1955 by the Israeli researchers Harry Lipkin and Alexander Kohn) and "Journal of Irreproducible Works".<sup>63</sup> Unfortunately, it never came to pass.

Jochen Martens later spent many months in Nepal and brought back a lot of new arthropod material from there in addition to his ornithological studies. I also worked on some of the beetle specimens (Carabidae: *Cychropsis*; Byrrhidae; Pyrochroidae). I was also able to describe as a new species the highest occurring butterfly in the

<sup>56</sup> [http://www.oegef.at/uploads/www.oegef.at/BEF\\_18\\_0185-0200.pdf](http://www.oegef.at/uploads/www.oegef.at/BEF_18_0185-0200.pdf)

<sup>57</sup> [http://www.european-arachnology.org/wdp/wp-content/uploads/2015/08/145-146\\_Juberthie.pdf](http://www.european-arachnology.org/wdp/wp-content/uploads/2015/08/145-146_Juberthie.pdf)

<sup>58</sup> Jochen Martens (June 10, 1941 in Jena) was a professor of zoology at Johannes Gutenberg University Mainz until 2012. He taught there between 1976 and 2012. He is a specialist in weavers and an outstanding ornithologist who has published a great deal of interesting research on birds and their songs in the Himalayas. On his 65th birthday: [https://arages.de/user\\_upload/psb\\_publicationmanagement/pdf/AM32\\_53\\_54.pdf](https://arages.de/user_upload/psb_publicationmanagement/pdf/AM32_53_54.pdf). Festschrift zum 80. Geburtstag: A Festschrift honouring Prof. Dr. Jochen Martens on occasion of his 80th birthday. In: JÄGER P., SCHWENDINGER P. & B. SHEAR (eds.): Zootaxa. No. 4984. Magnolia Press, Auckland, New Zealand 2021, 384 pp. MARTENS J. (2020): A harvestman with elaborate palpal pliers, *Thunbergia gretae* n. gen. n. sp. from China (Opiliones: Sclerosomatidae: Gagrellinae). - Zoologischer Anzeiger 287: 160-166.

<sup>59</sup> The well-known spider specialist Prof. Dr. Konrad Thaler died unexpectedly in 2005 on a student excursion in the Stubai Alps at the age of just 64. Obituary: [https://arages.de/fileadmin/import/pdf\\_bak/AM30\\_01\\_12.pdf](https://arages.de/fileadmin/import/pdf_bak/AM30_01_12.pdf)

<sup>60</sup> Prof. Dr. Günther Osche (1926-2009) was one of the leading evolutionary biologists in the German-speaking world: [http://www.dzg-ev.de/de/publikationen/mitteilungen\\_zoologie/2009/nachruf\\_osche\\_zoologie2009\\_77-79.pdf](http://www.dzg-ev.de/de/publikationen/mitteilungen_zoologie/2009/nachruf_osche_zoologie2009_77-79.pdf); [https://www.zoologicalbulletin.de/BzB\\_Volumes/Volume\\_56\\_1\\_2/003\\_005\\_BzB56\\_1\\_2\\_In\\_memoriam\\_G%C3%BCnther\\_Osche.PDF](https://www.zoologicalbulletin.de/BzB_Volumes/Volume_56_1_2/003_005_BzB56_1_2_In_memoriam_G%C3%BCnther_Osche.PDF)

<sup>61</sup> [https://de.wikipedia.org/wiki/Bernhard\\_Hassenstein](https://de.wikipedia.org/wiki/Bernhard_Hassenstein)

<sup>62</sup> Prof. Dr. Otto Freiherr von Helversen-Helversheim (1943-2009) was a researcher of grasshoppers with their songs and of bats (*Acta Chiropterologica*, 11(2): 467-469, 2009). His wife Dr. Dr.h.c. Dagmar von Helversen (1944-2003) was also a neuroethologist and worked primarily on the sound pattern of grasshoppers. [http://www.dzg-ev.de/de/publikationen/mitteilungen\\_zoologie/2009/nachruf\\_helversen\\_zoologie2009\\_73-76.pdf](http://www.dzg-ev.de/de/publikationen/mitteilungen_zoologie/2009/nachruf_helversen_zoologie2009_73-76.pdf); [http://www.zobodat.at/biografien/Helversen\\_Dagmar\\_von\\_Articulata\\_19\\_2004\\_0122-0126.pdf](http://www.zobodat.at/biografien/Helversen_Dagmar_von_Articulata_19_2004_0122-0126.pdf)

<sup>63</sup> In 1991, a similar journal was actually founded in the USA: "Annals of Improbable Research" (for research projects "that first make people laugh, and then make them think"): <https://improbable.com/whatis/about-marc-abrahams/> or [https://de.wikipedia.org/wiki/Annals\\_of\\_Improbable\\_Research](https://de.wikipedia.org/wiki/Annals_of_Improbable_Research). Here, even "alternative Nobel prizes (ig (=ignoble) Nobel prizes)" are awarded as "fun activities". My friend and colleague Prof. Dr. Ludwig Huber in my faculty and Anna Wilkinson from the University of Lincoln (England) had the honor of receiving such a prize for their research into whether "yawning is also contagious within turtles" (<https://www.derstandard.at/story/1317020016333/oesterreicher-ludwig-huber-freut-sich-ueber-seinen-ig-nobelpreis>).

world (4,500m) from the Shey Phoksundo National Park in Nepal, collected by Jochen Martens: *Paralasa nepalica* PAULUS, 1983 (Nymphalidae, Satyrinae). Only some beetles, bumblebees and especially Collembola occur at even higher altitudes (the latter up to 6,400m).

**Wissenschaftliches Kolloquium**  
 aus Anlass der 60. Geburtstage von  
**Prof. Dr. Otto von Helversen und Prof. Dr. Hannes Paulus**

am Samstag, den 8. Mai 2004  
 im Hörsaal A des Erlanger Biologikunns

10:00 Uhr **Prof. Dr. Bernd Ronacher, Berlin**  
 Variabilität neuronaler Antworten:  
 Ein Problem für Tiere – und Untersucher?  
**PD Dr. York Winter, München**  
 Blumenfledermäuse: singende Blüten und kognitive  
 Evolution  
 Pause  
**Prof. Dr. Manfred Ayasse, Ulm**  
 Chemische Mimikry als Bestäubungsstrategie bei  
 Sexualtäuschorchideen

**Feier**

in Neuhaus/Aisch

ab 17:00 Uhr im Schlossgarten und im Schloss



**Fig. 16:** On May 8, 2004, Otto von Helversen and I celebrated our respective 60th birthdays together at the Zoological Institute of the University of Erlangen in the form of a joint festive colloquium. Left is the program of the event. Right above: Otto von Helversen during a visit to my institute in Vienna in 2006. Right bottom: Birthday bouquet for Otto von Helversen from his faculty in Erlangen.

### My two ways to Vienna

1. when I was awarded the Hörlein Prize of the Association of German Biologists in 1966 and the award ceremony took place during the meeting of this society in Vienna (Fig. 7a), I decided that I would definitely go to Vienna later. As an enthusiastic collector of beetles and butterflies, I was attracted by the closer and wider surroundings of the city. So, in 1968, after completing my intermediate diploma in biology at the University of Mainz, I went to Vienna to "continue my studies for a year". There I quickly contacted Viennese entomologists through the weekly meetings of the Arbeitsgemeinschaft Österreichischer Entomologen, including Johann Probst<sup>64</sup> and Diethart Dauber<sup>65</sup> or Carolus Holzschuh<sup>66</sup> (Fig. 17), with whom I went on numerous beetle excursions in the greater Vienna area over the next two to three years.

<sup>64</sup> [http://www.zobodat.at/biografien/Probst\\_Johann\\_KOR\\_81\\_2011\\_0333-0335.pdf](http://www.zobodat.at/biografien/Probst_Johann_KOR_81_2011_0333-0335.pdf)

<sup>65</sup> [https://www.zobodat.at/pdf/LBB\\_0048\\_1\\_0005-0019.pdf](https://www.zobodat.at/pdf/LBB_0048_1_0005-0019.pdf)

<sup>66</sup> Carolus Holzschuh (born 1939), retired forest entomologist, was employed at the Federal Forest Research Institute, Institute for Forest Protection in 1131 Vienna. He specialized mainly in European and Asian Cerambycidae. He must have described around 800 new species.



**Fig. 17:** Horst Aspöck, Hannes Paulus, Anselm Kratochwil and Carolus Holzschuh, Entomologist conference, Schlossmuseum in Linz, November 2015; Foto Fritz Gusenleitner.

The encounters with Prof. Dipl.-Ing. Dr. Dr. h.c. Karl Mandl (1891-1989)<sup>67</sup>, the well-known *Carabus-Cicindela* specialist, were also very influential for me (Fig. 51). I also soon had intensive contact with the heads of the beetle collection at the Natural History Museum in Vienna. Dr. Friedrich Janczyk<sup>68</sup>, head of the beetle department, and after his sudden early death his successor Dr. Heinrich Schönmann (1948-2017)<sup>69</sup> gave me unrestricted access to the very extensive museum collection.

I was also impressed by my encounters with Eva Vartian in Vienna (Fig. 52). In addition to being a gifted painter, she was above all an enthusiastic butterfly collector who, as the wife of carpet dealer Assad Vartian, accompanied her husband on his carpet trading trips to the Middle East, Iran and Afghanistan. During these trips, she eagerly collected butterflies, especially moths. This enabled her to build up an extremely extensive collection over the years. I was allowed to visit her several times in her completely oriental furnished apartment in the Vienna road “Rechte Wienzeile” and admire the extensive carpet collection on the walls as well as the remaining parts of her moth collection. She was an extremely well-educated and knowledgeable woman who was always fascinating to talk to. Her very extensive collection of over 140,000 prepared moths was donated to the Natural History Museum Vienna in 1965, where it was given its own room. She herself only died in 2017 at the age of 93<sup>70</sup>.

<sup>67</sup> [http://verlag.nhm-wien.ac.at/pdfs/092B\\_291304\\_Fischer.pdf](http://verlag.nhm-wien.ac.at/pdfs/092B_291304_Fischer.pdf)

<sup>68</sup> [https://www.zobodat.at/pdf/ANNA\\_90B\\_0441-0444.pdf](https://www.zobodat.at/pdf/ANNA_90B_0441-0444.pdf)

<sup>69</sup> [http://www.coleoptera.at/uploads/www.coleoptera.at/KOR\\_88\\_2018\\_0281-0292.pdf](http://www.coleoptera.at/uploads/www.coleoptera.at/KOR_88_2018_0281-0292.pdf)

<sup>70</sup> [https://www.zobodat.at/pdf/EN\\_3\\_2\\_3\\_1996\\_0001-0005.pdf](https://www.zobodat.at/pdf/EN_3_2_3_1996_0001-0005.pdf); <http://objekte.nhm-wien.ac.at/objekt/th1967/ob1483>; [https://www.zobodat.at/biografien/Vartian\\_Sammlung\\_Entomologische-Zeitschrift\\_106\\_0206-0208.pdf](https://www.zobodat.at/biografien/Vartian_Sammlung_Entomologische-Zeitschrift_106_0206-0208.pdf); [https://www.zobodat.at/biografien/Vartian\\_Eva\\_Quad\\_14\\_0193-0214.pdf](https://www.zobodat.at/biografien/Vartian_Eva_Quad_14_0193-0214.pdf)

During my doctoral thesis in Vienna, I got to know other zoologists who worked at the Zoological Institute of the then University of Natural Resources and Life Sciences, including the later professors Dr. Hans Martin Steiner, Dr. Rainer Bösel, Dr. Peter Weish and Dr. Harald Tichy. The latter had a workplace there to carry out their doctoral thesis under Prof. Schaller, as one of the only two electron microscopes available in Vienna at the time was located here. Martin Steiner later became Head of Zoology at the University of Natural Resources and Life Sciences, which had since become the University of Natural Resources and Life Sciences. Peter Weish<sup>71</sup> was later an assistant lecturer at this Boku, among other things, but above all became the most prominent anti-nuclear opponent in Austria. Thanks in part to his tireless educational work and profound knowledge of the connections between nuclear energy and environmental risks, Austria still has no nuclear power plant in our country today<sup>72</sup>. Rainer Bösel first worked as a neuroanatomist at the Max Planck Institute for Developmental Biology in Tübingen, then moved to Berlin as an assistant professor at the Institute of Psychology at the Free University of Berlin. From 1980 to 2010, he was Professor of Psychology and Head of the Cognitive Neuropsychology Research Group at the Free University of Berlin and, until 2013, Professor of General Psychology at the International Psychoanalytic University Berlin.



**Fig. 18:** Speech by Hannes Paulus on the occasion of the 70th birthday of Prof. Dr. Friedrich Barth at the Zoology department Wien on 18.4.2008

Years later, Harald Tichy returned to Vienna from Regensburg as an assistant to the sensory physiologist and neurobiologist Prof. Dr. Friedrich Barth<sup>73</sup> (Fig. 18). Coming from Frankfurt, Barth had filled the long vacant chair of Prof. Dr. Wilhelm Kühnelt<sup>74</sup> in 1987 and now established it as the Department of Neurobiology in the Department of Zoology at the University of Vienna. Friedrich Barth was primarily concerned with sensory biology using the example of the large Central and South American

<sup>71</sup> [https://de.wikipedia.org/wiki/Peter\\_Weish](https://de.wikipedia.org/wiki/Peter_Weish)

<sup>72</sup> [https://www.akweb.de/ak\\_s/ak420/06.htm](https://www.akweb.de/ak_s/ak420/06.htm)

<sup>73</sup> <https://www.neuro.univie.ac.at/people/curriculum-vitae/>

<sup>74</sup> [https://www.zobodat.at/pdf/CAR\\_179\\_99\\_0319-0321.pdf](https://www.zobodat.at/pdf/CAR_179_99_0319-0321.pdf)

wandering spider *Cupiennius salei*<sup>75</sup>, and also with the communication system of stingless bees (Meliponini) in South America.

Together with Hans Martin Steiner<sup>76</sup>, his first wife Edith Steiner and Friederike Gruber from Vienna, my later first wife, I made a very successful journey by car from Vienna in 1971 via what was then Yugoslavia through Turkey into northern Iran to the Caspian Sea, the Talysh and Elburs Mountains and on to Mashhad near the border with Afghanistan. In the Elburs Mountains, I found almost fully-grown larvae of the newt *Batrachuperus persicus* EISELT & STEINER, 1970, which had previously only been described by small tadpoles, in the scree of a mountain stream. a pit viper (*Gloydius halys*) new to Iran at that time, a dragonfly (*Cordulegaster vanbrincki* LOHMANN, 1993) later described from my material and a new spider named after me (*Troglohyphantes paulusii* THALER, 2002; Dwarf canopy spiders: Linyphiidae)<sup>77</sup> were also found.

On this trip I met the well-known bumblebee specialist William F. Reinig from Nürtingen-Hardt in the middle of the Elbursgebirge mountains, who turned up in his car with his wife Lotte in a clearing next to the forest road right next to us one evening to pitch his tent in the immediate vicinity. While his wife was setting it up, he was already scouring the immediate vicinity of the shared campsite with an insect net in search of bumblebees. I was curious and excited to meet him in person, as I had only known him from literature. From this first encounter, a later close relationship and almost paternal friendship developed. At the time, he encouraged me to study bumblebees. It was only years later, as an assistant at the University of Freiburg to the probably best-known German-speaking evolutionary biologist Prof. Dr. Günther Osche, that I became aware that W. F. Reinig was one of the little-known pioneers of the modern synthetic theory of evolution<sup>78</sup>. Reinig had already published several important articles on evolutionary theory in the 1930s and had written particularly stimulating books combining biogeographical, evolutionary-biological and genetic considerations, such as "Elimination and Selection" (1938) and "Holarctic" (1937)<sup>79</sup>. The later textbooks on evolution by Bernhard Rensch ("Neuere Probleme der Abstammungslehre. Die transspezifische Evolution", 1947)<sup>80</sup> and "Zoogeographie" by Gustav de Lattin (1967) were significantly influenced by them. Reinig died in 1980 at the age of 76. His private bumblebee collection, probably the largest in the world, went to the Munich State Zoological Collection, which also contains all the bumblebees I subsequently collected for Reinig in the Elburs Mountains (N-Iran) and later many of the bumblebees collected in southern Europe.

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<sup>75</sup> A nice summary of his and his working group's work can be found in the book BARTH F. G.: Sinne und Verhalten: From the life of a spider. Springer-Verlag, 2002, 396 pp., or: BARTH F. G.: A spider in motion: facets of sensory guidance. - Journal of Comparative Physiology A (2021) 207: 239-255.

<sup>76</sup> Hans Martin Steiner (1938-2014) was later full professor of zoology at the University of Natural Resources and Life Sciences in Vienna. file:///D:/pdf-Data%2026.3.2015/iucn%20sidney%20in%20chatter.pdf

<sup>77</sup> THALER K. (2002): Mittl.Schweiz. Ent. Ges. 75: 51-55.

<sup>78</sup> William Frederick Reinig (1904-1980) was a German geneticist and evolutionary biologist; 1929 doctorate on: "Über das Manifestieren zweier Genovariationen bei *Drosophila funebris*". 1942 habilitation; he worked from 1930-1945 in Berlin at the "Prussian Academy of Sciences". His work on animal geography and evolutionary theory was often based on bumblebees as explanatory objects. 1949-1967 Editor-in-chief of the magazine "Kosmos".

<sup>79</sup> JUNKER T. (2004): Die zweite Darwin'sche Revolution. Geschichte des Synthetischen Darwinismus in Deutschland 1924 bis 1950. — Acta Biohistorica, Bd. 8 Marburg: Basilisken-Press, 635 pp, 25 Abb.

<sup>80</sup> Bernhard Rensch 21.1.1900 born in Thale (Harz), † 4.4.1990 in Münster, Zoologist and Evolutionary Biologist at the University of Münster (Germany) ([https://de.wikipedia.org/wiki/Bernhard\\_Rensch](https://de.wikipedia.org/wiki/Bernhard_Rensch)).



My later work, especially on the flower biology of bumblebees, resulted in a series of diploma and doctoral theses in Freiburg and later also in Vienna, including those by Peter Sowig (1988) on bumblebee raceme lengths and competition avoidance and Johann Neumeyer on the ecology of alpine bumblebees in the Hohe Tauern National Park (NEUMEYER & PAULUS 1999) (Fig. 83). But I also worked on other aspects of flower biology in Freiburg, including the remarkable doctoral thesis on the synoecology of flower-insect communities by Anselm Kratochwil (1983) (650 pages!)<sup>81</sup>, or the one on moth-flower relationships by Thomas Esche (1989)<sup>82</sup>. As my very first student at the time, Anselm Kratochwil later became Professor of Ecology at the University of Osnabrück (Fig. 19).



**Fig. 19:** Prof. Dr. Anselm Kratochwil (University of Osnabrück) in my study at the Institute on 27.9.2012. Anselm Kratochwil was my very first doctoral student in Freiburg. In the background several photos of pseudocopulations on *Ophrys* and a cartoon (dancing *Mantis*) by Klaus Pitter (Vienna).

2. Otto von Helversen, Klaus-Peter Sauer and myself each habilitated at intervals of one year and celebrated them together at the Lichteneck castle ruins north of Freiburg. Dagmar von Helversen had illustrated a beautiful poster (Fig. 20). After my habilitation in Freiburg, I started looking for a job, as in Germany this qualification often meant that my own position as an assistant was terminated. You were given another two years in which to find a professorship at another university if you wanted to continue your academic career at the university. At that time, the newly created temporary C2 professorships were available as "interim positions". Fortunately, I was

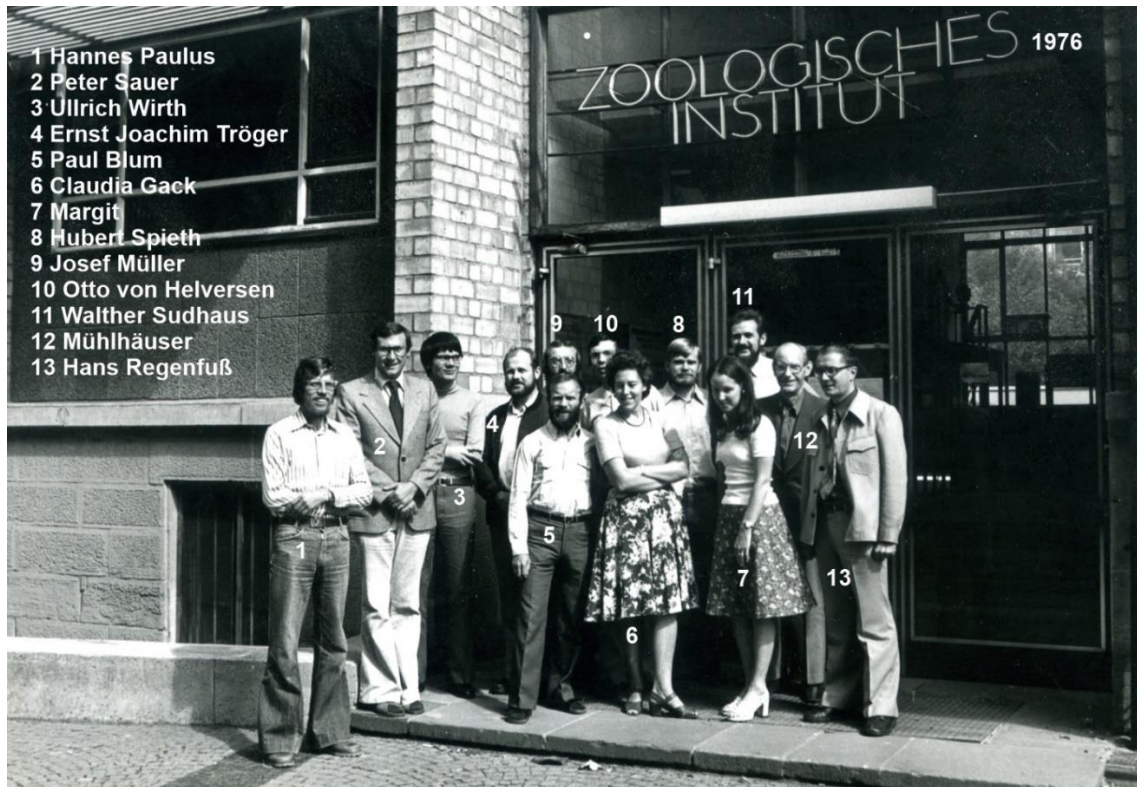
<sup>81</sup> In 1983, he received the Goedecke Research Prize of the University of Freiburg, one of the highest awards in the field of natural sciences in the city of Freiburg, for this work, which was initiated and supervised by me (with co-supervision by Prof. Dr. Ottilie Wilmanns).

<sup>82</sup> [https://www.zobodat.at/pdf/Neue-Entomologische-Nachrichten\\_35\\_0001-0194.pdf](https://www.zobodat.at/pdf/Neue-Entomologische-Nachrichten_35_0001-0194.pdf)



**Fig. 20:** Hand-painted poster by Dagmar von Helversen of our joint habilitation ceremony at the Lichtenneck castle ruins north of Freiburg on July 20, 1979. Otto von Helversen had just accepted his professorship at the University of Erlangen, Klaus-Peter Sauer was still busy with his negotiations with the University of Bielefeld, which were successful shortly afterwards, while I myself was allowed to take up a professorship in Freiburg with Günther Osche. Otto had successfully completed his habilitation with work on the song pattern of field crickets, Klaus-Peter on sexual selection in scorpion flies, and I myself on the evolution of arthropod eyes.

quite successful with my applications, as I immediately achieved various places on the list for C4 professorships (full professorships), for example in Osnabrück, Tübingen and Erlangen. This gave me the opportunity of a permanent professorship in Freiburg. In 1990, I was appointed to the Department of Zoology at the University of Vienna, thus fulfilling my old but secret wish. Looking back, my succession to the Chair of Zoology seems almost "fateful". My last biology teacher Helmut Meyer was a doctoral student of Schaller, Schaller was a student of Wolfgang Buddenbrock, Buddenbrock was one of the butterfly experts who supported and inspired me. My butterfly work led to the Hörlein Prize, which Prof. Schaller of all people presented to me in Vienna. Years later, this led to my doctoral thesis with Schaller.



**Fig. 21:** Zoology (Biology I) staff in Albertstrasse 21A (today "Weissmann-Haus") at the University of Freiburg in 1976: My fellow assistants were Peter Sauer (2), Otto von Helversen (10), Walter Sudhaus (11) and Hans Regenfuß (13). The others were doctoral students at the time (3, 9, 8, 5, 6), Mr. Mühlhäuser (12) was our gifted animal keeper.

When I was appointed to the University of Vienna, I initially founded the Department of Evolutionary Biology as one of ten departments in Zoology. This was later rededicated as a separate department, as were several other departments. After negotiations with the Ministry, I was granted two new assistant positions and two new technical assistant positions. This was remarkable in that it was surprisingly generous compared to my experiences in Germany, even though I had already been able to take over four or five such positions from my predecessor Prof. Schaller. However, these had already been filled by established and scientifically well-qualified people, and on a permanent basis. These were Prof. Dr. H. Tunner (frog genetics), Doz. Dr. H. Kratochvil (bioacoustics), Doz. Dr. Günther Pass (circulatory systems in Arthropoda) and Dr. Walter Hödl (reproductive strategies in tropical frogs). One of my first tasks was to help Walter Hödl obtain his habilitation. For the new appointments, I brought in Dr. Manfred Ayasse from Tübingen to cover my newly established field of work, namely olfactory communication in pollination biology, which he did with flying colors. Thanks to our joint research in the orchid genus *Ophrys*, he is now a professor at the University of Ulm. The second assistant position was to cover another new field, namely functional morphology of the mouthparts of flower-visiting colors. Thanks to our joint research in the orchid genus *Ophrys*, he is now a professor at the University of Ulm. The second assistant position was to cover another new field, namely functional morphology of the mouthparts of flower-visiting insects. Dr. Harald Krenn was an ideal candidate for this position. He has also made

an excellent name for himself with his studies. However, this meant that I had decided to leave my previous field of work, the evolution of arthropod eyes. Both assistants later habilitated. When Manfred Ayasse accepted his appointment at the University of Ulm, I was able to fill his position again with an outstanding new assistant, Dr. Johannes Spaethe. He represented the sensory side of the flower-insect relationship in research and teaching and is now at the University of Würzburg.

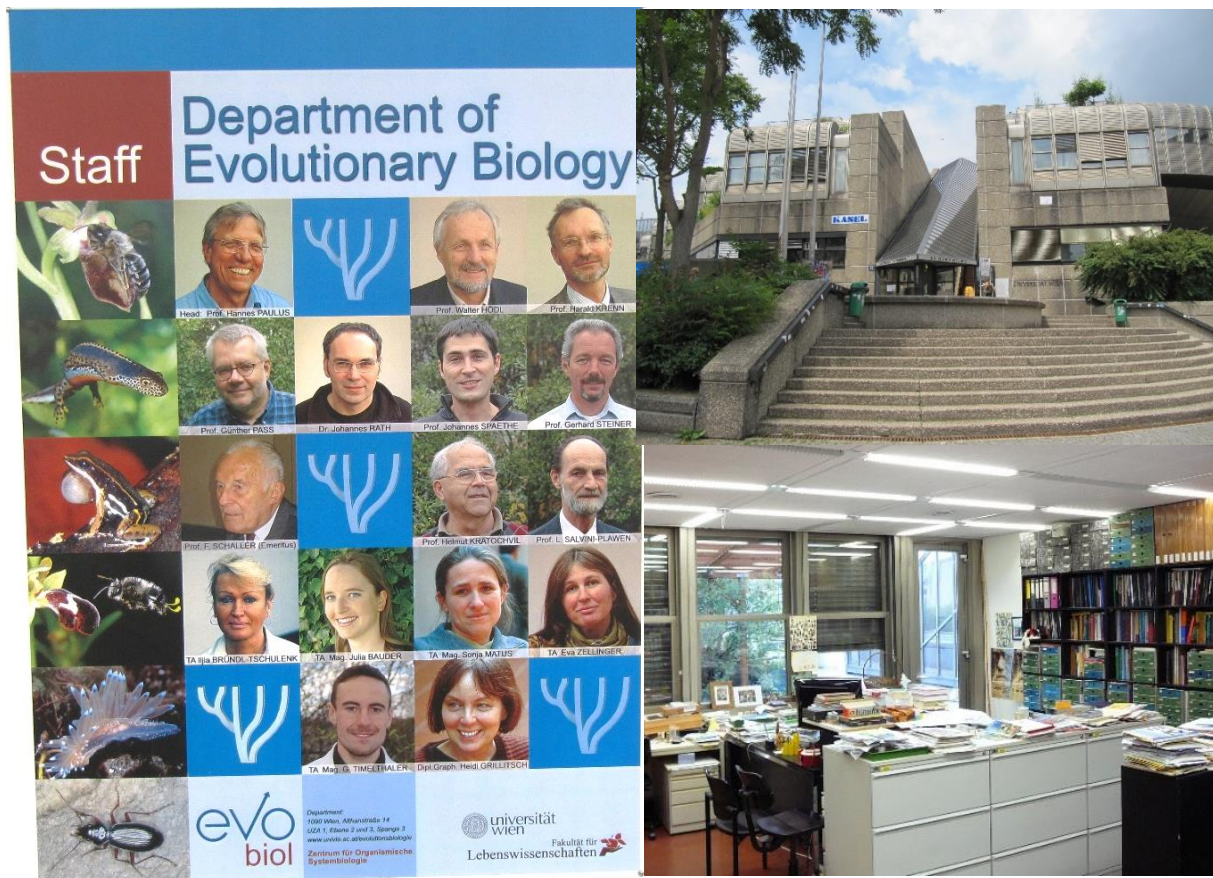
Treffen der „alten“ Zoologen aus Freiburg 26.2.1994



**Fig. 22:** Group photo on the occasion of a meeting of current and former zoologists from Biology I at the University of Freiburg at Neuhaus Castle near Erlangen. From left to right: Prof. Dr. Peter Weygoldt († 23.10.2021), Prof. Dr. Peter Sauer (Univ. Bonn, † 12.11.2022), Mrs. Elisabeth Osche († 2010) (wife of G. Osche), Prof. Dr. Otto von Herversen (Univ. Erlangen, † 2.3.2009), Dr. Claudia Gack (Zoology, Freiburg), Prof. Dr. Hannes Paulus (Univ. Vienna, emeritus 1.10.2012), Mrs. Karin Sudhaus (wife of Walter Sudhaus, Berlin), Prof. Dr. Norbert Elsner (Univ. Göttingen, † 16.6.2011), Mrs. Elsner (wife of Norbert Elsner), Dr. Dagmar von Herversen (Univ. Erlangen, wife of Otto von Herversen, † 20.7.2003), Prof. Dr. Walter Sudhaus (Univ. Berlin), Urte Paulus (wife of Hannes Paulus, Vienna), Prof. Dr. Günther Osche (Univ. Freiburg, † 2.2.2009), Mrs. Helma Hassenstein (wife of Bernhard Hassenstein, Freiburg, † 2016), Sylvia Weygoldt (wife of Peter Weygoldt, Münstertal), Prof. Dr. Peter Götzt (Univ. Berlin), Prof. Dr. Bernhard Hassenstein (Univ. Freiburg, † 16.4.2016, obituary: <https://docplayer.org/78867465-Zoologie-mitteilungen-der-deutschen-zoologischen-gesellschaft.html>)

professor at the University of Ulm. The second assistant position was to cover another new field, namely functional morphology of the mouthparts of flower-visiting insects. Dr. Harald Krenn was an ideal candidate for this position. He has also made an excellent name for himself with his studies. However, this meant that I had decided to leave my previous field of work, the evolution of arthropod eyes. Both assistants later habilitated. When Manfred Ayasse accepted his appointment at the

University of Ulm, I was able to fill his position again with an outstanding new assistant, Dr. Johannes Spaethe. He represented the sensory side of the flower-insect relationship in research and teaching and is now at the University of Würzburg.



**Fig. 23:** (left) Poster of the staff my Department of Evolutionary Biology in Vienna, 2010; (right above) Entrance to the old Zoology department in Althanstrasse (ca. 2013); (right bottom) My office shortly before clearing out in the course of my retirement in 2013

My colleagues in Zoology were Prof. Dr. Friedrich Barth, who succeeded Prof. Dr. Kühnelt in 1986 and named his department Neurobiology, from 1988 Prof. Dr. John Dittami (Behavioral Biology), Prof. Dr. Ruppert Riedl (Theoretical Biology and Marine Biology) (until 1995, then Prof. Dr. Jörg Ott as Marine Biology) and Prof. Dr. Heinz Löffler (Limnology) (until 1995, from 1997 as successor Prof. Dr. F. Schiemer). The historical separation within Botany into Systematic Botany (Rennweg) and Plant Physiology (Althanstrasse) led to rather curious assignments of Terrestrial Ecology (with Doz. Dr. Karl Sängler, Doz. Dr. W. Waizbauer and Doz. Dr. G. Spitzer) outside Zoology. This prevented a reorganization into disciplines that had long been represented internationally, namely a combination of evolutionary biology and ecology. This "curiosity" continued even after the reappointment of Prof. Dr. Konrad Fiedler as a population biologist, who in fact represented the terrestrial ecology of animals and ultimately ended up as a department with the botanists at Rennweg. My two technical assistants deserve special mention: Ilija Bründl-Tschulenk and Sonja Matus, who have accompanied me in all the last years at the institute (Fig. 24).



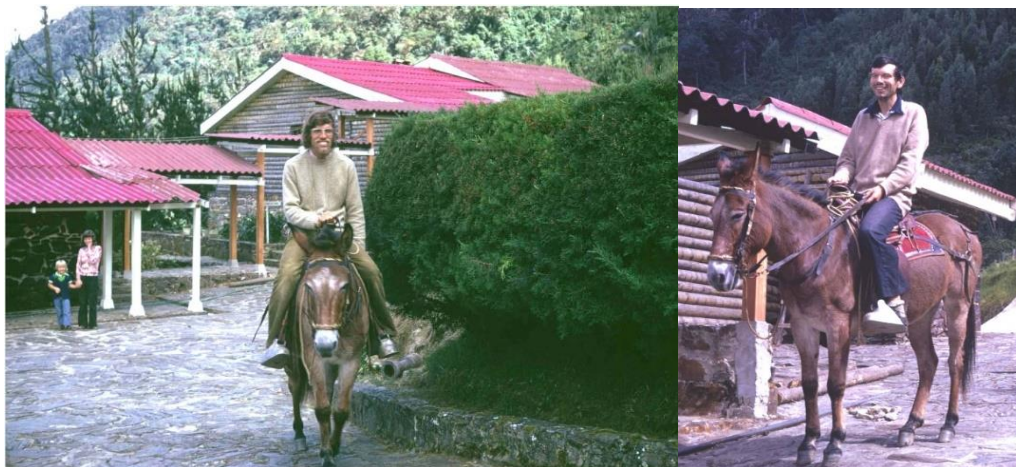
**Fig. 24:** Ilija Bründl-Tschulenck (left) and Sonja Matus (right) accompanied me as extremely helpful colleagues until my retirement in 2012



**Fig. 25:** Door posters until 2013 at my institute in the Biology Center 1090 Vienna, Althanstraße.

## Further journeys

My first major trip took me to Lebanon in May 1966 together with Prof. Dr. Klaus Rose in Mainz. At that time, Lebanon was still considered the "Switzerland of the Middle East" until the political turmoil brought this beautiful country to the brink of ruin. Our focus here was on butterflies and beetles. The results were a publication on blue butterflies (PAULUS & ROSE 1971) and the discovery of two beetle species new to science: *Phytoecia (Helladia) paulusi* HOLZSCHUH<sup>83</sup>, 1971 (Cerambycidae) and *Tanyproctus paulusi* PETROVITZ, 1980 (Scarabaeidae)<sup>84</sup>. In the late summer of 1967, while still in Mainz, I undertook a trip with Jochen Martens (later Professor of Zoology at the University of Mainz) to the Eastern and Western Alps, the Pyrenees and the Cantabrian Mountains. The first stop was the first meeting of German-speaking arachnologists in the Hohe Tauern (Stubachtal, 15.8.-22.8.1967). They then went on to the Pyrenees (cave visits), the Cantabrian Mountains and the Picos de Europa. In the Pyrenees, while searching for longhorned beetle larvae in wood, I discovered already hatched imagines of an apparently new stag beetle, which after much hesitation I redescribed as *Platycerus pseudocaprea* (PAULUS, 1970; 1974), a form between *Platycerus caraboides* and *P. caprea*<sup>85</sup>. In 1970 I made a five-week trip to Norway and southern Sweden together with Ernst Hüttinger (Purgstall) (Fig. 100). The aim was to obtain "topotypical insect material in Linné's footsteps". I was supposed to receive financial support from the Austrian Theodor Körner Fund<sup>86</sup>, but this failed because it was only now "discovered" that I was German and not Austrian<sup>87</sup>. According to the statutes, this prize was only intended for Austrians and



**Fig. 26:** During our research stay in N-Colombia (Sta. Martha) in December 1973, we climbed to the upper regions of the Sierra Nevada to San Lorenzo to the research station of the Inderena (Instituto Nacional de los Recursos Naturales Reno-vables y del Ambiente = National Institute of Renewable Natural Resources and Environment (Colombia) at 2,300 m above sea level, also with mules as mounts. Hannes Paulus, in the background Dagmar von Helversen. On the right: Otto von Helversen.

<sup>83</sup> HOLZSCHUH C. (1971): Bemerkenswerte Käferfunde in Österreich. — Mitt. Forstl. Bundesversuchsanstalt Wien 94: 1-65.

<sup>84</sup> PETROVITZ R. (1980): Österreichisch-entomologische Expeditionen nach Persien und Afghanistan. Beiträge zur Coleopterenfauna. Teil XII. Weiteres über Lamellicornia aus Iran. — Annls. Naturhist. Museum Wien 83: 597-638.

<sup>85</sup> I had already planned the new description in 1969 in the Annals of the Natural History Museum Vienna. However, the manuscript was apparently "misaid" and did not reappear until 1974.

<sup>86</sup> History of the Theodor-Körner Fonds: <http://www.theodorkoernerfonds.at/ueber-den-fonds/>;  
[https://www.theodorkoernerfonds.at/tkf/tkf/PreistraegerInnen/PreistraegerInnen\\_1954-2013.html](https://www.theodorkoernerfonds.at/tkf/tkf/PreistraegerInnen/PreistraegerInnen_1954-2013.html)

<sup>87</sup> When I was appointed to the Chair of Zoology at the University of Vienna in 1991 as a German citizen, I also became an Austrian virtually overnight.

for research with an Austrian connection. The typical Austrian way out was to award it pro forma to Prof. Dr. Karl Mandl<sup>88</sup>, but in double the amount, so that the funding was secured. This trip took us via Denmark, Oslo, central Norway to central and southern Sweden and back via Uppsala, Stockholm and Malmö to Germany and finally Vienna.

From June 26 to August 11, 1971, I went on a long road trip to the Caspian Sea and the Elburs Mountains in Iran together with Friedrike Gruber, my later first wife (Friederike Paulus-Gruber, †2000), Hans-Martin Steiner (later Professor of Zoology at the University of Natural Resources and Life Sciences in Vienna), his then first wife Edith Steiner and Harald Tichy (later Professor of Animal Physiology in the Department of Neurobiology at the University of Vienna). This was followed in late 1973/early 1974 by an almost three-month stay in Sta. Martha in northern Colombia together with Dagmar and Otto von Helversen and my first wife. Our main focus was on the bat flower (Figs. 61, 62). The discovery of a new species and genus of the firefly family Phengodidae was entomologically significant: *Penicillophorus ctenotarsus* PAULUS, 1975, which is even a representative of a new subfamily: Penicillophorinae. Our first excursion to Andalusia on the Costa del Sol from March 4 to 18, 1976 was seminal for my further field research. Here I began my research on the female mimicry orchid genus *Ophrys*. In the course of further annual spring trips up to the present day, it has taken me to all regions of the Mediterranean, including the first visits to Israel (1984), Cyprus (1986), Tunisia (1996) and Turkey (1998).

In addition, there were repeated summer trips to southwest France (Alpes Maritimes: hay insect excursion with Otto von Helversen), northern and western Greece (including the first ascent of Smolikas in 1978, which until then had been a restricted military area in Greece), central Italy (Abruzzo and Monti del Matese: Bats, beetles and grasshoppers, together with Dagmar and Otto von Helversen and students), northern and central Spain. As I had inherited a small apartment from my aunt Hannelore Paulus in Gran Canaria (Arguinegin-Patalavaca), our first tour took us there in 1988. This was followed by further trips to Tenerife, Fuerteventura (Fig. 95) and Lanzarote. In addition to the general fauna and flora, we were particularly interested in wolf spiders (Lycosidae). This later resulted in a new description of *Alopecosa thaleri* from Gran Canaria and a summarizing publication on the wolf spiders of Gran Canaria (HEPNER & PAULUS 2007, 2009) in the course of a further diploma thesis by Martin Hepner in Vienna (2004).

I often accompanied my wife Urte Paulus to her international archery competitions throughout Europe, e.g. to Scotland, Wales, Portugal, Finland, Estonia or Hungary in addition to Austria, Germany and Switzerland. These were all European or World Championships, where she almost always won medals, several times even the title of European Champion and once even the title of World Champion<sup>89</sup>.

Long-distance travel first began in 1973 with our research trip to Colombia (with stays in Barbados, Trinidad and Curaçao). This was followed by visits to Nigeria (1976),

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<sup>88</sup> Have a look in FISCHER M. 1991, Seite 293: [http://verlag.nhm-wien.ac.at/pdfs/092B\\_291304\\_Fischer.pdf](http://verlag.nhm-wien.ac.at/pdfs/092B_291304_Fischer.pdf)

<sup>89</sup> <https://www.gettyimages.at/detail/nachrichtenfoto/austrian-gold-medalist-of-individual-longbow-women-nachrichtenfoto/74479597>



Kenya and Tanzania (1978, 2016), Uganda (2019: incl. Visit to the mountain gorillas and chimpanzees), Seychelles (2017), Dubai (Emirates) (2016), Egypt (2018, 2020, 2022), Morocco (2020), Malaysia (Borneo-Sabah) and Brunei (2015), Bali, Flores, Komodo Island (2017), India (Rajasthan) (2018), Cuba (2016), Oman (2021/22) and Central China (2023).

### **My path to Schaller and Vienna**

After attending school in Mainz and my great interest in insects, especially butterflies and beetles, it was only logical that I studied biology in Mainz from 1966. My most important teachers there were Prof. Dr. Stefan Vogel, Prof. Dr. Helmut Risler and Doz. Dr. August-Wilhelm Steffan. However, my first encounter with Prof. Friedrich Schaller was during the annual meeting of the Association of German Biologists, which took place in Vienna in 1966. I was presented with the medal by the then president of this association, Prof. Dr. Friedrich Schaller (Fig. 7a). I had no idea at the time that this was a kind of fateful encounter. What I also didn't know at the time was that my biology teacher was also a student of Schaller, who had written a doctoral thesis on collembolans with him when Schaller was a lecturer in Mainz<sup>90</sup><sup>91</sup>. What I also didn't know at the time was that Schaller himself had habilitated under Wolfgang von Buddenbrock. However, he had already moved to the University of Braunschweig in 1958, so I was no longer able to see him in Mainz. From there, Schaller finally followed a call to Vienna in 1968, where he worked until his retirement in 1987.<sup>92</sup>



**Abb. 27:** Prof. Dr. Friedrich Schaller in his Vienna apartment on 20.9.2015 at the age of 95 with Hannes Paulus.

<sup>90</sup> As Friedrich Schaller also lived in the so-called Kettlersiedlung in Mainz's upper town at the time, it is likely that I played "together in the sandpit" with the eldest daughter at least, without suspecting anything of their later acquaintance.

<sup>91</sup> MAYER H. (1957): Zur Biologie und Ethologie einheimischer Collembolen. — Zoologische Jahrbücher 85: 502-570.

<sup>92</sup> Prof. Dr. Dr.h.c. Friedrich Schaller died on 5.5.2018 at the age of 97.

After completing my intermediate diploma in 1968, I made my plans a reality and initially went to Vienna for a year. I immediately sought contact with Prof. Schaller and other zoologists (including the mite specialist Prof. Dr. Eduard Piffel and Prof. Dr. Herbert Franz at the University of Natural Resources and Applied Life Sciences), who all gave me a very warm welcome. After a year in Vienna, however, I was so enthusiastic about the city and its insect-rich environment that I decided to finish my studies here. In 1970, Schaller suggested that I write my dissertation on a fine-structure study of the collembolan eyes, a group of small proto-insects about whose senses very little was known. I had a job at the Institute of Anatomy and Physiology of Domestic Animals in the main building of the School of Natural Resources and Applied Life Sciences (Hochschule für Bodenkultur)<sup>93</sup>, where one of the two existing electron microscopes in Vienna was located at the time. I spent my time at this institute until the end of my doctorate in 1971, meeting Prof. Dr. Schubert-Soldern<sup>94</sup> (affectionately called "Bossi" by all of us), Prof. Dr. Hans Adam ("Hans-Uncle")<sup>95</sup> (although he had already received an appointment as professor of zoology in Salzburg in October 1968, he still spent a lot of time in Vienna at first), the secretary Grete Schulz ("Schulz-Tant"). The latter was a gifted draughtswoman and produced some of the drawings and graphics in my publications at the time. The eye topic subsequently lent itself to a very successful study of the evolution of the compound and frontal eyes of insects and other arthropods (e.g. Fig. 45). After a postdoctoral fellowship from the DFG, I was able to take up an assistant position in Freiburg i. Br. with the well-known evolutionary biologist Prof. Dr. Günther Osche in 1973. In 1978 I habilitated here with the topic "Evolution of arthropod eyes". In 1981<sup>96</sup>, I was appointed Professor of Zoology in Freiburg under Osche and was then Head of the Department of Electron Microscopy in Freiburg until I was appointed to Vienna in 1991 (Fig. 22).

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<sup>93</sup> Die Hochschule für Bodenkultur wurde erst 1975 in Universität umbenannt.

<sup>94</sup> Prof. Dr. Rainer Schubert-Soldern (1900-1974) was head of the Institute for Anatomy and Physiology of Domestic Animals at the University of Natural Resources and Life Sciences in Vienna from 1950 to 1970. A well-known book by him is: "Philosophie des Lebendigen", published by Anton Pustet Graz-Salzburg-Vienna, 1951, 276 pp.

<sup>95</sup> 1925-2013; [http://www.zobodat.at/biografien/Adam\\_Hans\\_ENTAU\\_0021\\_0287-0288.pdf](http://www.zobodat.at/biografien/Adam_Hans_ENTAU_0021_0287-0288.pdf)

<sup>96</sup> What was curious at the time was that the faculty initially habilitated me in biochemistry due to a typing error. The mistake could only be corrected in another session.



**Fig. 28:** My professorship successors to my position at the Department of Zoology in Freiburg: left: Prof. Dr. Josef ("Jupp") Müller (ecology of carrion beetles, etc.) and his successor, right: Prof. Dr. Oliver Niehuis (son of my friend Manfred Niehuis) (phylogenomic analysis of Apoidea, etc.).

My successors in Freiburg were Prof. Dr. Josef Müller<sup>97</sup> (fig. 28 left) and, since October 2019, Prof. Dr. Oliver Niehuis<sup>98</sup> (fig. 28 right).

### **My encounters with personalities and their influence on my scientific development**

I started studying insects, especially butterflies and beetles, as a schoolboy without having any formative role models. The first person who later influenced me was Prof. Dr. Klaus Rose in Mainz, whom I met one day on the Mainz sands. His way of collecting and evaluating initially had a strong influence on me. We went on many excursions together, including a trip to Lebanon in 1966. At the beginning of my biology studies in Mainz, I very quickly came into contact with Prof. Dr. Konrad Schmitt and especially Prof. Dr. August Wilhelm Steffan<sup>99</sup>. He introduced me to the scientific study of beetles, especially Elmidae and Byrrhidae. From 2010, I was allowed to edit his journal "Entomologia Generalis", which he founded, until 2018. My later friendships, first with Jochem Martens in Mainz and then above all with Otto von Helversen in Freiburg, shaped my way of thinking and the scientific way of looking at nature. Otto's mother once said that Otto had also been strongly influenced by me. However, the meeting with Prof. Dr. Günther Osche in Freiburg and the occasional meetings with Ernst Mayr during his visits to Freiburg were decisive for my future path. Both influenced and shaped my thinking in evolutionary biology, so that my call

<sup>97</sup> [https://www.researchgate.net/profile/Josef\\_Mueller2](https://www.researchgate.net/profile/Josef_Mueller2)

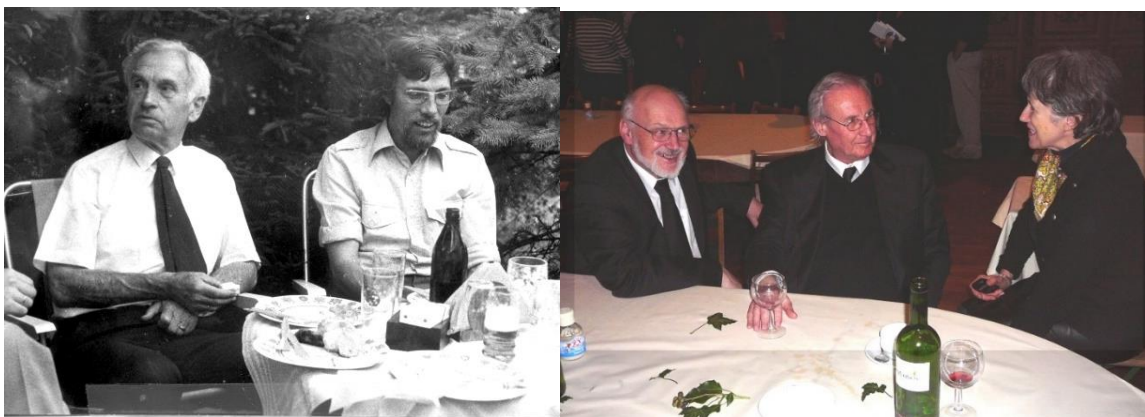
<sup>98</sup> [https://www.researchgate.net/profile/Oliver\\_Niehuis/experience](https://www.researchgate.net/profile/Oliver_Niehuis/experience). Oliver Niehuis is the son of Manfred Niehuis, whom I already knew during my time in Mainz. Among other things, he published an edition of the beetle fauna of the Mainz sands, to which I contributed a lot of my own data. [https://www.rng-mainz.de/images/MNArchiv25-Mainzer\\_SandT2\\_ab273.pdf](https://www.rng-mainz.de/images/MNArchiv25-Mainzer_SandT2_ab273.pdf); <http://gnor.de/wp-content/uploads/2019/07/Diehl-Niehuis-Geburtstag.pdf>

<sup>99</sup> [https://www.zobodat.at/biografien/Steffan\\_August\\_Wilhelm\\_DGaaE\\_Nachr\\_31\\_1.pdf](https://www.zobodat.at/biografien/Steffan_August_Wilhelm_DGaaE_Nachr_31_1.pdf)

to Vienna was only logical when I founded the first Institute of Evolutionary Biology in Austria<sup>100</sup>.



**Fig. 29:** (left) Prof. Dr. Günther Osche (University of Freiburg) (2009) and his facial expressions during lively discussions. (right) Prof. Dr. Ernst Mayr with Prof. Dr. Günther Osche during one of his several visits to Freiburg (1989) (Photos: H. Paulus).



**Fig. 30** Ernst Mayr, next to Hannes Paulus during one of his visits to Freiburg (1980). During his visits, there were always heated discussions about species problems and phylogenetic systematics. **Right Fig. 31:** Prof. Dr. Norbert Elsner (left: neurobiologist, University of Göttingen, †16.6.2011), Prof. Dr. Klaus-Peter Sauer (middle:

<sup>100</sup> My friend and co-assistant Klaus-Peter Sauer had already founded an Institute for Evolutionary Biology at the University of Bielefeld in Germany in 1979.

evolutionary biologist, University of Bonn, †12.11.2022), Nele Ronacher (right) (Berlin), wife of Prof. Dr. Bernhard Ronacher (neurobiologist).



**Fig. 32:** Hannes Paulus, Norbert Elsner and Friedrich Barth (right) in Vienna on 18.4.2007. Norbert had given a lecture on “Sexual selection in field locusts” at the Academy of Austrian Sciences in Vienna.

Of course, various colleagues had very different influences on my way of working and thinking. I was close friends with Otto von Helversen (Erlangen), but also with Prof. Dr. Klaus-Peter Sauer (Bonn) and Prof. Dr. Norbert Elsner (Göttingen). I last saw both of them at Otto von Helversen's funeral service at Neuhaus Castle near Erlangen (Fig. 31, 32).

### **Other private matters**

I got to know Friederike Gruber and her extended family during my doctoral thesis in Vienna. She had five siblings. She was also writing her "Hausarbeit" (= state examination thesis) on the vertebrate brain at the zoology department of the University of Natural Resources and Applied Life Sciences. After completing my doctoral thesis in 1971, she followed me to Freiburg, where I had found my first job as a university assistant to Prof. Dr. Günther Osche at the Department of Biology I (Zoology). While still in Vienna, she initially worked as a secondary school teacher for biology and sport. Unfortunately, she was unable to find a suitable position in Freiburg, as school bureaucratic hurdles prevented this. After teaching at private schools in Freiburg, she turned to other activities and finally became a passionate potter with a large workshop ("Fabrik" in Freiburg)<sup>101</sup>. The marriage ended in 1993 without children.

<sup>101</sup> <https://www.fabrik-freiburg.de/keramikwerkstatt>

My appointment in spring 1991 as Full Professor of Zoology-Evolutionary Biology at the University of Vienna was also associated with a change in my private life (Fig. 3). In 1993 I married Urte Freitag, who had secretly followed me from Freiburg to Vienna in a furniture van in 1991. This marriage produced two children: Maria (1993) and Marko (1995). Maria completed her master's degree in astrophysics in Glasgow (Scotland) and a doctorate in Munich/Garching in 2021, Marko wrote a master's thesis on "Possibilities for unsealing our soils in Austria" in 2023 in the master's program in spatial planning and regional planning at the Vienna University of Technology. My wife Urte Paulus initially continued to study spiders. This resulted in the publication of her diploma thesis on wolf spider successions in the glacier foreland of the Hornkees in the Zillertal Alps in 1997<sup>102</sup>. As already mentioned, we collected mainly wolf spiders during numerous stays in Gran Canaria, which were processed in the course of a diploma thesis by Martin Hepner together with material also collected by him (HEPNER & PAULUS 2009). Urte preferred to stay at home because of the children, but was also involved in spider, insect ("Insects for kids") and dance projects at kindergartens and schools in Vienna (especially in Mauer). From 2000, Urte Paulus devoted herself more and more to archery (longbow) and achieved the highest national and international successes (world champion, multiple European champion, multiple Austrian champion). She was the national coach for the Austrian squad and is currently a national and international coach trainer. She has just published a comprehensive standard work on archery<sup>103</sup>. I myself am still an archer in my spare time. After years of intensive activity in a jazz dance group, she switched to a Viennese hula dance group that cultivates the tradition of Hawaiian dances. She even won another European championship title with this group in 2018. In her versatility, she has also repeatedly written poetry. In 2020, a small illustrated volume of poetry was published in English, in which she played a leading and significant role<sup>104</sup>. In 2021, another volume of poetry was published in German, with numerous illustrations by her (Fig. 34)<sup>105</sup>.

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<sup>102</sup> PAULUS URTE & PAULUS H. F. (1997): [https://www.zobodat.at/pdf/BERI\\_84\\_0227-0267.pdf](https://www.zobodat.at/pdf/BERI_84_0227-0267.pdf)

<sup>103</sup> PAULUS U. (2019): Das große Buch vom Bogensport. Lehrbuch für Anfänger, Hobby-, Wettkampf-, Leistungsschützen und Trainer. ISBN: 978-3-938921-65-4, 1. Auflage, 568 Seiten, farbige Fotos und Abbildungen.

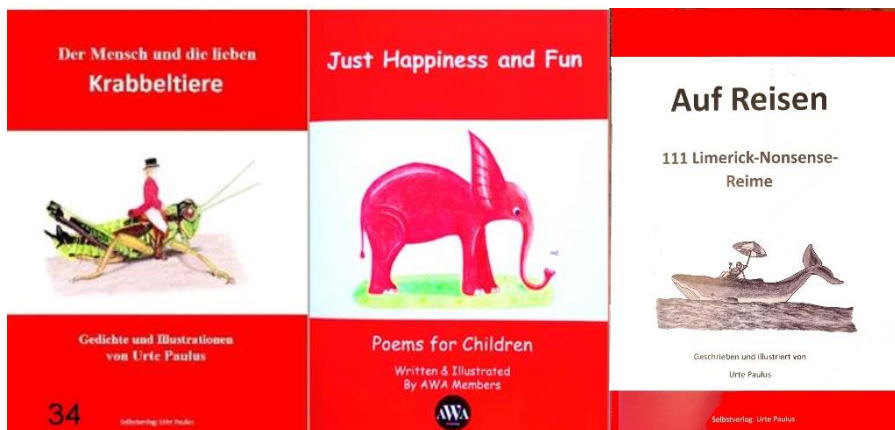
[https://bogenschiessen.de/bogenschiessen/de/verlag/buecher/neue\\_buecher.php](https://bogenschiessen.de/bogenschiessen/de/verlag/buecher/neue_buecher.php). An English edition will appear in 2024.

<sup>104</sup> „Just Happiness and Fun – Poems for Children” written by AWA Members (ISBN 978-3-200-07315-9). AWA = International Womens Association in Vienna. Of the 54 poems presented here, 46 are from her pen.

<sup>105</sup> „Der Mensch und die lieben Krabbeltiere”, 78 poems with 80 illustrations from the author, 80 pages (self-published).

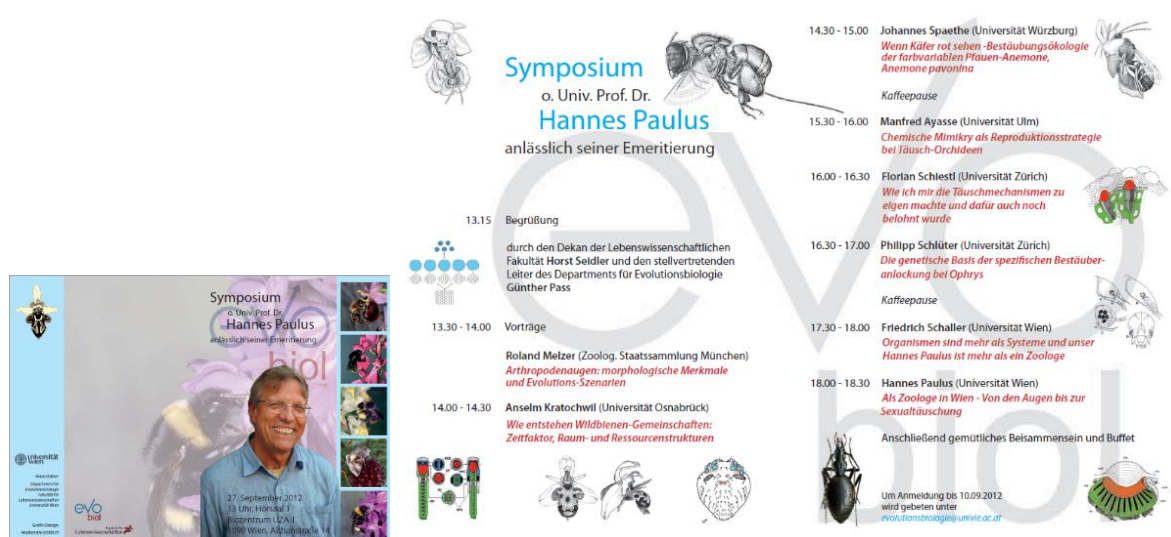


**Fig. 33:** Hannes Paulus and Urte Paulus as archers (longbow); Ireental near Vienna (25.3.2006 and 27.12.2023).



**Fig.34:** Five books by Urte Paulus: three volumes of poetry (bottom), the large and small textbook on archery (above).

Until my retirement in autumn 2013, I myself headed the Department of Evolutionary Biology, which my successor Prof. Dr. Dr. Andreas Wanninger initially renamed the Department of Integrative Zoology in 2013, but later changed its name back to Evolutionary Biology. Since September 2021, most of the biology department has been located in the new building at Djerassiplatz 1 in 1030 Vienna.



**Fig. 35:** Folder and program of the symposium on 27.9.2012 on the occasion of the retirement of o. Univ.-Prof. Dr. Hannes Paulus in Vienna.



**Fig. 36: (left):** Prof. Dr. F. Schaller at my retirement ceremony on 27.9.2012 in the main lecture hall of my institute in Vienna, Althanstrasse. In the background you can see (from left to right): Ernst Gügel (Munich, orchid researcher), Prof. Dr. Florian Schiestl (Zurich), Prof. Dr. Günther Pass (one of my assistants in Vienna), Prof. Dr. Andreas Wanninger (my successor in Vienna), Prof. Dr. Roland Melzer (Munich, my last doctoral student from eye research). **(right):** F. Schaller gave a keynote speech: "Organisms are more than systems and our Hannes Paulus is more than a zoologist"



Some of my students went on to become professors: Prof. Dr. Anselm Kratochwil (Professorship of Ecology, University of Osnabrück), Prof. Dr. Roland Melzer (Professorship of Zoology, University of Munich) (Fig. 47), Prof. Dr. Manfred Ayasse (Chair of Chemical Ecology, University of Ulm) (Fig. 74), Prof. Dr. Florian Schiestl (Institute of Botany, University of Zurich) (fig. 74), Prof. Dr. Johannes Spaethe (Behavioral Physiology and Sociobiology, University of Würzburg) (Fig. 75). Prof. Dr. Philipp Schlüter (initially assistant to Florian Schiestl in Zurich, then appointed to the Chair of Biochemistry of Plant Secondary Metabolism, University of Hohenheim) (Fig. 68, 76), Johannes Stökl should have taken up the professorship of Applied Entomology at the University of Hohenheim, but went to the University of Bayreuth instead. With the exception of Anselm Kratochwil and Roland Melzer, all of them emerged from Ophrys research. Anselm Kratochwil (Fig. 17, 20) was the first of my research groups to work intensively on wild bees in his extensive doctoral thesis under my supervision (completed in 1983).

My close connection with the Natural History Museum in Vienna and my efforts to attract capable staff to teach at my university led to three prominent habilitations at my instigation (Fig. 37): Prof. Dr. Ulrike Aspöck (world specialist of Raphidioptera and Neuropterida)<sup>106</sup>, lecturer Dr. Elisabeth Haring (head of the central research laboratories) and lecturer Dr. Anita Gamauf<sup>107</sup> (Department of Ornithology). She died far too early in 2018 at the age of just 56.



**Fig. 37:** During my time in Vienna, I helped three prominent scientific ladies from the Natural History Museum in Vienna to gain their habilitation (from left to right): Prof. Dr. Ulrike Aspöck (world specialist of Neuropterida), Doz. Dr. Anita Gamauf (Ornithology) and Doz. Dr. Elisabeth Haring (Molecular Systematics), here on the occasion of my retirement ceremony on 27.9.2012 at my Institute of Evolutionary Biology in Vienna.

<sup>106</sup> Documentations of her scientific publications: [https://www.zobodat.at/pdf/LBB\\_0048\\_2\\_1011-1079.pdf](https://www.zobodat.at/pdf/LBB_0048_2_1011-1079.pdf)

<sup>107</sup> [http://verlag.nhm-wien.ac.at/pdfs/121B\\_005008\\_Winkler.pdf](http://verlag.nhm-wien.ac.at/pdfs/121B_005008_Winkler.pdf)

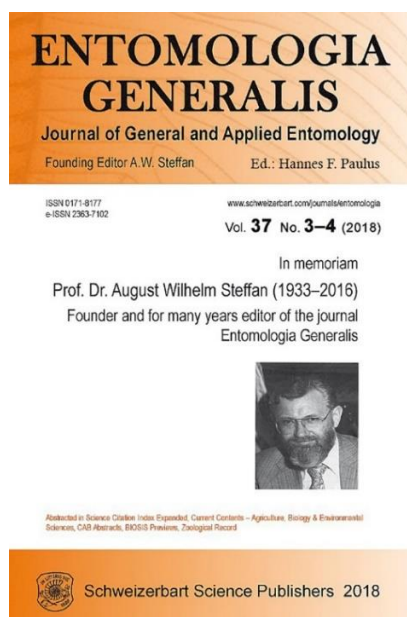
Of course, all my assistants also habilitated in Vienna: Prof. Dr. Walter Hödl (1990, amphibian-reptile reproductive biology), Prof. Dr. Günther Pass (arthropod circulatory organs, molecular phylogeny of basal Hexapoda), Prof. Dr. Harald Krenn (functional morphology of the mouthparts of flower-visiting insects), Prof. Dr. Manfred Ayasse (chemical ecology and scent communication) (now University of Ulm), PD Dr. Johannes Spaethe (sensory ecology) (now University of Würzburg). I have already taken over Prof. Dr. Helmut Kratochvil (Fig. 23, 25).

I am/was editor of two international journals:

1. "Zoologica" (founded in 1888), Schweizerbart Verlag, Stuttgart:  
<http://www.schweizerbart.de/series/zoologica>, for monographs or comprehensive manuscripts from the entire field of zoology (Fig. 38).



**Fig. 38:** 10 volumes of the "Zoologica" series 2011-2020 edited by Hannes Paulus.



**Fig. 39:** "Entomologia Generalis" (founded in 1978 by A. W. Steffan, initially as Entomologica Germanica), for scientific papers from the entire field of entomology: <http://www.schweizerbart.de/journals/entomologia>. Last issue edited by Hannes F. Paulus: Volume 37 (3-4), 2018.

2. "Entomologia Generalis" (founded by A. W. Steffan, initially as "Entomologica Germanica"), for scientific works from the entire field of entomology: <http://www.schweizerbart.de/journals/entomologia>. From 2018, I handed over the management to N. Desnieux. I am currently still a member of the editorial board (Fig. 39).

Other functions at journals and associations:

Member of the editorial board of: "Journal of Phylogenetics & Evolutionary Biology"<sup>108</sup>, Zeitschrift der Arbeitsgemeinschaft Österreichischen Entomologen, Zoomorphology, Zoologischer Anzeiger, Zeitschrift für zoologische Systematik und Evolutionsforschung.

1982-1991 only German member of the European Committee "Conservation of Nature and Natural Resources (Invertebrata)" of the Council of Europe in Strasbourg (France)<sup>109</sup>,

1996-1999 President of the ÖEG (Austrian Entomological Society),

2001-2013 Member of the KIÖS (Commission for Interdisciplinary Ecological Studies of the Austrian Academy of Sciences),

1994-2013 Member of the Scientific Advisory Board of the Schönbrunn Zoo.

## **My university teaching**

### Freiburg:

Lectures: Introduction to the Histology of Vertebrates, Fauna of Central Europe, Pollination Biology, Biology of Insects, Main Lecture Special Zoology, Introduction to the Principles of Phylogenetic Systematics.

Exercises (all from 1974-1991): Histology course, large practical course I (morphology, systematics of animals) and II (ecology), III (behavior, physiology) each full day, with field exercises in S-France.

Excursions: Native fauna, excursions to the Mediterranean region (S-Spain: Andalusia, S-Portugal, S-France, Crete, Rhodes, Lesbos, Naxos, Karpathos, Peloponnese),

Seminars: Recent work from pollination biology, animal-plant interactions, co-evolution, new results from evolutionary biology.

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<sup>108</sup> <https://www.hilarispublisher.com/phylogenetics-evolutionary-biology/editorial-board.html>

<sup>109</sup> This met twice a year in Strasbourg to plan conservation projects for EU-wide invertebrates, especially insects.

## Vienna:

**Lectures:** Introduction to Evolutionary Biology (2 hrs.) (1992-2018), Sexual Selection (2 hrs.) (1993-2019), Introduction to Zoology (STEOP: "Studieneingangs- und Orientierungsphase")<sup>110</sup> (2007-2013), Pollination Biology (2 hrs.) (1992-2019), Native Fauna (1992-2019), Speciation and Coevolution-Concepts and Case Studies (2008-2016), Scientific Thinking - interdisciplinary lecture series.

**Exercises:** Establishment and management of Introductory Biology Exercises I with field trips (compulsory for all students in the first semesters), Zoology Exercises (parts Coelenterata, Plathelminthes, Arthropoda), Entomology Courses, Animal Identification Exercises.

**Excursions:** In addition to numerous small excursions in the greater Vienna area, there were Alpine excursions (partly together with Harald Krenn and Barbara Gereben-Krenn) (High Tatras - together with Prof. Dr. Josef Rusek , Budweis<sup>111</sup>: Institute of Landscape Ecology-Soil Biology), Zillertal Alps: Berliner Hütte, Totes Gebirge, Hohe Tauern: Weisssee, Rudolfshütte and above all many years at the Haus Alpine Naturschau research station on the Gross Glockner High Alpine Road etc.), numerous excursions to the Mediterranean region (Fig. 40).



**Fig. 40:** Examples of excursions to the Mediterranean region led by Hannes Paulus (N Greece: Lake Prespa, Mallorca, North Thessaly: Olympus region,).

<sup>110</sup> [https://www.oesterreich.gv.at/themen/bildung\\_und\\_neue\\_medien/universitaet/5/Seite.160105.html](https://www.oesterreich.gv.at/themen/bildung_und_neue_medien/universitaet/5/Seite.160105.html)

<sup>111</sup> Prof. Dr. Josef Rusek was a visiting professor at my institute for many years and gave various lectures on soil biology. [https://cs.wikipedia.org/wiki/Josef\\_Rusek](https://cs.wikipedia.org/wiki/Josef_Rusek). I had already met him during my doctoral thesis in 1970 at the various "Colloque internationales sur les Collemboles" in Brunoy near Paris and later in Prague as a leading specialist in the order Collembola.



## Philosophisch-theologisch-biologisches Seminar 300073 SE

Huber L., Janauer G., Kampits P., Kallhoff A., Kattmann U., Klein A., Langthaler R., Lengauer E., Markl P., Paulus H., Kastner O., Popp M.

### Was ist der Mensch?

- 15.03.12 Die biologische Natur des Homo sapiens.  
Zu einem funktionalen Verständnis des heutigen Menschen.  
(Prof. Dr. H. Paulus)
- 22.03.12 Was ist der Mensch?  
Zur schwierigen Frage der Interaktion von biologischer und kultureller Evolution.  
(Prof. Dr. L. Huber)
- 19.04.12 Die Rechtfertigung unseres Tuns. Eine kantische Perspektive auf den Menschen.  
(Mag. O. Kastner)
- 26.04.12 Was ist der Mensch?  
Zur Fraglichkeit und Autonomie des Menschen.  
(Prof. Dr. A. Klein)
- 03.05.12 Genetische Vielfalt des Menschen – Überlegungen zu "Rassen" und Rassismus.  
(Prof. Dr. U. Kattmann)
- 04.05.12 (14 Uhr) - 06.05.12 (12 Uhr) Seminar im Bildungshaus Stift Zwettl

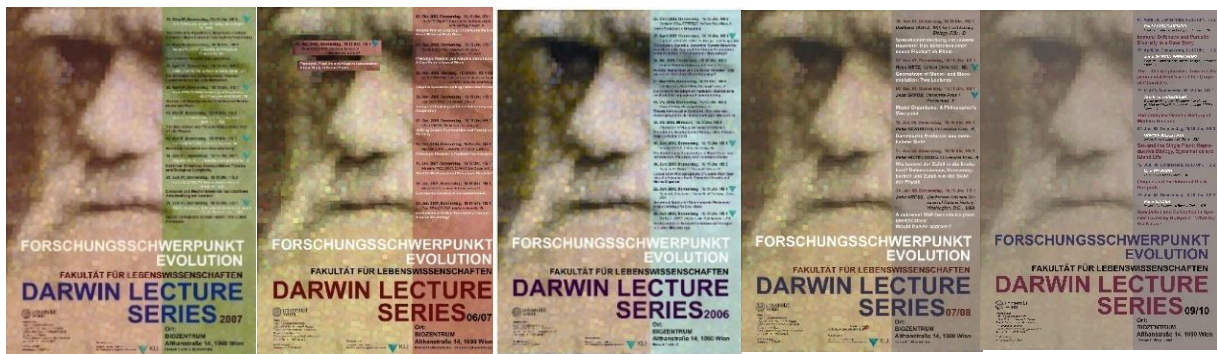
jeweils um 18:15, HS 2, Biozentrum, Althanstrasse 14, 1090 Wien

Die Teilnahme an den Donnerstag-Vorlesungen in Wien ist notwendige Voraussetzung für die Seminartage in Stift Zwettl.  
Anmeldung bitte während der Vorbesprechung am 08.03.12

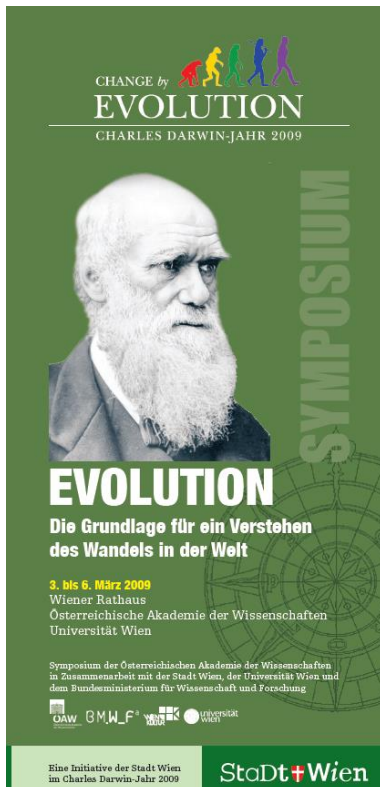
**Fig. 41:** Example of a program of the "Philosophical-Theological-Biological Seminar in Vienna and Zwettl Monastery", organized mainly by Prof. Dr. Marianne Popp, here from the summer semester 2012.

Seminars: Twice a year "Zoological Colloquium" (together with Prof. Dr. Friedrich Barth, Head of the Department of Neurobiology) (1992-2013), departmental seminar (recent results of evolutionary biology research), philosophical-theological-biological seminar (at Zwettl Monastery) - discussions on current topics at the intersection of philosophy, theology and biology (Fig. 41).

Project practicals with seminars: Pollination biology, wild bee internship (annually since 1994 together with Manfred Ayasse), pollination biology in the Alps (Hohe Tauern) with a focus on bumblebees (together with Johannes Spaethe).



**Fig. 42:** Program posters of the lectures of the "Darwin Lecture Series" organized by Hannes Paulus at the Department of Evolutionary Biology at the University of Vienna from 2006-2010.



**Fig. 43:** A "personal" meeting with Charles Darwin only took place on May 20, 2008 at Madame Tussauds in London to get advice on the upcoming Darwin Year. Unfortunately, he remained silent.

# PROGRAMM

3. bis 6. März 2009 / Wiener Rathaus / Österreichische Akademie der Wissenschaften / Universität Wien

**Dienstag, 3. März 2009**  
Wiener Rathaus, Festsaal, Feststiege I  
Lichtenfelsgasse 2, 1010 Wien

**19:00 Uhr** Eröffnungsvortrag im Rahmen der Wiener Vorlesungen  
Svante PÄÄBO, Leipzig  
*Ursprung des Menschen aus molekulargenetischer Sicht*

**Mittwoch, 4. März 2009**  
Österreichische Akademie der Wissenschaften, Festsaal, Dr. Ignaz Seipel-Platz 2, 1010 Wien

**10:00 Uhr** Begrüßung  
Peter SCHUSTER  
Präsident der Österreichischen Akademie der Wissenschaften

Johannes HAHN  
Bundesminister für Wissenschaft und Forschung  
*Vorstellung der Studie: „Wie denkt Österreich über Evolution?“*

**10:30 Uhr** Peter HAMMERSTEIN, Berlin  
*Darwin heute*

**12:00 Uhr** Herbert JÄCKLE, Göttingen  
*Mechanisms of development in the light of evolution*

**14:30 Uhr** Eörs SZATHMÁRY, Budapest  
*Darwin extended. From molecules to man*

**15:30 Uhr** Eva JABLONKA, Tel Aviv  
*Epigenetic inheritance in evolution*

**17:00 Uhr** Gerd MÜLLER, Wien  
*Evolutionäre Entwicklungsbiologie und die Erweiterung der Synthetischen Theorie*

**19:00 Uhr** Vortrag in Kooperation mit den Wiener Vorlesungen  
Kardinal Christoph SCHÖNBORN, Wien  
*Schöpfung und Evolution – zwei Paradigmen und ihr gegenseitiges Verhältnis*

**Donnerstag, 5. März 2009**  
Universität Wien, Zoologie, HS I  
Althanstraße 14, 1090 Wien

**9:30 Uhr** Hannes PAULUS, Wien  
*Selektionstheorie*

**10:30 Uhr** Horst SEIDLER, Wien  
*Evolution zum Homo Sapiens. Morphologie und Großhirn*

**12:00 Uhr** Sebastian BONHOEFFER, Zürich  
*Die Evolution der sexuellen Reproduktion*

**14:30 Uhr** Ludwig HUBER, Wien  
*The tree of mind. On the evolution of cognitive abilities in human and non-human animals*

**15:30 Uhr** Karl SIGMUND, Wien  
*Evolution und Spieltheorie*

**17:00 Uhr** Erich STREISSLER, Wien  
*Evolution. How far was Darwin an economist*

**Freitag, 6. März 2009**  
Österreichische Akademie der Wissenschaften, Sitzungssaal  
Dr. Ignaz Seipel-Platz 2, 1010 Wien

**9:30 Uhr** Kurt DOPFER, St.Gallen  
*Von der Zelle zum Bewusstsein des Homo Sapiens Oeconomicus: Universalität und Kontingenz in der Evolution*

**10:30 Uhr** Arthur ROSENAUER, Wien  
*Evolution in der Kunstgeschichte*

**12:00 Uhr** Peter MARKL, Wien  
*Evolutionstheorie und die Irritation durch Design ohne Designer*

**13:00 Uhr** Peter SCHUSTER, Wien  
*Abschließende Worte*

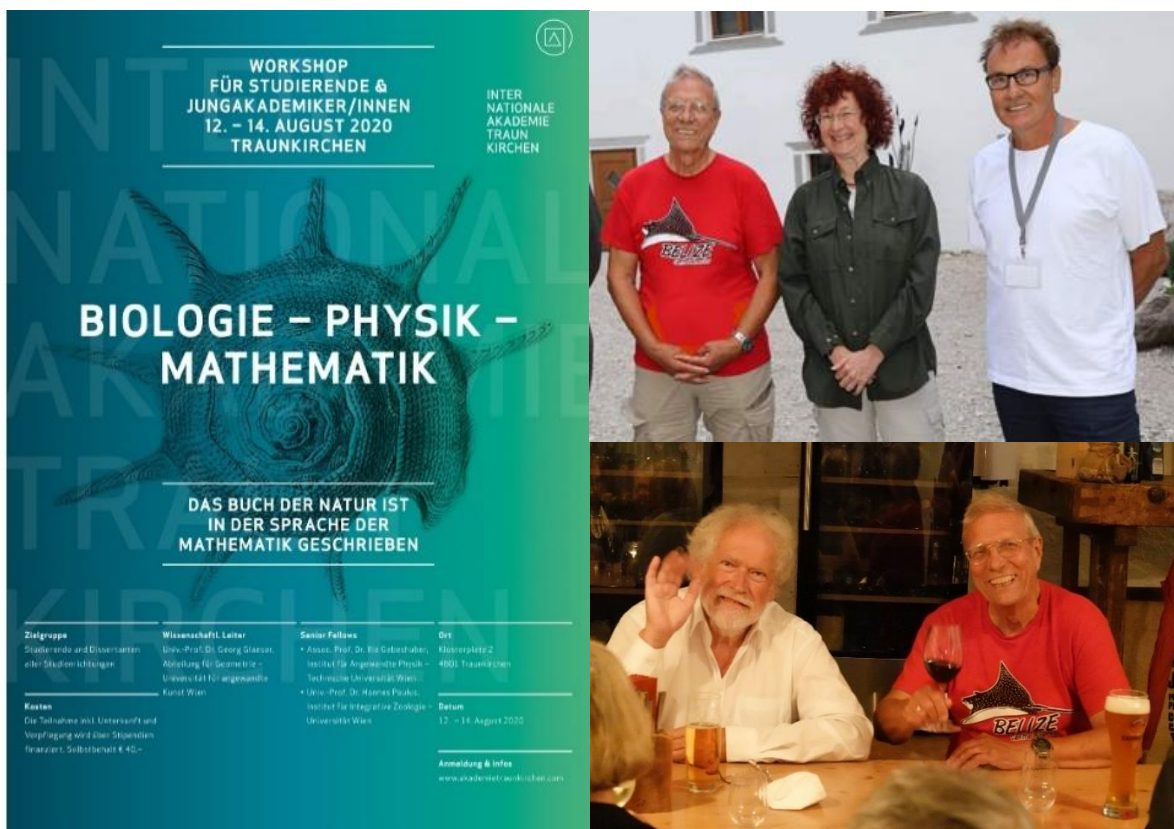
**Fig. 44:** Program for the Darwin Year 2009 organized by the Austrian Academy of Sciences (Prof. Dr. Peter Schuster) and my Department of Evolutionary Biology (Prof. Dr. Hannes F. Paulus), sponsored by the City of Vienna, among others.

## Further events:

Foundation and organization of the interdisciplinary lecture series "Darwin Lecture Series" (2007-2013) with numerous international speakers (Fig. 42).

Darwin Symposium from 3-6 March 2009 in Vienna: Evolution - The Foundations for Understanding Change in the World (together with Prof. Dr. Peter Schuster, President of the Austrian Academy of Sciences) (Fig. 44). As the opening speaker we had invited the later Nobel Prize winner Svante Pääbo (Fig. 13b).

As the last seminar for the time being, we organized "Biology - Physics - Mathematics: The book of nature is written in the language of mathematics" together with Georg Gläser (Geometry) and Ille Gebeshuber (Applied Physics) at the International Academy Traunkirchen from 12-14.8.2020. At the end of the event, we were joined by Prof. Dr. Anton Zeilinger. He had founded this academy years earlier. We had an intensive discussion about evolution and quantum physics (Fig. 45). Zeilinger is one of the internationally renowned quantum physicists at the University of Vienna. On October 4, 2022, he was finally awarded the Nobel Prize in Physics together with two other quantum physicists.

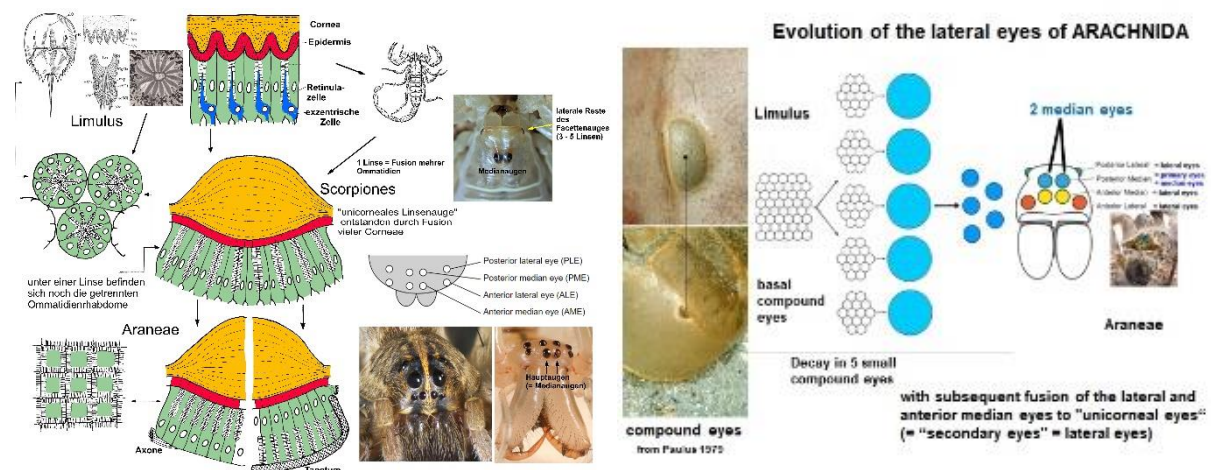


**Fig. 45: (left):** "Biology-Physics-Mathematics" workshop in Traunkirchen (Austria) on 14.8.2020. **(right, above):** Organizers of the workshop "Biology-Physics-Mathematics" at the International Academy Traunkirchen; from left to right: Hannes Paulus, Ille Gebeshuber (Applied Physics, TU Vienna) and Georg Gläser. **(right, bottom):** Prof. Dr. Anton Zeilinger (Nobel price in physics in 2022) and Hannes Paulus in the follow-up session to our workshop (Photo: G. Glaeser).

## Research activities

### Phylogeny of arthropod eyes

Based on studies of the rudimentary eyes of the ground-dwelling arthropod *Collembola*, I was able to show that the eight "ocelli" are in fact remnants of an original compound eye, as they contain exactly all the elements of a mandibulata ommatidium. In Freiburg, I started an extensive comparative ultrastructural analysis of numerous other insects, myriapods and some crustaceans to show the clear homology of the ommatidia between crustaceans and insects. According to the tracheal concept advocated at the time, the myriapod eyes did not fit into this argument, as they are built completely differently. Since insect larvae often have similarly structured lateral stemmata as Myriapoda, I was able to show through a further comparative study of numerous Holometabola larvae that these also evolved from modified ommatidia. I used this as a model to show that similar modifications could also have taken place within the Myriapoda. Only later was the Pancrustacea or Tetraconata (4 cone cells in the crystalline cone is a synapomorphic character of Hexapoda + Crustacea) concept developed, mainly on the basis of molecular-phylogenetic data, according to which the Insecta and Crustacea are sister groups and the Myriapoda are the original Mandibulata. The modification model for the larvae of Holometabola remained unaffected, as did the Myriapoda, even if they now had a mandibulata ommatidium at the base. Examinations of the eyes of the genus *Scutigera*, the only Myriapoda with compound eyes, at the base of the Chilopoda showed that they probably had a mandibulate ommatidium.



**Fig.46:** Diagrams of the evolution of Arachnida eyes based on an original compound eye in the marine Xiphosurus (*Limulus*). Illustrations from the lecture H. Paulus. "Introduction to Zoology", based on the data from PAULUS (1979) and the comparative studies of my Freiburg graduate student Ingeborg GEBHARDT (1983).

The modification model for the larvae of Holometabola remained unaffected, as did the Myriapoda, even if they now had a mandibulata ommatidium at the base. Studies on the eyes of the genus *Scutigera*<sup>112</sup>, the only Myriapoda with compound eyes, at

<sup>112</sup> PAULUS (1979) and later Carsten MÜLLER (2008): Vergleichend-ultrastrukturelle Untersuchungen an Augen ausgewählter Hundertfüßer (Mandibulata: Chilopoda) und zur Bedeutung von Augenmerkmalen für die phylogenetische Rekonstruktion



the base of the Chilopoda showed that they are probably also derived from an ommatidium with a four-part crystal cone (Tetraconus<sup>113</sup>). My investigations also within the Arachnida eyes showed that they are also derived from basal compound eyes of the Chelicerata (Fig. 46). From the beginning, I argued against prominent opponents for the monophyly of the Arthropoda, which was later clearly proven by the numerous molecular data.



**Fig. 47:** Roland Melzer's doctorate at the University of Freiburg (1990): from left to right: Prof. Dr. K.-F. Fischbach (Developmental Genetics), Roland Melzer, H. Paulus (supervisor) and Prof. Dr. Klaus Vogt (Sensory Physiology, successor to Prof. Dr. B. Hassenstein). In 2023 Prof. Dr. Roland Melzer was professor of Systematic Zoology at the University of Munich and section manager of the "Arthropoda varia" in the Bavarian State Collection for Zoology (ZSM).

All these investigations were supported by many of my students, who did outstanding work in their diploma and doctoral theses. Roland Melzer (Fig. 47) in particular worked on the larval eyes of many dipterans and was even able to show that the remarkable so-called Bolwig organ in the reduced larval head of higher dipterans represents modified stemmata. This organ played a special role in the emerging field of developmental biology, as it could be shown that this organ plays a kind of guideline for the growth of new axons during the recruitment of new nerve tracts (neurogenesis) in the pupal phase. This fitted in very well with the research of Prof. Dr. Karl-Friedrich Fischbach<sup>114</sup> and, above all, my friend Prof. Dr. José Campos-

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der Euarthropoda. Doctoral thesis, Faculty of Natural Sciences, University of Rostock, 138 p. + 140 p. in appendix, Cuvillier Verlag, Göttingen, ISBN 978-3-86727-484-5.

<sup>113</sup> The later renaming of a mandibulata group "Tetraconata" is based on this.

<sup>114</sup> [https://de.wikipedia.org/wiki/Karl-Friedrich\\_Fischbach](https://de.wikipedia.org/wiki/Karl-Friedrich_Fischbach)

Ortega<sup>115</sup> who initially worked on such issues in Freiburg and later at the University of Cologne in genetics and became famous for his work: “kind of guideline for the growth of new axons”.

One participant in the first full-day project internship in behavioral ecology, which I and Otto von Helversen were the first to design, did their doctoral theses under José Campos-Ortega and went on to become well-known neurobiologists, including Prof. Dr. Claudia Stürmer<sup>116</sup> (University of Konstanz) and Prof. Dr. Alois Hofbauer<sup>117</sup> (University of Würzburg, died in 2021). I had a friendship with Claudia Stürmer during her student days. Among other things, she was with us on our field internship in the south of France (Camargue) to study the courtship behavior and visual orientation of the red jumping spider *Philaeus chrysops*. After completing her doctorate, she moved to the Max Planck Institute for Developmental Biology in Tübingen, and from 1990 to the University of Konstanz as a full professor of developmental neurobiology. Her main focus was on the growth and regeneration of nerve fibers.

Roland Melzer continued his eye research on arthropods very successfully and is still a professor and group leader of the Arthropoda Varia at the Zoological State Collection in Munich<sup>118</sup>.

The move to the University of Vienna was also associated with an increased focus on my field of pollination biology. A book on the evolution of vision together with the Professor of Geometry at the University of Applied Arts and enthusiastic photographer Georg Gläser from Vienna (Fig. 47) was the last publication on eyes to date.<sup>119</sup> A Chinese edition was even published in 2021 (Fig. 85).

## Systematics and phylogeny

Phylogenetic systematics, species concepts and speciation have occupied me since my late school days and then especially in the course of my university research. Numerous discussions with my Freiburg teacher Günther Osche and my Freiburg assistant colleagues (especially Walter Sudhaus, Peter Sauer, Michael (Theo) Schmitt) sharpened my and everyone else's understanding of phylogenetic processes. My visits to the "Phylogenetic Symposia"<sup>120</sup>, which took place almost annually in different Central European university towns, were important here from the beginning of 1970. Here I got to know the big names in these disciplines at the time and took part in the sometimes-heated discussions. I was even allowed to give a keynote lecture three times:

1. 20th Symposium in Hamburg, 28-29.11.1975: topic co-evolution: "Co-evolution between flowers and their animal pollinators".
2. 31th symposium in Freiburg im Breisgau, 25-27.11.1988: Homology:

<sup>115</sup> [https://www.biospektrum.de/blatt/d\\_bs\\_pdf&\\_id=934338](https://www.biospektrum.de/blatt/d_bs_pdf&_id=934338)

<sup>116</sup> <https://www.biologie.uni-konstanz.de/stuermer/prof-dr-claudia-stuermer/>

<sup>117</sup> Alois Hofbauer later was Professor of Neurobiology at the University of Würzburg (Germany)

<sup>118</sup> <https://zsm.snsb.de/sektion-mitarbeiter/prof-dr-roland-melzer/>

<sup>119</sup> With him as photographer and the biophysicist Prof. Dr. Werner Nachtigall from Saarbrücken, another book was written: "Evolution des Fliegens" (<https://www.springer.com/de/book/9783662498989>). Werner Nachtigall is one of the founders of bionics. He turned 85 years old on 7.6.2019. (<https://www.uni-saarland.de/nc/universitaet/aktuell/artikel/nr/20909.html>). This book was also published in chinese in 2021.

<sup>120</sup> A summary of the history of these symposia has been compiled by Michael SCHMITT & Walter SUDHAUS (2018): 60 years of Phylogenetisches Symposium, a scientific meeting with a difference. — Annals of the History and Philosophy of Biology Vol. 21 (2016): 247-308. [https://www.univerlag.uni-goettingen.de/bitstream/handle/3/eissn-2512-5923\\_annals21/Annals21.pdf?sequence=1&](https://www.univerlag.uni-goettingen.de/bitstream/handle/3/eissn-2512-5923_annals21/Annals21.pdf?sequence=1&)

„Homologizing ultrastructures“

3. 41th Symposium in Vienna (Austria), 19-21.11.1999: Large-scale systematics: Homology and convergences: "The Myriapoda-Crustacea-Insecta problem: Do the structures of the photoreceptors offer a solution?"

In addition, our "Zoological Colloquia" in Freiburg were often followed by meetings and discussions at Günther Osche's home. The occasional meetings with the famous evolutionary biologist Prof. Dr. Ernst Mayr, who was often in Freiburg with his sister and then always visited Osche and us assistants at home, were also formative (Figs. 29, 30, 48).



**Fig 48:** Hannes Paulus with Prof. Dr. Ernst Mayr during one of our occasional meetings at Prof. Günther Osche's apartment, where Mayr repeatedly visited his sister in Freiburg (Freiburg 1988).

**Fig. 49:** Prof. Dr. Peter Weygoldt (University of Freiburg i Brg.), during my visit to his house in the Münstertal south of Freiburg on 8.7.2014. He died on 23.10.2021 at the age of 88.

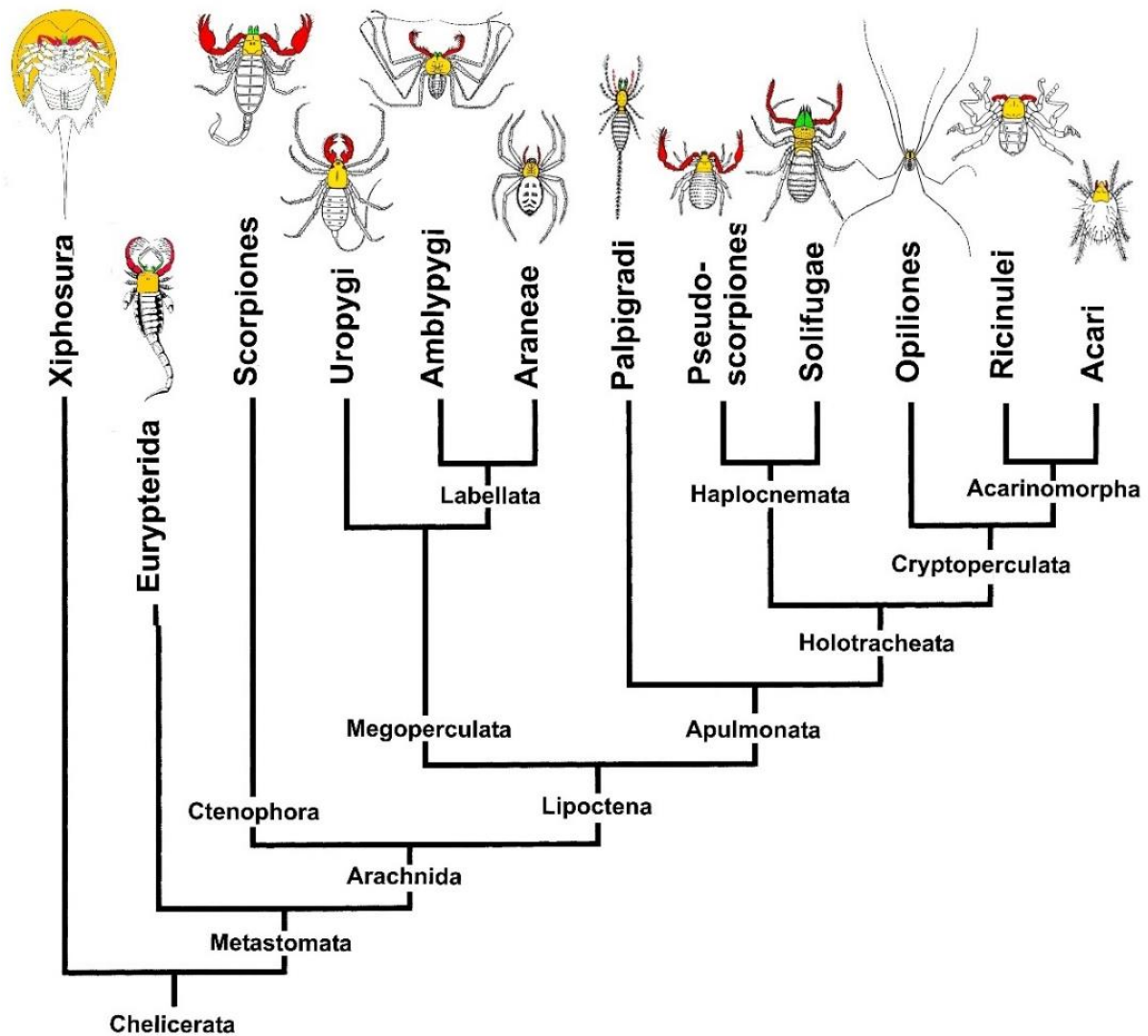
**Three large groups were the subject of such treatments:**

### **Chelicerata**

In collaboration with my friend Prof. Dr. Peter Weygoldt<sup>121</sup> in Freiburg, my work on the phylogeny of the Chelicerata (Figs. 49, 50), which is still widely cited, arose from the study of the evolution of eyes. The proposed phylogenetic tree based on morphological characteristics is still essentially valid today. New large taxa names were also introduced here: Euchelicerata WEYGOLDT & PAULUS, 1979 (= Xiphosura + Metastomata) and Metastomata WEYGOLDT & PAULUS, 1979 (= Eurypterida + Arachnida). I also had many private connections with Peter's family during my time in Freiburg. I am the godfather of his youngest son Hans Weygoldt<sup>122</sup>.

<sup>121</sup> Peter Weygoldt lived with his wife Sylvia in his house in Münstertal, south of Freiburg. He died on 23.10.2021 at the age of 88.

<sup>122</sup> He now lives as Hans Whygold in North Carolina and works as: "Breathwork facilitator and life coach".



**Fig. 50:** Phylogenetic tree of the Chelicerata according to the works of WEYGOLDT & PAULUS (1979) and PAULUS (2004).

As my friend Otto von Helversen had also studied wolf spiders in addition to his research into the sound biology of grasshoppers in Freiburg, I had also developed an interest in this family. We had a small apartment in the south of the Canary Island of Gran Canaria. Together with my wife Urte Paulus, I collected wolf spiders on this island for many years. From this, Martin Hepner<sup>123</sup> in Vienna, together with his own collections, was able to write a diploma thesis with me, in which even a new species *Allopecosa thaleri* was described<sup>124</sup>. Together with Claudia Gack and Ulrich Schaible, I also worked on the ultrastructure and significance of the strange head appendages in dwarf spiders (Linyphiidae), whose males compete for females with head secretions during courtship.

<sup>123</sup> I got him a scholarship for a three-month stay in Gran Canaria.

<sup>124</sup> [www.researchgate.net/publication/273219214\\_Alopecosa\\_thaleri\\_a\\_New\\_Wolf\\_Spider\\_from\\_Gran\\_Canaria\\_Araneae\\_Lycosidae](http://www.researchgate.net/publication/273219214_Alopecosa_thaleri_a_New_Wolf_Spider_from_Gran_Canaria_Araneae_Lycosidae)

## Coleoptera

I collected my first beetles in Mainz in the summer of 1956 at the age of 13. As I didn't know any better at the time, small beetles were glued onto self-cut paper plates with eagle owl. I continued to eagerly collect beetles during various summer stays in Wickstadt near Friedberg in Upper Hessen, where we went from my nursery school in Mainz as a country stay. Here we were even "allowed" to "smoke" blackberry leaf tea against the omnipresent mosquito plagues. In 1959, I started keeping diary entries<sup>125</sup>. At that time, of course, I initially wanted to see large longhorned beetles, jewel beetles, doll predators or rhinoceros beetles. During a visit to my great-aunt Martha von Reitzenstein<sup>126</sup> in Berlin in March 1959, I visited Pfaueninsel (Peacock Island)<sup>127</sup>, which at that time still had many very old oak trees, on which there were many feeding traces of the large oak longhorn beetle (*Cerambyx cerdo*); in the hollow trunks I found remains of the hermit beetle (*Osmoderma eremita*), wing covers of the large oak longhorn beetle and even wing covers of the forest caterpillar hunter (*Calosoma sycophanta*). A visit to the aquarium in the Zoological Garden in Berlin was very exciting for me because there were living and several dead rhinoceros beetles in a terrarium with large toads. I asked the keeper if I could have some dead animals and he actually gave me a dead pair of *Oryctes nasicornis*. Years later, many of the old oak trees on this peacock island had unfortunately fallen victim to a "clean-up operation", along with the many rarities living in them. I later experienced something similar in the Schwanheim Forest near Frankfurt<sup>128</sup>, which I often visited from Mainz. At the beginning of the 1960s, there were still many of the so-called "1000-year-old oaks" (their actual age was probably up to 500-600 years). Around 30 of these trees are still standing today. After all, the remainder is now an FFH conservation area. Here, too, the great oak bucks and many large stag beetles were bustling about in June. On a large tree stump lay many dozens of heads with prothorax of the large stag beetle, some of which were still moving. Birds (mainly jays) had eaten the abdomens. I used part of this collection of male stag beetle heads as an example of intraspecific size variation in one of the showcases of the Natural History Museum in Mainz as part of the development of a display collection<sup>129</sup>.

I dealt with systematics and taxonomy from the very beginning of my work with insects. The in-depth study of the European Byrrhidae led to the editing of this family in the then newly conceived work "Die Käfer Mitteleuropas" by Freude-Harde-Lohse. Here I also presented the Nosodendridae, which in our country has only one species (*Nosodendron fasciculare*), as well as the Limnichidae, which were previously regarded as Byrrhidae. The encounters with the various beetle specialists that I met again and again, especially at the insect exchange days in Frankfurt, Munich or Vienna, were also stimulating. As I was particularly interested in Carabidae, especially the species of the genera *Carabus* and *Cychnus*, I had intensive contact

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<sup>125</sup> My excursion diaries, which have been carefully kept from then until now, are mostly scanned.

<sup>126</sup> Sister of my maternal grandmother. The noble family of the Reitzensteins is an old Franconian nobility.

<sup>127</sup> This is despite the fact that the island or parts of it have been a nature reserve since 1924 at the instigation of the famous entomologist Wolfgang Stichel (specializing primarily in bugs). However, Stichel was also notorious for his Nazi past, which cost his colleague Walther Arndt his life. He was executed in 1944 after being denounced.

<sup>128</sup> <https://frankfurt.de/media/pdf/gruenguertel>; [https://www.zobodat.at/pdf/Berichte-der-Senckenberg-naturf-Ges-Frankfurt\\_1913\\_0236-0265.pdf](https://www.zobodat.at/pdf/Berichte-der-Senckenberg-naturf-Ges-Frankfurt_1913_0236-0265.pdf)

<sup>129</sup> I published later „Einige Vorschläge für Hilfsprogramme unserer gefährdeten Käfer“ (PAULUS 1980).

with Walter Heinz (Schwanfeld near Schweinfurt) (1925-2023)<sup>130</sup>, Armin Korell<sup>131</sup>, Carl Ludwig Blumenthal, Prof. Dr. Karl Mandl (Vienna)<sup>132</sup> and occasionally Stephan von Breuning.



**Fig. 51** Karl Mandl, honorary doctorate in Vienna at 1986.

**Fig. 52:** The married couple Eva and Assad Vartian in Vienna 1977, right Carl von Demelt (Klagenfurt, Austria), behind: the couple Legorsky (Vienna) and right behind: Dr. Fritz Kasy in the lecture hall of the Wien-Ottakring Adult Education Center (Volkshochschule). (Fotos: Zobodat).

I spent some time several nights with C. L. Blumenthal<sup>133</sup> in shared rooms on the occasion of various conferences. Here I was able to listen with excitement to his adventurous stories, which he had experienced in the course of his *Carabus* research, especially in Turkey. His visits to southeastern Turkey in the restricted area of the Kurds were not without danger. However, politics was far from his mind. He only wanted to find a previously lost *Carabus* in the border region. His pride and joy was the business card he had designed, on which he had added many imaginative titles to his name, in Arabic script of course, knowing the oriental soul. In addition to his actual title, some of these included "honorary Prussian district forester", "retired senior district forester", "general entomologist" and the like. Walter Heinz also risked a lot for his *Carabus* (W. Heinz died on 3.1.2023 at the age of 97; see the obituary by W. SCHAWALLER (2023): *Integrative Systematics* 6 (1): 113-119). The search for the nominate form of *Carabus stroganowi* ZOUBKOFF, 1837 and *Carabus (Cyclocarabus) kuznetzovi* SEMENOV, 1903 in the border region of northern Iran to what was then Russia, now Turkmenistan<sup>134</sup>, was quite adventurous. On my trip to

<sup>130</sup> <https://bioone.org/journals/integrative-systematics-stuttgart-contributions-to-natural-history/volume-6/issue-1/2023.484664/In-Memoriam-Coleopterist-Dipl-Ing-Walter-Heinz-19252023/10.18476/2023.484664.full>

<sup>131</sup> FRISCH J. (2014): Armin Korell (1928-2014) — ein Nachruf mit Verzeichnis seiner entomologischen Schriften. — *Entomologische Zeitschrift*, Stuttgart 124 (4): 203-207.

<sup>132</sup> [https://www.zobodat.at/pdf/ANNA\\_92B\\_0291-0304.pdf](https://www.zobodat.at/pdf/ANNA_92B_0291-0304.pdf); In his honor, I described *Cychropsis mandli* from Nepal in 1975.

<sup>133</sup> Carl-Ludwig Blumenthal (1917-1989) war hochdekoriertes Hauptmann und Oberstleutnant und zuletzt Kommandeur des Wachbataillons in Siegburg: MÜTING D. unter Mitarbeit von A. KORELL (1990): Nachruf auf Carl L. Blumenthal (20.12.1917-9.3.1989). — *Ent. Z. (Frankfurt/Main)* 100: 158-159.

<http://www.koleopterologie.de/arbeitsgemeinschaft/historie/biografien/enkel/blumenthal.html>

<sup>134</sup> This region is highly interesting biogeographically:

[https://www.academia.edu/19872845/Biogeography\\_and\\_Ecology\\_of\\_Turkmenistan?auto=download](https://www.academia.edu/19872845/Biogeography_and_Ecology_of_Turkmenistan?auto=download)

Iran, I had been commissioned by him to find out whether there was still forest in this border mountain range, the Kopet Dagh. The information from the Iranian forestry authority was clear; there were no more forests on the Iranian side, only sporadic remnants on the Russian (now Turkmen) side of the border mountain range. As far as I remember, Walter Heinz<sup>135</sup> was actually able to find these *Carabus* forms in baited traps on the Russian-Turkmen side, although this border, as part of the "Iron Curtain", was heavily guarded with watchtowers at the time. His very extensive carabid collection is now in the Stuttgart Natural History Museum.

I last met Stephan von Breuning<sup>136</sup>, the famous *Carabus* and Cerambycidae-Lamiinae specialist, at a conference in Vienna, where he had attracted attention by presumably stealing an as yet undescribed *Carabus* species from Karl Mandl, or so Karl Mandl suspected at the time. Breuning was known for his engaging nature and was therefore banned from various museums. As a "k.u.k.-Altösterreicher" (he was born in Vienna in 1894 and had also studied biology in Vienna before leaving the country for Paris in 1945, where he died in 1983), Breuning was a charismatic personality with a remarkable knowledge of entomology. He first became known for his "Monograph of the genus *Carabus* (1932-1937)" or his revision of the Dorcadionini (1962, 665 pages!). However, during his long life as a private scholar in Paris, he tirelessly and ceaselessly described new species and forms, with 7,894 new species in the Cerambycidae/Lamiinae alone.

Based on the studies on the biology of *Agapanthia violacea* still in Mainz, work on other beetle larvae followed in Vienna, initially mainly longhorn beetles, and in 1970 the already mentioned first discover of Limnichidae larvae, which I was able to find in laborious search work in the river gravel of the then not yet dammed Drau near Ferlach in Carinthia. Finally, in Vienna, the first new species of beetle was described, namely *Pseudochelonarium kalimantanense*, a representative of the strange Dryopoidea family Chelonariidae, which were also previously regarded as relatives of the Byrrhidae. I was less interested in the new descriptions than in comparative morphological studies of mouthparts, wing veins etc. in order to find out more about their phylogenetic position. This was followed by further descriptions of new Byrrhidae, including new genera from Nepal. From Freiburg I had lively and friendly contact with Dr. Walter Wittmer<sup>137</sup>, who worked as curator of beetles at the Natural History Museum in Basel. He aroused my interest in his families (Cantharoidea). So, I

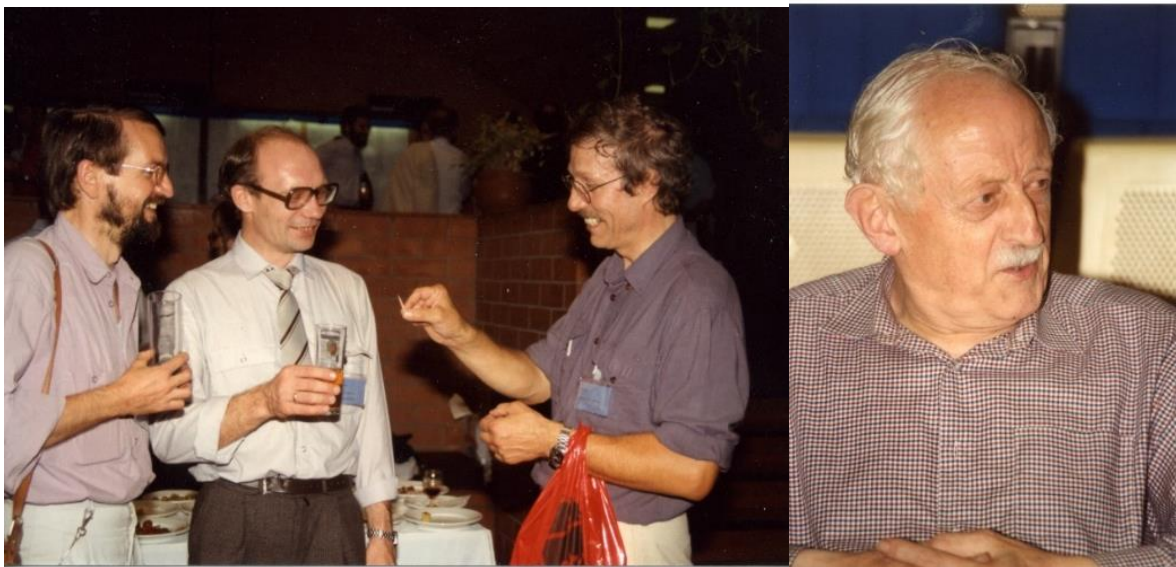
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<sup>135</sup> 2015: Walter Heinz 95th birthday: [https://www.schwanfeld.de/download/Kembachkurier\\_2020-15.pdf](https://www.schwanfeld.de/download/Kembachkurier_2020-15.pdf)

<sup>136</sup> Stephan von BREUNING (1894-1983): Blumenthal C. L. & W. Heinz (1984): Zum Gedenken an Stephan von Breuning. — Entomologische Zeitschrift 94: 32; TÉOCCHI P. (1984): Stephan von Breuning (1894-1983). — Bulletin de la Société Entomologique de Mulhouse (janvier-mars): 16. von Breuning, Stephan (1984). "Stephan von Breuning 1894-1983". Notice autobiographique et liste des publications". — Bulletin de la Société Sciences Nat. 41: 1-17. MEUNIER Jean-Yves & Pierre TÉOCCHI (2015): Addenda et corrigenda à la liste des publications de Stephan von Breuning (1894-1983) avec une notice biographique. — L'Entomologiste 71(5): 317-320.

<sup>137</sup> Dr. Walter Wittmer (1915-1998) was a well-known specialist of the Cantharoidea, especially the families Cantharidae, Malachiidae, Phengodidae and Drilidae, as well as other groups of the so-called Malacodermata (soft-bodied beetles). Meantime, the family Drilidae was recognized as "disguised" Elateridae on the basis of molecular-genetic studies (KUNDRATA R. & L. BOCAK 2011: The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? — Zoologica Scripta 40(4): 364–378, doi:10.1111/j.1463-6409.2011.00476.x); or: Zoological Journal of the Linnean Society, 2019, XX, 1-40. As curator, Wittmer also endeavored to expand the museum's collections. For example, the museum purchased the extensive *Carabus* collection of Karl Mandl (Vienna), Dr. Hermann Priesner (Linz) (1891-1974, Biography: <https://www.zobodat.at/personen.php?id=4175&bio=full>) the beetles from Egypt, from the Thysanoptera-, Pompilidae- and ichneumon wasp specialist, or the extensive staphylinid collection (40,000 specimens) of Julius Lautner (Zurich), who died in 1972. ([https://www.zobodat.at/biografien/Lautner\\_Julius\\_Mitt-Schweiz-Ent-Ges\\_1972\\_45.pdf](https://www.zobodat.at/biografien/Lautner_Julius_Mitt-Schweiz-Ent-Ges_1972_45.pdf)) Obituary: BRANCUCCI, M. (2005): Dr. h.c. Walter Wittmer — a coleopterist to the bone. — Entomologica Basiliensia 27: 60 pp.

was able to describe a tiny representative of the South American family Phengodidae as a new genus and species: *Penicillophorus ctenotarsus*, which I was able to find by light myself during our almost three-month stay in Colombia in 1972/1973. Walter Wittmer achieved a special "highlight" for the museum by purchasing what is probably the largest private collection of beetles from Walter Frey ("Loden-Frey") in Tutzing, south of Munich. As I was friends with Walter Wittmer, I experienced this at first hand. It was preceded by a curious legal dispute, as the Bavarian State Collection in Munich wanted to prevent this purchase<sup>138</sup>. I was even supposed to be involved as an expert for the Munich collection, but I refused because of various conflicts of interest.



**Fig. 53: (left):** Meeting during the 1st Coleopterological Congress in Barcelona in September 1989: from left to right: Dr. Michael ("Theo") Schmitt (today in Greifswald, Germany), Alexander Kirejtshuk from St. Petersburg, Hannes Paulus (in Freiburg at that time). **(right)** Prof. Dr. Roy Crowson (University of Glasgow)

I was also interested in other beetle families: Pyrochroidae, Cebrionidae, Phengodidae from Colombia, Carabidae, Scarabaeidae (*Trox*) or, more recently, Lymexylidae, as I was informed by my friends Hubert and Renate Rausch (Scheibbs) (Fig. 99) I was able to describe as a new genus (*Urtea graeca* PAULUS, 2004) a sensational find for Europe in northern Greece of a tertiary tropical relict of the otherwise tropical subfamily Atractocerinae<sup>139</sup>. From Nepal I was able to describe *Pyrrhochroa nepalensis* and two new species of the genus *Ischalia* with the new subgenus *Pseudohomalitus* (*martensi* and *nepalensis*) based on material collected by Jochen Martens from the Pyrrhochroidae/Anthicidae. *Pseudohomalitus* was later assigned to the genus *Eupleurida* (GUSAKOV & TELNIKOV 2007)<sup>140</sup>, which was previously only known from the Nearctic, within the Ischaliidae, now separated as a separate family. Other new discoveries included *Cychropsis mandli* (1971) (Carabidae, Cychrini), *Trox dhaulagiri* (1972) (Trogidae) and the new genus and species *Chrysosimplocaria nepalensis* (1982) (Byrrhidae). This genus of Byrrhidae

<sup>138</sup> e.g. <https://www.zeit.de/1994/30/streit-um-tote-kaefer>

<sup>139</sup> The animal was found in northern Halkidiki in NE Greece, far from any likelihood of dispersal.

<sup>140</sup> Systematic changes and new species of Ischaliidae. — Folia Heyerovskiana 15: 39-46.



later proved to be a species-rich endemic of the Himalayas with at least 17 different species. The representatives of the genus *Cychropsis* have also expanded from four species (1971) to 38 species with a total of 25 subspecies (2014)<sup>141</sup>.

In the course of my more intensive involvement with the large-scale systematics of beetles, I was in active correspondence with the old masters of the phylogeny of the order, above all Roy A. Crowson<sup>142</sup> from the University of Glasgow in Scotland (Fig. 53). His book "The natural classification of the families of Coleoptera", London, 1955, was for a long time the "bible" of the major systematics of beetle science. However, a personal meeting did not take place until September 1989 at the only "International Congress of Coleopterology" in Barcelona to date. R. A. Crowson proved to be an undisputedly competent discussant, but also an almost irascible opponent if one did not share his opinion. Clarke Scholtz from Pretoria (South Africa) (Department of Zoology and Entomology, specialist in Scarabaeoidea, especially Trogidae) was present at most of our discussions and wrote in a letter dated October 16, 1989: "Dear Hannes, it was good meeting you and talking about scarabs in Barcelona. I trust you have recovered from your meeting with Crowson!" However, Crowson had already apologized to me the next day for his behaviour.



**Fig. 54:** Prof. Dr. Michael Schmitt, Dr. Alexander Kirejtshuk from St. Petersburg and myself in Freiburg in 1989 (after attending the 1st International Congress of Coleopterology of Barcelona).

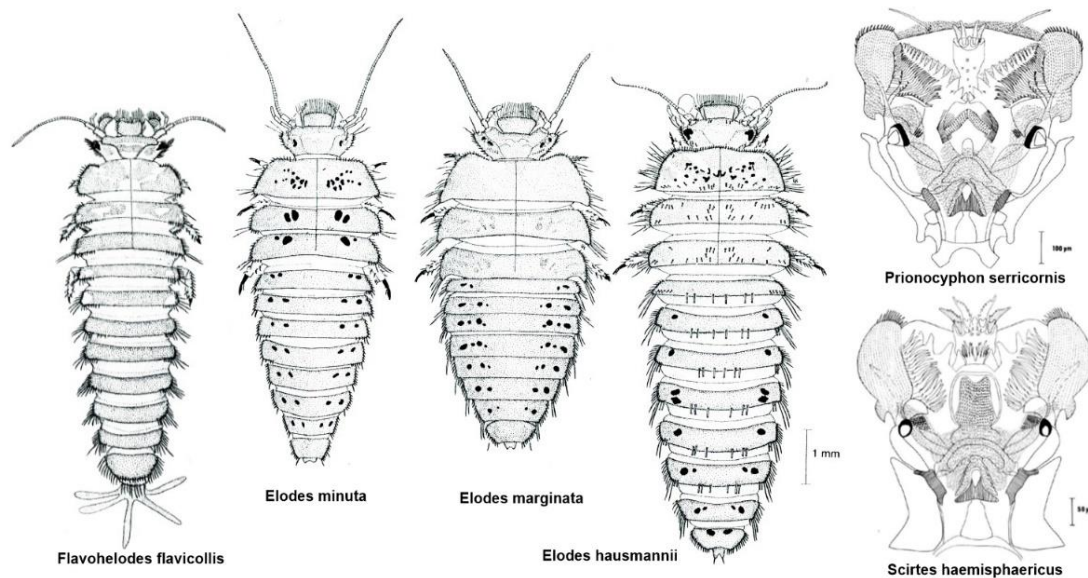
In Barcelona I also met the Russian nitidulid specialist Alexander Kirejtshuk from St. Petersburg (then still Leningrad: Zoological Institute, Russian Academy of Sciences) (Fig. 53, 54)<sup>143</sup>. He was in the "West" for the first time and felt "like he was on the

<sup>141</sup> DEUVE T. (2013): Note sur le sous-genre *Cychropsis* du genre *Cychrus* et descriptions de nouveaux taxons du Népal Central (Coleoptera, Carabidae). — Coléoptères 19(1): 1-15.; HÄCKEL & SEHNAL (2014): Studies and Reports. — Taxonomical Series 10(2): 393-402 (Prague).

<sup>142</sup> orbitary: [https://www.zobodat.at/pdf/KOR\\_70\\_2000\\_0225-0226.pdf](https://www.zobodat.at/pdf/KOR_70_2000_0225-0226.pdf)

<sup>143</sup> <https://www.zin.ru/animalia/coleoptera/eng/kirejtsh.htm>

moon", as he told me himself, because of the numerous "innovations" such as photocopiers or the fact that you could go into a photo store and an hour later already have all the paper prints. He was already a specialist in the Cucujoidea, especially Nitidulidae. He accompanied me to Freiburg at the end of the congress. As he was completely destitute, I invited him to sleep in our apartment. Together with Michael ("Theo") Schmitt, who worked with me at the institute as an assistant to Prof. Dr. G. Osche, we spent several highly interesting days of discussion. He also gave a lecture in Freiburg on the phylogeny of beetles.



**Fig. 55:** Drawings by Ursula Hannappel in the course of her diploma and doctoral thesis on the larvae of the Scirtidae (Coleoptera). Here larvae of Central European genera (from HANNAPPEL & PAULUS 1994), on the right detailed structures of the hypopharynx (from HANNAPPEL & PAULUS 1987).

In Barcelona, I presented a lecture based on material from Borneo and Sumatra on a then still undescribed Lucanid as *Nosodendroides sumatraensis* nov. gen. et nov. spec. (nomen nudum!), which was then independently described by Wilhelm Zelenka as the new genus *Echinoaesalus*<sup>144</sup> in 1993 due to the delay until a valid publication caused by the move to the University of Vienna. Like the representatives of the genus *Nosodendron*<sup>145</sup>, these strange little stag beetles from the *Aesalus* family live in the sap flowing from trees and therefore show some remarkable convergences with this family. Twelve species of this genus are now known from SE Asia. In the course of these convergences I took a closer look at the species of the family Nosodendridae. A revision of the family together with Frank Steinheimer has remained unpublished to this day. Frank Steinheimer<sup>146</sup> was already a passionate ornithologist at the time and, after an honorable position as curator of the bird collection of the Natural History Museum in London/Tring, is now head of the Central Stacks of Natural History Collections at Martin Luther University Halle-Wittenberg. Starting in Freiburg, I later worked with my colleague Ursula Hannappel, who was

<sup>144</sup> [https://www.zobodat.at/pdf/KOR\\_63\\_1993\\_0235-0237.pdf](https://www.zobodat.at/pdf/KOR_63_1993_0235-0237.pdf)

<sup>145</sup> HUANG & CHEN 2015: Zootaxa 3920(1): 173-170.

<sup>146</sup> [www.naturkundemuseum.uni-halle.de/mitarbeiter/dr.\\_frank\\_d.\\_steinheimer/](http://www.naturkundemuseum.uni-halle.de/mitarbeiter/dr._frank_d._steinheimer/)

already working in Freiburg and then also in Vienna, on the aquatic larvae of the Scirtidae (formerly Helodidae), where we were particularly interested in the functional anatomy of the highly complex food filtering apparatus of the mouthparts. This resulted in several extensive publications, including the treatment of the larvae in the "Freude-Harde-Lohse" larvae section, edited by Bernhard Klausnitzer in 1994. They are also characterized by the captivating drawings by Ursula Hannappel (Fig. 55). She had also begun an extensive dissertation on this subject. For personal reasons, she discontinued this very promising work.

Most of my earlier trips were devoted to researching the faunistics and systematics of beetles. As I had inherited a tiny apartment in the south of the island of Gran Canaria, many trips took us to this island.

In the course of my *Ophrys* trips to the Mediterranean, I often collected beetles. Worth mentioning are my findings of *Bolbelasmus* (Geotrupidae) on Crete and Rhodes. The first find was in March 1984, when one of these beetles suddenly flew into my car while I was camping in the evening and landed in my glass of red wine, of all things. The following year something similar happened again; this time an animal landed in my soup. I found the last animals on March 14, 2005 when they drowned in a small swimming pool at our accommodation near Agios Nikolaos. Incidentally, several of the endemic camel-necked fly *Fibla (Reisserella) pasiphae* H. ASPÖCK & U. ASPÖCK, 1971 (Inocelliidae) were also swimming here. Further individuals of this enigmatic beetle genus were also found in Rhodes: Koskinou, flown to the light in the car, 30.3.1987; Profitis Elias, 30.3.1999, under a stone. Here it turned out to be *Bolbelasmus nireus* (REITTER, 1895)<sup>147</sup>, which was previously only known from southern Anatolia and northern Iraq. There is another specimen in my collection, which Jochen Martens found in Karpathos (Pigadia 8.4.1963). The species was only newly described in 2011 by MIESSEN & TRICHAS as *Bolbelasmus keithi* from the small island of Kasos and Crete<sup>148</sup>. It had previously been cited as *Bolbelasmus unicornis* from Crete (OERTZEN 1886)<sup>149</sup> and Rhodes (MIKSIC 1959). *Bolbelasmus* is also worth mentioning because the species *B. unicornis* is one of the few beetles listed as a species of special conservation concern in the Habitats Directive of the European Union.

## Beetles as flower visitors

Flower-visiting beetles, especially longhorn beetles and various members of the Scarabaeoidea, aroused my interest early on. After initially focusing on collecting, I soon became interested in what the beetles eat there and what adaptations they have to eating pollen. As part of the large-scale zoological internships in Freiburg, I was often assigned topics that involved comparative morphological studies of the mouthparts of flower-seeking insects. A final major project from Vienna was the study of the pollinator guild of polymorphic anemones in Greece. Here I had already observed the glaphyrid genus *Pygopleurus* busily visiting red poppies and especially the red flowers of *Anemona pavonina*, *A. coronaria* and *Ranunculus asiaticus* on our

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<sup>147</sup> SOMMER et al. (2021): *Zootaxa* 4920 (3): 380-394.

<sup>148</sup> MIESSEN & TRICHAS (2011): *Lambillionea* 111(2): 182-188.

<sup>149</sup> OERTZEN E.v. (1886): Verzeichnis der Coleopteren Griechenlands und Cretas. — *Berliner ent. Zeitschr.* 30: 189-293.

early excursions starting in 1982. The other-colored flowers of the same species (the species have white, yellow, purple or mixed-colored flowers in addition to bright red ones) were not visited at all or much less frequently. I concluded from this that the beetles should actually see red, which would generally be an exception for insects. Like humans, they are trichromats, but their compound eyes lack red receptors and instead have UV receptors. Initial experiments with the red lid of our thermos flask seemed to confirm this. The beetles eagerly flew over this lid during our breakfasts at the campsite. However, we could not rule out the possibility that, as with the red poppy seed, the red was mixed with UV.



**Fig. 56:** Together with my colleagues on the southwest flank of the Greek Mount Olympus on May 1, 2008 at approx. 700m. From left to right: Wilhelmi, Sarah Pfaphigan (later Sarah Streinzer), John Plant, Johannes Spaethe, Martin Streinzer, unknown, Hannes Paulus and Linde Morawetz.

**Fig. 57:** Color dish experiments to test the color selection frequencies of *Pygopleurus* (Glaphyridae) on *Anemona pavonina*. East Greece, foot of Mount Olympus, southwest side, 30.4.2010.

It wasn't until years later that my colleagues Johannes Spaethe and Martin Streinzer and I took up the subject again. In addition to testing the red visibility of some *Pygopleurus* species, we were actually able to show that these beetles are the most important pollinators of the red flowers, while the other-colored flowers are mainly visited by bees. In addition, to choose experiments with color bowls (Fig. 57), we checked the correlation between the frequency of anemone color morphs and the occurrence of *Pygopleurus* along an altitudinal transect of the serpentine road up to the Olympic Ski Center on the southwest flank of Mount Olympus. We had noticed that at an altitude of around 1000 m the anemones are only purple, while red is completely absent. The lower you move down into the valley, the frequency of red flowers increases continuously, becoming dominant from about 300 m upwards. The frequency of *Pygopleurus* was similar. The result suggests that *Pygopleurus* selects the anemone color red (STREINZER et al. 2019).

## Butterflies

I got into entomology by collecting butterflies. As already mentioned, I was already intensively involved with butterflies as a student. This led to my first publications on the local faunistics of the Mainz area, in particular the later Mainzer Sande nature reserve. In 1966, I received the Hörlein Prize from the Association of German Biologists for this work, which was awarded in Vienna and had a decisive influence on the course of my later life. My close connection to Prof. Dr. Klaus Rose (University of Mainz) (Fig. 59), whom I met one day on the Mainz sands, was a motivating factor.



**Fig. 59:** Prof. Dr. Klaus Rose (Mainz, 3.6.1928-13.12.2021).

**(left)** <https://www.abebooks.de/Parnassiinae-World-Part-Errata-Addendum-Vols/18844672801/bd#&gid=1&pid=2>; **(right)** as Emeritus in Mainz (<https://www.aussenwirtschaft.vwl.uni-mainz.de/123.php>).

This developed into a kind of fatherly friendship with me. We went on a number of collecting trips, initially in southern Germany, then mainly to Valais in Switzerland and finally even on a joint trip to Lebanon. Helga Luckenbach<sup>150</sup>, who was initially an assistant to Prof. Rose at the University of Mainz and then went on to become a professor of economics at the University of Giessen, was also often part of the group. Her collection later went to the Natural History Museum in Mainz. Klaus Rose later also worked intensively on the systematic taxonomy of butterflies. His monographic work on the Apollo butterflies (Parnassiinae) is particularly noteworthy<sup>151</sup>. He died on 13.12.2021 at the age of 93. His extensive collection went to the König Research Museum in Bonn. Systematically-taxonomically, however, I have only marginally dealt with butterflies. Blue butterflies from Lebanon (PAULUS & ROSE 1971) and in 1983 the new description of *Paralasa nepalica*, a Nymphalidae/Satyrinae from the high altitudes of NW Nepal, were the only such publications (Fig. 60). The animals had been caught by Jochen Martens in the course of his numerous expeditions to Nepal in the Dolpo District in the easternmost foothills of the subalpine coniferous

<sup>150</sup> [https://de.wikipedia.org/wiki/Helga\\_Luckenbach](https://de.wikipedia.org/wiki/Helga_Luckenbach); siehe auch in RENKER & HENRICH (2009): 411

<sup>151</sup> ROSE K. & J.-C. WEISS (2011): The Parnassiinae of the World. Vol. 5, Keltern, Verlag Goecke & Evers.

forest zone at an altitude of about 3,700 meters. However, the species has only rarely been found again to this day<sup>152</sup>.



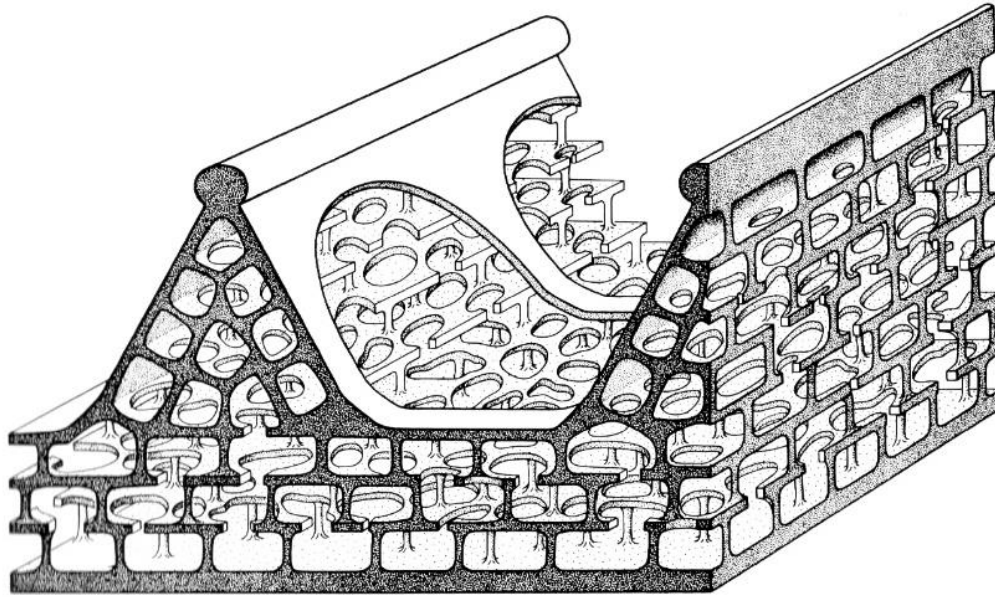
**Abb. 60:** Paratype of *Paralasa nepalica* PAULUS, 1982 (Nymphalidae, Satyrinae) from the high altitudes of NW Nepal, Dolpo District in the easternmost foothills of the subalpine coniferous forest zone at about 3,700 m (leg. J. Martens).

However, I was fascinated by the colors of butterflies from an early age. A publication on the fine structure of blue butterfly scales (SCHMIDT & PAULUS 1970) and a diploma thesis in Vienna on the distribution of UV and especially polarization patterns in butterflies (SCHNEIDER 2012) are worth mentioning here. My enthusiasm at the time for butterflies and especially for blue butterflies led me to wonder how male blue butterflies produce their characteristic blue tones. We already knew that these are so-called iridescent or structural colors. But how do you create such nuanced, different and even species-specific shades of blue between the males of *Polyommatus icarus*, *P. coridon*, *Plebejus argus* or *Celastrina argiolus*? Although we provided an electron-optical study of the fine structure of various types of scales (Fig. 61), the physics behind this was not clarified until many years later<sup>153</sup>.

The fine structure of butterfly proboscis with its remarkable Sensilla styloconica also occupied me in Freiburg. When I moved to Vienna, this was a reason to bring Harald Krenn on board as my new assistant. He had written a doctoral thesis on the functional morphology of the butterfly sucking weevil. I published part of my

<sup>152</sup> file:///C:/Users/TEST/Downloads/3814-Fullarticletextwithauthoranddetails-21831-2-10-20190128.pdf

<sup>153</sup> e. g. WILTS et al. (2009): Imaging scatterometry and microspectrophotometry of lycaenid butterfly wing scales with perforated multilayers. — J. Royl. Soc. Interface 6: 185-192.



**Fig. 61:** Section of a block diagram of the iridescent scale of the blue butterflies (*Lycaenidae*) of the genera *Lysandra* or *Plebejus* (from SCHMITT & PAULUS 1970).

preliminary work on these sensilla with him. Harald Krenn has since then concentrated very successfully on the functional morphology of the mouthparts of flower-visiting insects. The decision to employ Harald Krenn as an assistant was not easy for me at the time, as it was in competition with my last doctoral student from Freiburg, Roland Melzer<sup>154</sup>. I had brought him to Vienna with me as a postdoc. He had done his doctorate on the comparative ultrastructures of dipteran larval eyes. The decision not to take him on as a new assistant ultimately resulted from the decision to devote myself more to pollination biology in the future and to limit or even end the very successful years of work on the evolution of arthropod eyes. However, Roland Melzer found a good position at the Zoology Department of the University and the Zoological State Collection in Munich and has now successfully continued his work on the evolution of eyes. In particular, he has recently continued the work I started on the eyes of the Chelicerata. The decision to employ Harald Krenn as an assistant has proved to be a successful one. He and his colleagues are now among the leading functional morphologists of the mouth parts of insects<sup>155</sup>.

## Apoidea

My interest in wild bees resulted from my first encounter with W. F. Reinig in the Elburs Mountains in northern Iran in 1971, at whose suggestion I began collecting bumblebees, initially in Iran (especially at the Chalus Pass at an altitude of 2000 m). All the bumblebees collected here and in Turkey can be found in the Reinig Collection. Later, I always took bumblebees and other wild bees with me on my various summer trips to the Mediterranean region (especially northern Spain, the Pyrenees, Greece and Italy). Another encounter encouraged me to take a closer look

<sup>154</sup> <http://de.syszoo.bio.lmu.de/mitarbeiter/mitarbeiter/glawfrank1/index.html>

<sup>155</sup> A readable summary of this line of research can be found in: KRENN H. W. (ed.) (2019): *Insect Mouthparts: Form, Function, Development and Performance*. — Springer International Publishing.

at other bees. In 1972, in the Kaiserstuhl region near Freiburg, I met Dr. phil. habil. Otto Rebmann from Frankfurt a. M., who mainly collected Megachilidae there, but also Chrysididae. I actually knew him as a Nitidulidae specialist from the beetle meetings in Ludwigsburg or the entomologists' meetings in Frankfurt. Since then, I have also increasingly observed and collected other bees. This knowledge later helped me in the course of my work on the pollination biology of orchids. This was reflected in my numerous publications on the pollination biology of the genus *Ophrys*. In Freiburg, my interest in bees gave rise to diploma and doctoral theses, the first of which was the extensive dissertation by Anselm Kratochwil, who I entrusted with the difficult task of finding connections between pollinator communities and flower communities. Anselm Kratochwil had such an extensive collection of data that his dissertation was almost not accepted because it was too large. Fortunately, I was able to convince the committee that extensive data is not an argument against the quality of a thesis. After all, I can say that the topic I presented to Anselm Kratochwil turned out to be a kind of pioneering achievement, as the topic has received an international boost since the publication of the so-called "Krefeld Study" (2017)<sup>156</sup> on insect mortality. A separate center was even founded in Leibzig for this type of research (German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig), where my doctoral student Demetra Rakosy (coming from *Ophrys* research) is a member of staff. This was followed by further studies by Renate Maddocks (née Ullrich) on quantitative aspects of pollen collection in the breeding biology of *Anthophora acervorum* (now *plumipes*) and *Osmia rufa* (now *bicornis*). Studies on "optimal foraging" in bumblebees started with diploma and doctoral theses in Freiburg (Günter Lützenkirchen, Peter Sowig), which finally ended in Vienna with Karin Farnberger (bumblebees at Eichkogel near Mödling, FARNBERGER & PAULUS 1996), Karin Hermann (Perchtoldsdorfer Heide near Vienna) and above all with Johann Neumayer (Hohe Tauern) (NEUMAYER & PAULUS 1999) (Fig. 83). Suggestions for further work with bumblebees arose in the course of the special bee practical courses I organized annually in Vienna, in which I always had bumblebee identification components. These skills were practiced and deepened on the numerous alpine excursions from the zoology department in Vienna. The identification key of Austria's bumblebees, which was created under the supervision of my assistant Prof. Dr. Harald Krenn, his wife Dr. Barbara Gereben-Krenn and above all Dr. Johann Neumayer and the diploma thesis of Joseph Gokcezade, should be mentioned here in particular (GOKCEZADE et al. 2016). Further work on bumblebees was carried out in the course of the field internships I led in the Hohe Tauern in the Großglockner region. Here, among other things, work was started on the difficult *Bombus lucorum-cryptarum* species group (BOSSERT 2015, BOSSERT et al. 2016). The results of my travels and stays in the Austrian Alps were also incorporated here. This was followed by studies by Martin Streinzer, Johann Neumayer and Johannes Spaethe on the altitudinal distribution of bumblebees in the eastern Himalayas<sup>157</sup>.

My summer stays in the Niedere Tauern near Oppenberg deserve special mention here. I spent several summers here with my first wife together with the very

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<sup>156</sup> <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0185809>

<sup>157</sup> <https://www.researchgate.net/project/Bumblebees-of-North-East-India>



successful Austrian artist Ingeborg Strobl<sup>158</sup> from 1981, first on the Seifriedalm near Mößna (Sölktal), then on the Plienten- or Plieten-Alm near Oppenberg. We herded up to 80 cows from the various surrounding farms, so-called one-year-old calves, in the large valley basin. While I was mainly interested in bumblebees as well as beetles, Ingeborg collected impressions and ideas from nature and alpine life. Much of this later flowed into her artistic works and could and can be seen in her numerous exhibitions (e.g. at the Vienna Secession or the Lentos Art Museum in Linz). The precision with which she researched her works is also evident in the design of a house façade in Novaragasse in Vienna's 2nd district, near the Taborstrasse underground station, Novaragasse exit: the plants depicted on huge enamel plates on the entire side of the house façade are a reminder that the street, which was renamed Novaragasse in 1862, was previously called Gartenstrasse and later Gärtnerstrasse, and that these plants are also intended to commemorate the famous Austrian Novara expedition of 1857-1859<sup>159</sup>. Her façade design in Schrems near Gmünd in the northern Waldviertel is also well-known: the UnterWasserReich Ramsar is a visitor and research center for raised bogs in the Waldviertel. In 2004, Ingeborg Strobl won the architectural competition to design the glass façade with depictions of the pond frog, sand lizard and adder screen-printed on the glass outer skin over a background ornament of white amphibian skeletons<sup>160</sup>. In March 2020, an exhibition dedicated to her works was launched at the MUMOK (Museum of Modern Art in Vienna).

I worked on the morphology and large-scale systematics of the Apoidea themselves mainly together with my student, the American Dr. Dr<sup>161</sup>. John Plant (Figs. 56, 91, 94), who first came to Freiburg with me and then to Vienna in 1991. The final result of this fruitful collaboration is his extensive doctoral thesis on the phylogeny of the Apoidea, which was published in English as a book in Zoologica (Stuttgart) (PLANT & PAULUS 2014) (Fig. 84).

I compiled an extensive collection of Mediterranean Apoidea as "incidental-catches" of my pollination biology studies of the orchid genus *Ophrys*. In particular, I collected evidence of males of various bee genera and species that had been observed in the pseudocopulation on *Ophrys* species throughout the Mediterranean region.

## Pollination biology

My first scientific work on the pollination of flowers was carried out together with the couple Otto and Dagmar von Helversen during our almost three-month stay (Dec. 1973 - Feb. 1974) in Sta. Marta/Colombia. We stayed at the Punta Betin Marine Biological Station near the port of St. Martha (Fig. 62). Here we mainly collected data on bat pollination. In addition to observations in the field, we also caught roosting Glossophaginae (leaf-nosed bats) during the day in caves and in the rainwater pipes

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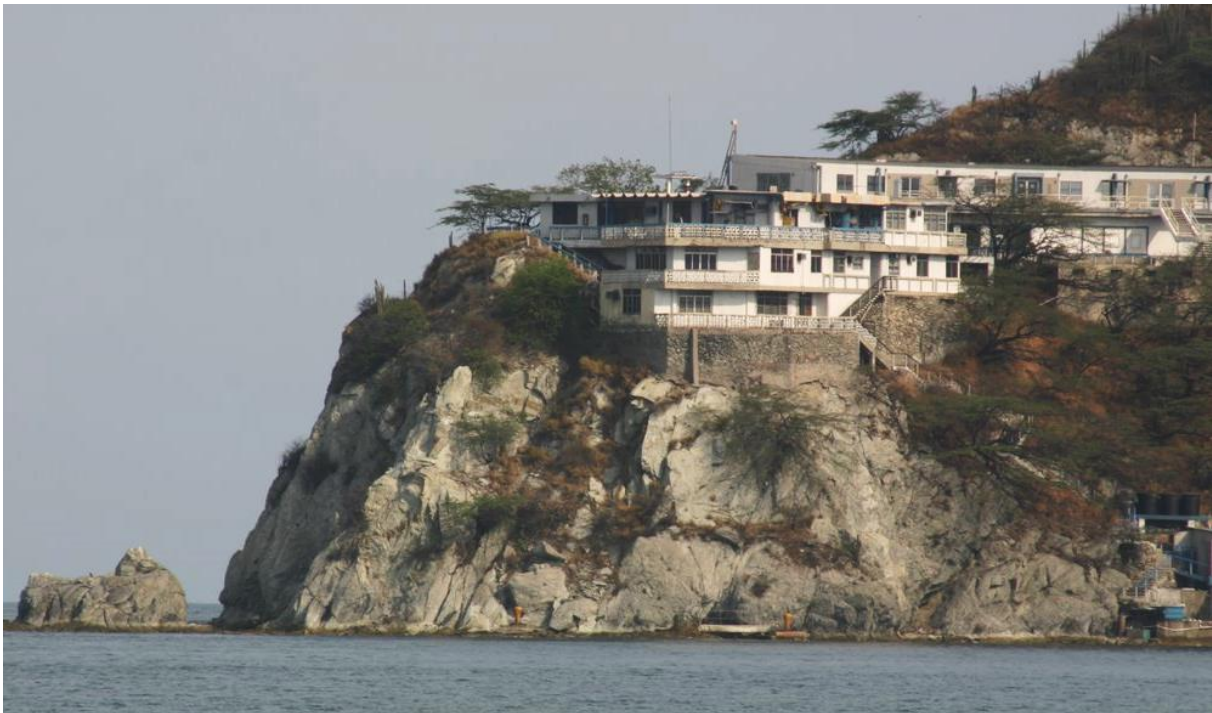
<sup>158</sup> Inge Strobl passed away at the age of just 67 on April 9, 2017. <http://www.artmagazine.cc/content98541.html>; <https://www.derstandard.at/story/2000043645823/vom-staunen-der-tiere-ueber-den-als-tier-verkleideten-menschen>

<sup>159</sup> <http://www.novara-expedition.org/de/geschichte.html>; <https://de.wikipedia.org/wiki/Novara-Expedition>

<sup>160</sup> [http://www.architektur-online.com/wp-content/uploads/2009/01/archiv\\_05\\_06\\_34\\_39\\_Unterwasserreich\\_neu.pdf](http://www.architektur-online.com/wp-content/uploads/2009/01/archiv_05_06_34_39_Unterwasserreich_neu.pdf)

<sup>161</sup> John Plant received his first doctorate in 1994 with a thesis on the culture of the Plains Indians in the Department of Ethnology at the University of Freiburg: [https://www.anjol.de/documents/100802\\_heyoka\\_neu.pdf](https://www.anjol.de/documents/100802_heyoka_neu.pdf). [https://www.researchgate.net/profile/John\\_Plant2](https://www.researchgate.net/profile/John_Plant2)

under the streets in order to observe them flying freely in our rooms as quasi flight rooms in the Acuario at Punta Betin (today Instituto de Investigaciones Marinas) in Sta. Martha. This is where the first high-quality flight photos were taken with *Glossophaga*, *Carollia* and *Phyllostomus* during various flower visits. We had previously collected different bat flowers in bloom. We were more interested in the behavior of the animals during visits to *Pseudobombax septenatum*, *Ochroma* or *Lemeiocereus* sp. (Fig. 63). A first publication with pictures of these findings can be found in PAULUS (1976, 1978). Otto von Helversen later decisively continued studies on bat flowering after his move to the University of Erlangen as full professor of zoology.



**Fig. 62:** Marine Biological Station Punta de Betin above the harbor of Sta. Marta, N-Colombia, December 1973. We spent almost three months here during our research trip to Colombia.

At that time, I gave a lecture in the university's main lecture hall on the results of our research into bat flowering in Colombia. I was particularly touched at the end of the lecture when the old Fritz Knoll jumped up and said enthusiastically, slapping his thighs: "That I was still able to see how "his" bat research" has been continued so successfully". Together with the later Stefan Vogel, Prof. Knoll was one of the pioneers of pollination biology. He died on 14.3.1981.

Our research led me back to Prof. Dr. Stefan Vogel<sup>162</sup>, whom I had already come to appreciate as a young student in Mainz. I had attended his various lectures, especially his ecological-botanical lectures, which included pollination biology as well as ant symbioses with plants. He was Professor of Botany at the University of Mainz

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<sup>162</sup> O.Univ. Prof. Dr.Stefan Vogel ( 1925-2015): <file:///D:/pdf-Data%2026.3.2015/Biografien/Stefan%20Vogel%20283-Artikeltext-503-1-10-20180201.pdf>; Vogel\_Stefan\_STAPFIA\_0103\_0003-0004.pdf or [https://www.researchgate.net/publication/305740320\\_Stefan\\_Vogel\\_1925-2015](https://www.researchgate.net/publication/305740320_Stefan_Vogel_1925-2015)

until 1973, then Professor at the FU in Berlin from 1973 to 1977, before moving to Vienna until 1981. He then returned to Mainz, where he retired in 1990. However, as his children had remained in Vienna, he returned to Vienna with his wife to continue working there as a visiting professor at the Botanical Institute until his death on November 5, 2015. This is where I met him again after my appointment in Vienna. He was very interested in the results of our research on chiropterophily in Colombia. Stefan Vogel was undoubtedly one of the pioneers of pollination biology and discovered many incredible things for the first time in his life and studied them in detail. These include discoveries such as the pollination syndromes of oil flowers and oil bees, fungus gnats and fungus mimetes. He was the first to intensively study chiroptero-gamy in South America and the relationship between euglossines (magnificent bees) and their perfume-producing orchids in South America. He was also the one who first recommended to me that I should try to attract the bees by applying essential oils, e.g. eucalyptol or cineol, somewhere on the bark of a standing tree. We did this several times in Colombia and were amazed that dozens of males of different species of honeybees appeared within a very short time and diligently tried to collect this oil. I was particularly amazed because I had never seen a single animal flying in the biotopes before.



**Fig. 63: (left):** *Anoura geoffroy* (Phyllostomidae, Glossphaginae) approaching the bat flower *Erythrina fusca* (Fabaceae): Cienaga sw. Sta. Martha, N-Columbia (PAULUS 1978); **(right)** *Glossophaga longirostris* hovering in front of *Pseudobombax septenatum* (Malvaceae, Bombacoideae): N-Colombia, Parque Nacional Natural Tayrona north of Sta. Martha, January 1974 (Photos: H. Paulus).

Stefan Vogel's publications were always whole books with numerous excellent drawings by him. I was able to visit him and his wife in Mainz and later in Vienna at his house in Maria-Enzersdorf near Mödling. During my time as a professor in Freiburg, I was able to invite him several times to lectures and symposia. Incidentally, he himself had repeatedly tried to see the pseudocopulation with *Ophrys*. He very much regretted that he had never succeeded and admired the fact that I obviously had fewer problems with this. In Vienna, however, I was able to show him a pseudocopulation of *Andrena nigroaenea* on *Ophrys sphegodes*. On the green roof terrace of my institute in Vienna's 9th district, *Andrena nigroaenea* males regularly flew in search of their females in spring. In his presence, I presented a plant of the

“Early Spider Orchid” (*Ophrys sphegodes*) from Bisamberg opposite Vienna to these flying males. It didn't take long before several males landed on a flower and began to copulate vigorously. Stefan Vogel was incredibly excited and almost childlike in his joy at being able to witness this (Fig. 64).



**Fig. 64:** Prof. Dr. Stefan Vogel and his wife on March 14, 2009 on the occasion of the funeral of my friend Otto von Helversen at Schloss Neuhaus near Erlangen (Photo: H.F.Paulus).

The studies of the bumblebees also marked the beginning of some investigations into the pollination biology of individual plant genera. For example, I gave Jacqui Shykoff, who came from Canada, the task of studying the gynodioecia in *Salvia pratensis* (Fig. 64), which had already been discovered by Darwin, as part of a longer stay in my working group in Freiburg. She then went to Paul Schmidt-Hempel at the University of Basel, where she initially worked on parasitic flies in bumblebees as part of her doctoral thesis, but then returned to my original basic question of the significance of gynodioecia. The hypothesis was that gynodioecia<sup>163</sup> is favored when all-female plants are fitter mothers than hermaphrodites. The ratio of female to hermaphrodite is then determined by two factors: the frequency-dependent disadvantage of all-female plants, as there is little pollen available when the proportion is high, and the disadvantage of hermaphrodite mothers due to self-fertilization or the consumption of resources for the pollen. Jacqui Shykoff later became famous for these further

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<sup>163</sup> Gynodioecia is a form of sex distribution in flowering plants in a population: there can be purely female plants and also hermaphrodite plants (with hermaphrodite flowers).

studies, especially on carnations (*Silene*), and is now a professor at the University of Paris<sup>164</sup>. Later, in Vienna, I again sent two graduate students to work on a comparative pollination biology of the genus *Salvia*. Enikő Tweraser<sup>165</sup> then continued her research in a doctoral thesis with Prof. Dr. Regine Claßen-Bockhoff at the Institute for Special Botany at the University of Mainz<sup>166</sup>.



**Fig. 65:** Jaqui Shykoff spent some time with me in Freiburg (here in my laboratory, ca. 1980) before she first went to Basel and finally worked as a professor in Paris. <https://research.com/u/jacqui-a-shykoff>. (Photo: H.F.Paulus)

### Research and collecting trips

Numerous trips have taken me to Southern Europe and the Middle East in particular. The trip to Iran has already been mentioned. With the couple Otto and Dagmar von Helversen, I undertook summer trips to Spain and above all to Greece. The first trip

<sup>164</sup> e. g.: SHYKOFF J. et al. (2003) Effects of male sterility on reproductive traits in gynodioecious plants: a meta-analysis. — *Oecologia* 135:1-9. SHYKOFF J. A. (1992): Sex polymorphism in *Silene acaulis* (Caryophyllaceae) and the possible role of sexual selection in maintaining females. — *American Journal of Botany* 79: 138-143.

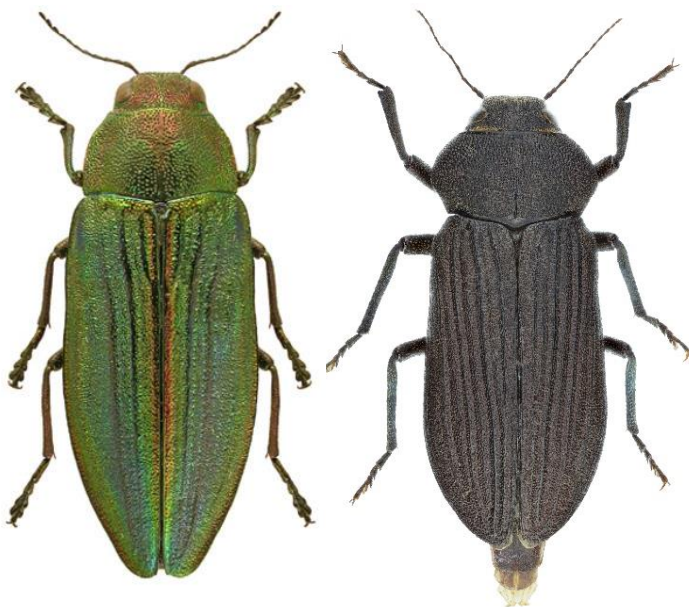
<sup>165</sup> TWERASER Enikő (2000): Vergleichende Untersuchungen zur Blütenbiologie der Gattung *Salvia* in Ost-Österreich. Teil I: Blütenmorphologie, Palynologie und Bestäubung. 80 pp. + 47 Tafeln, Diplomarbeit Universität Wien (Betreuer H. F.Paulus).

WEININGER S. (2000): Vergleichende Untersuchungen zur Blütenbiologie der Gattung *Salvia* in Ost-Österreich. Teil II: Bestäubungsbiologie und ökologische Sonderung, 179 pp. Diplomarbeit Universität Wien (Betreuer H. F.Paulus).

TWERASER E. & S. WEININGER-HÖLLRIGL (2001): Isolating mechanisms among six sympatric *Salvia* species in eastern Austria. 15th Symposium Biodiversität und Evolutionsbiologie, Bochum (poster abstract).

<sup>166</sup> e. g. CLAßEN-BOCKHOFF R., SPECK T., TWERASER E., WESTER P., THIMM S. & M. REITH (2004): The staminal lever mechanism in *Salvia* L. (Lamiaceae): a key innovation for adaptive radiation? — *Organisms Diversity & Evolution* 4 (3): 189-205.

in July 1978 together with Martina and Thomas Esche<sup>167</sup>, Klaus-Gerhard Heller<sup>168</sup> and Marianne Volleth<sup>169</sup> to the Smolikas area in northern Greece was remarkable. This was shortly after the area was opened to public transport. Until then, the region had been a Greek restricted military area. In fact, highly remarkable finds were made here, e.g. *Buprestis splendens* (previously lost for at least 100 years). At the foot of the Smolikas I noticed two butterflies that were newly described by Brown a little later (*Pseudochazara graeca* ssp. *coutsisi* BROWN, 1978 and *Pseudochazara tisiphone* BROWN, 1981)<sup>170</sup>. Both species were surprisingly common here, so I was surprised that nothing was known about these species until then. My preoccupation with these species made me realize on the spot that they had obviously not yet been described. However, I didn't feel well enough versed in this complex group of species with several very similar species from the southern Balkans to Turkey and the Asian mountains. Above all, it seemed difficult to separate it from the Turkish *Pseudochazara mniszechii*. A little later, John Brown, a better expert on this species group, described it as an independent species.



**Fig. 66: (left):** *Buprestis splendens* (Foto ZoBodat). **(right):** *Strigopterooides aegyptiaca* Gmelin, 1790, 11 mm (syn. *S. hellenica*, *S. depressa*) (Buprestidae, Polycestinae), here a specimen from Syria (Deir ez Zor, 17.6.2006, leg. A. Kotán & N. Rahmé: <http://rahme.blogspot.com/2006/11/strigopterooides-aegyptiaca.html>). Gerhard Heller and I found this species for the first time in Europe in Greece dead in a *Platanus* tree.

<sup>167</sup> Thomas ESCHE later (1996) wrote his extensive doctoral thesis with me: "Do moths compete for flowers? Studies on niche separation and pollination efficiency (Insecta, Lepidoptera)" ([https://www.zobodat.at/pdf/Neue-Entomologische-Nachrichten\\_35\\_0001-0194.pdf](https://www.zobodat.at/pdf/Neue-Entomologische-Nachrichten_35_0001-0194.pdf)): „Konkurrieren Nachtschmetterlinge um Blüten? Untersuchungen zu Nischentrennung und Bestäubungseffektivität (Insecta, Lepidoptera)“ ([https://www.zobodat.at/pdf/Neue-Entomologische-Nachrichten\\_35\\_0001-0194.pdf](https://www.zobodat.at/pdf/Neue-Entomologische-Nachrichten_35_0001-0194.pdf)).

<sup>168</sup> Klaus-Gerhard Heller later completed his doctoral thesis in Erlangen under Otto von Helversen: HELLER K.-G. (1988): Bioacoustics of European locusts. Ecology in research and application (in German). Vol. 1 Josef Margraf, Weikersheim (pp. 360).

<sup>169</sup> Marianne Volleth later worked on chromosome evolution in bats in the Otto von Helversen research group in Erlangen: e. g. VOLLETH M. (1987): Differences in the location of nucleolus organizer regions in European vespertilionid bats. — Cytogenet Cell Gen 44: 186-197.

<sup>170</sup> BROWN J. (1981): On the status of a little known satyrid butterfly from Greece. — Entomologist's Record and Journal of Variation 92: 280-281.

On this trip, Gerhard Heller and I found a hitherto unknown jewel beetle, about 13 mm in size, dead and in bad condition, cut out of an old plane tree in the Tauropos river valley west of Karpenision near Kalesmenon (38°57'03.02"/21°41'06.60", 300m) on 2.8.1978 alongside a number of *Macrotoma scutellaris* longhorn beetles. This individual later caused quite a stir as nobody knew which genus it might belong to. Only the Spanish jewel beetle specialist Antonio Cobos<sup>171</sup>, to whom the animal had been sent for identification, recognized it as a new species for Europe. He initially identified this animal as *Pseudocastalia aegyptiaca* GMELIN, 1788 from the subfamily Polycestinae. Later, he created the new genus *Strigopteroides* COBOS, 1981 and described the animal as the new species *Strigopteroides hellenicus* COBOS, 1990, which was probably too much, because today the Greek occurrence is considered to belong to *Strigopteroides depressa* F. (with *aegyptiaca* as a synonym) (Fig. 65). Nevertheless, a few years later, Gottfried Novak, a specialist in jewel beetles well known to me from the Arbeitsgemeinschaft österreichischer Entomologen in Vienna, was able to describe another new species of this genus from southwest Crete: *Strigopteroides margotanae* NOVAK, 1995.<sup>172173</sup>

### Travels to the tropics

While my main focus is on the Mediterranean region, I have also made several trips to the tropics. My first trip was to Colombia. Here I was together with Dagmar and Otto von Helversen and my later first wife Friederike Gruber at the marine biology station in Santa Martha (Fig. 26, 61). We spent almost three months here from 18.11.1973-24.1.1974. The trip also took us to the islands of Barbados, Trinidad and Curaçao. Above all, we carried out studies on bat flowering (Fig. 62). From the beetle specimens I was able to describe a tiny, presumably myrmecophilous new genus of the firefly family Phengodidae (*Penicillophorus ctenotarsus* PAULUS, 1975), which is even a representative of a new subfamily Penicillophorinae. Another trip in 1976 took me together with Friederike Gruber to southern Nigeria (University of Ibadan) to observe, among other things, further bat pollination with fruit bats. Trips to Kenya and Tanzania (1978 together with my then colleagues from the Zoological Institute in Freiburg - and again in 2016 with my wife Urte and daughter Maria) were mainly photo safaris. This was followed by further stays in the Seychelles (Mahe and Praslin) (2014), North Borneo (Sabah) (2015), Dubai (2016), Bali - Komodo Island (Komodo giant monitor lizards) - Flores Island (2017), Egypt (2017, 2020), NW India (2018), Jordan (2018), Morocco (2020) and as a further highlight in Uganda (including chimpanzees and especially mountain gorillas) (2019). Here I was able to experience a mountain gorilla family up close and personal with Urte and Maria. One of the frolicking young animals fell directly onto my head along with the breaking branch. Our guides were quite frightened as they weren't sure how the mother would react. But she only gave her young a "tired look" and continued to eat her fresh branch with relish. Fortunately, I only had a minor laceration on my head.

<sup>171</sup> Antonio COBOS SANCHEZ (1922-1998): Graellsia 57(2):191-210: <https://docplayer.es/39517685-Necrologica-obituary.html>

<sup>172</sup> NOVAK G. (1995): *Strigopteroides margotanae* n. sp. von Kreta und *Strigopteroides depressus turcicus* n. ssp. aus der Türkei (Coleoptera: Buprestidae). – Schwanfelder Coleopterologische Mitteilungen 10: 1-10.

<sup>173</sup> Gottfried Novak died on June 2, 2015 at the age of 79 as a result of a stroke. Shortly before this, we happened to spend a hospital stay in the same room. [http://www.entomologie.at/uploads/www.entomologie.at/67\\_198-199\\_barries\\_dostal\\_nachruf\\_novak.pdf](http://www.entomologie.at/uploads/www.entomologie.at/67_198-199_barries_dostal_nachruf_novak.pdf)

## Ophrys research

From 1976 onwards, in addition to general questions of pollination biology, I was particularly interested in clarifying pseudocopulation in the Mediterranean orchid genus *Ophrys*. This was triggered by a conversation with the well-known plant physiologist Prof. Dr. Hans Mohr in Freiburg, whose statement that the whole story of female imitation by flowers was "nonsensical" or simply "over-interpreted". So, the next spring I organized an excursion to Andalusia to check the pollination biology directly on site. On this first trip to southern Spain at the beginning of March 1976, I was accompanied by Prof. Dr. Günther Osche, the later professors Peter Sauer (Bonn) (Fig. 22) and Walter Sudhaus (Berlin) (Fig. 22) as well as Claudia Gack (Fig. 22). The latter later became an important colleague for me in the *Ophrys* research started in Freiburg. Already on this first trip we were able to confirm Pouyanne-Kullenberg's hypothesis that *Ophrys* flowers imitate female wild bees that are willing to mate and that attracted males attempt to mate on them. On further excursions to Andalusia, I also took Klaus Lunau<sup>174</sup> with me, who, initiated by Prof. Osche and elaborated by Claudia Gack in her doctoral thesis, later wrote a doctoral thesis on stamen imitations and their sensory stimulus effectiveness in pollination biology. He later became Professor of Animal Physiology (Sensory Ecology) at the University of Düsseldorf. I had also noticed Florian Schiestl (now Professor of Botany at the University of Zurich) on excursions to the Austrian Alps and then especially during our first *Ophrys* tour to northern Tunisia.

However, Bertil Kullenberg had not drawn the conclusion that a species-specific relationship should exist by imitating the sexual attractants of these wild bees. However, initial choice test experiments in Andalusia confirmed this assumption. It was surprising and astonishing to me that two different flower sizes of a single species known as *Ophrys fusca* were common in and around Marbella. As these were also visited by two different bees, the small one by *Andrena flavipes* and the larger one by *Colletes cunicularius*, it was immediately clear to me that they must be two separate biological species<sup>175</sup>. Their respective isolation mechanism consisted precisely in the two separate bee species transferring the pollen only within "their" *Ophrys* species. These pollinators act as a pregamic isolation mechanism. Little did I know that this concept, which was completely obvious to an evolutionary biologist, would later revolutionize the entire *Ophrys* systematics. So, it was obvious to me that the *Ophrys holoserica* subsp. *elator* discovered and described by Dr. Reinhart Gumprecht from Freiburg at the Isteiner Klotz must be an independent biospecies. After all, the plants only flowered from mid-July, long after the "normal" late spider orchid had faded, had much smaller flowers and were surprisingly tall. I therefore made every effort to find the specific pollinator. I soon succeeded. It was the small *Tetraloniella salicariae* long-horned bee. As the name given by Gumprecht was unfortunately invalid, I later validated it as *Ophrys elator* GUMPRECHT ex PAULUS 1996. Reinhart Gumprecht was particularly pleased when I was able to show him a pseudocopulation of *T. salicariae* on "his" *Ophrys* (Fig. 66a, b).

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<sup>174</sup> Until his retirement, he was head of the Institute for Sensory Ecology at Heinrich Heine University in Düsseldorf (Germany)

<sup>175</sup> Only 34 years later did we describe this fusca form as a new species: *Ophrys malacitana* LOWE, PHILLIPS & PAULUS 2010.



**Urte Paulus: Der Mensch und die lieben Krabbeltiere  
2021, Selbstverlag**

**Betrug**

Wer denkt, allein der Mensch sei schlecht,  
besonders falsch und ungerecht,  
der hat die Masche nicht gesehen,  
mit der ein Typ von Orchideen  
Vertrauen und Verstand zerreibt  
und Täuschung ohne End' betreibt.

Die Opfer sind, wie könnt es sein,  
nur Männchen, die, ganz allgemein,  
von solitärer Bienenart,  
alleine leben ohne Staat  
und deshalb auch, meist souverän,  
privat auf Weibchensuche gehn.

Und hier nun fängt der Schwindel an,  
der Wind trägt einen Duft heran,  
der durch Verlockung pur besticht  
und eine schöne Maid verspricht,  
die nicht weit weg, noch Jungfrau ist  
und sehnsuchtsvoll 'nen Mann vermisst.

So stürzt der Bienenmann voll Gier  
sich auf's vermeintlich hübsche Tier  
und merkt nicht, dass die holde Frau  
zwar riecht, auch aussieht haargenau  
wie eins der Weibchen, das er will,  
doch sonst sehr wortkarg ist und still.

Vor Liebe blind der junge Mann  
betastet erst galant, doch dann,  
getrieben von der Leidenschaft,  
er rücksichtslos, mit ganzer Kraft



das Wesen packt und rasch vollzieht  
die Paarung, ehe es entflieht.

Doch irgendetwas läuft ganz schief,  
das Weibchen ist so inaktiv  
und auch die Paarung nicht gelingt,  
was bei ihm ziemlich Stress bedingt.  
Egal wie er sich müht und plagt,  
sein Traumziel bleibt ihm doch versagt.

Zum Schluss wird es ihm zu kurios,  
frustriert lässt er das Weibchen los,  
zudem sieht er letztendlich ein,  
die Frau ist nur gefälschter Schein,  
und er ein „Blumen“-Opfer ist,  
betrogen durch 'ne Täuschungslist.

So fühlt das Männchen sich ganz matt  
und spürt, dass man ihn nicht nur hat,  
durch Trug in seinem Stolz verletzt,  
sondern ihm auch hat aufgesetzt  
zwei Hörnchen, die voll Pollenkorn  
und in ihm wecken noch mehr Zorn.

Der Ärger jedoch bald vergeht,  
da wieder durch die Lüfte weht  
der Duft, versprechend eine Maid,  
und's Männchen denkt: „Schicksal entscheid',  
ob es wird Liebe oder List,  
'ne Frau oder 'ne Ragwurz ist.“

Ragwurz: Orchideengattung *Ophrys*: Bestäubungsstrategie: Weibchenmimikry u.  
Pseudokopulation Gewidmet o.Univ.Prof. Dr. Hannes Paulus

**Fig. 67:** Poem by Urte Paulus: "Betrug" from her book of poems "Der Mensch und die lieben Krabbeltiere" ("Humans and the dear creepy-crawlies") (2021) (in German, fig. 34).



**Fig. 68:** (left) Hannes Paulus with *Ophrys elatior* for test purposes in a vase together with Reinhart Gumprecht in the Taubergießen north of Freiburg 17.7.1988 (Photo: Claudia Gack). (right) *Tetraloniella salicariae* male in the pseudocopulation with *Ophrys elatior*. Taubergießen north of Freiburg 17.7.1988 (Photo: H. Paulus).

My first destination for *Ophrys* studies was, as already mentioned, Andalusia. In 1982 I decided to visit the island of Crete as my next new destination. Here I was

accompanied by Prof. Osche, Claudia Gack and my student Anselm Kratochwil. I was inspired to visit this island by Stefan Vogel's publication on *Ophrys* pollination as a result of a student excursion to Crete<sup>176</sup>. He described here that he was able to catch various male bees with pollinaria, but not a single observation of a pseudocopulation. However, I confirmed his assumptions as to which *Ophrys* species could have been pollinaria donors, with one exception. In fact, we remained faithful to this goal for many years and several scientific investigations started here. Phillip Schlüter, Kerstin Steijskal, Martin Streinzer and Demetra Rakosy wrote their doctoral thesis on *Ophrys fusca* aggr., *Ophrys heldreichii* and the complex *Ophrys tenthredinifera* relationship mainly here<sup>177</sup>.



**Fig. 69** Some of my staff members in our *Ophrys* projects: **(left)** Philipp and Berit Schlüter in Vienna (2012), **(right)**: Martin Streinzer, Hannes Paulus, Demetra Rakosy, Johannes Spaethe (at my 80th Birthday party in the University of Vienna, 21.10.2023) (Photo: zobodat).



**Fig. 70: (left)**: Hans Salkowski (Valendar near Koblenz) during a visit to Vienna on 15.8.2007 (Photo Paulus). **(middle)**: Claudia Gack and Hannes Paulus, **(right)**: Claudia Gack and Manfred Ayasse (at my 80th Birthday party in the University of Vienna, 21.10.2023) (Photo: zobodat).

Through my numerous trips to the Mediterranean region, first with Claudia Gack (Freiburg) and changing students from Freiburg, later from Vienna with Manfred Ayasse (fig. 70), Florian Schiestl and Johannes Stökl, later with Hans Erich

<sup>176</sup> VOGEL Stefan (1976): Zur *Ophrys*-Bestäubung auf Kreta. — Jahresberichte des Naturwissenschaftlichen Vereins Wuppertal 29: 131-139.

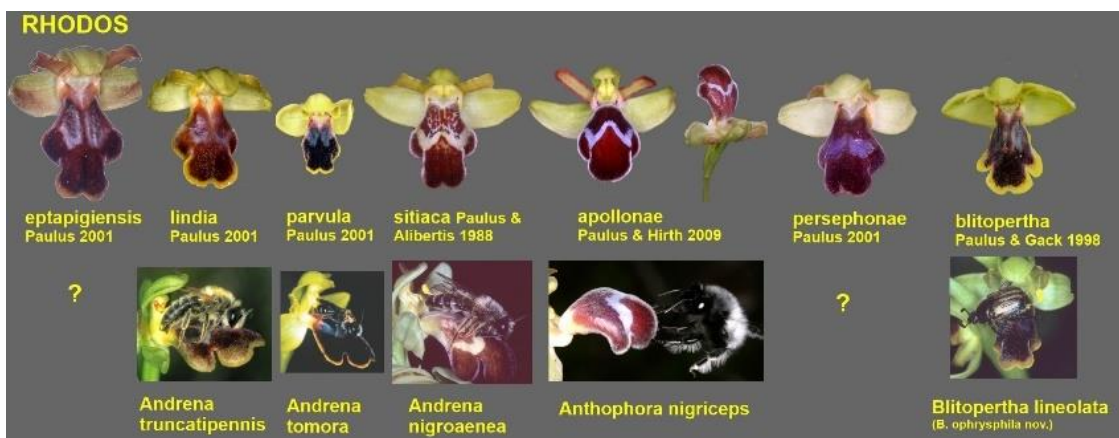
<sup>177</sup> Z. B. RAKOSY et al. 2017:

[https://www.researchgate.net/publication/318992969\\_Looks\\_matter\\_Changes\\_in\\_flower\\_form\\_affect\\_pollination\\_effectiveness\\_in\\_a\\_sexually\\_deceptive\\_orchid](https://www.researchgate.net/publication/318992969_Looks_matter_Changes_in_flower_form_affect_pollination_effectiveness_in_a_sexually_deceptive_orchid)

Salkowski (from Vallendar near Koblenz, 30.9.1935 - 23.11.2013) (Fig. 70) and many of the last years with Monika Hirth (from Freiburg) (Fig. 78, 89B), I was able to show for many of the *Ophrys* species that they have only one effective pollinator. However, closely related bees often occur as so-called secondary pollinators, but their frequency in the pollination process is so low that they do not exert any significant selection.



Jan	Febr	März	April	Mai	<i>Ophrys</i>	Bestäuber	Lippenlänge
	—	—			sitiaca	nigroaenea	13,3 ± 1,0
	—				mesaritica	nigroaenea	15,6 ± 1,4
		—			creticola	?	15,0 ± 1,3
		—			thriptiensis	bicolor	12,0 ± 0,8
		—			cinereophila	cinereophila	11,4 ± 0,6
			—		iricolor	morio	18,4 ± 1,5
			—		creberrima	creberrima	13,7 ± 1,3
			—		cressa	merula	11,7 ± 0,6
			—		pallidula	combinata	12,9 ± 0,4
				—	phaidra	?	13,9 ± 0,6
				—	kedra	variabilis	16,5 ± 0,8



**Fig. 71:** The species of the *Ophrys fusca* group are represented by at least 15 species on the Aegean islands of Crete (**above**) and Rhodes (**bottom**) all of which were described by H. Paulus as new biospecies. They are all reproductively isolated by their own specific pollinators. Originals: H.F. Paulus.

Early excursions to Italy (especially to the Monte Gargano area<sup>178</sup>), Crete and Rhodes led to the realization that many more *Ophrys* species exist here than previously recognized. In particular, a first trip to Crete in February led to the discovery of six undescribed *Ophrys* species (*O. cretica*, *sitiaca*, *mesaritica*, *thriphitiensis*, *basilissa*<sup>179</sup>, *cinereophila*) (Fig. 71). Similar results were found on the island of Rhodes, which I visited again for the first time in 1999 in the course of a university excursion (Fig. 71). Here, too, I found previously unnoticed, undescribed *Ophrys* species from the *fusca* group: *O. persephone*, *lindia*, *eptapigiensis*<sup>180</sup>, *parvula* and later even another species from the *omegaifera* group: *O. apollonae*. In conjunction with flower morphological differences coupled with further ecological evidence, I was able to show and suggest that the genus *Ophrys*, which at that time consisted of around 30 known species, now actually comprises almost 300 species.



**Fig. 72:** The crime novel by Robert Roden 1986 (alias Horst Focken from Holzminden): Gargano - Geschichte einer Flucht (“Gargano – A story of an escape”) describes astonishingly detailed one of (our ?) *Ophrys* journeys in the Gargano region in southern Italy.

In the course of my numerous "*Ophrys* journeys" I met many colleagues who deal with Mediterranean orchids. I first met Antonis Alibertis from Heraklion in Crete in the spring of 1984, where we went on excursions together with his first wife<sup>181</sup>. In 1988 he showed me the "Winter *Ophrys*" in Crete. Antonis eventually wrote an impressive work on the orchids of Greece<sup>182</sup>. I also met and corresponded many times with the Greek doctor and orchid expert from Thessaloniki, Zissis Antonopoulos (Fig. 77).

<sup>178</sup> Unbeknownst to me, a crime novel by Robert RODEN (alias Horst Focken from Holzminden) was written here in 1986: Gargano - Geschichte einer Flucht. - Fischer paperback, 239 pages (ISBN 3-596-28200-4). Obviously my *Ophrys* excursions in the Gargano region were described here as a framework story.

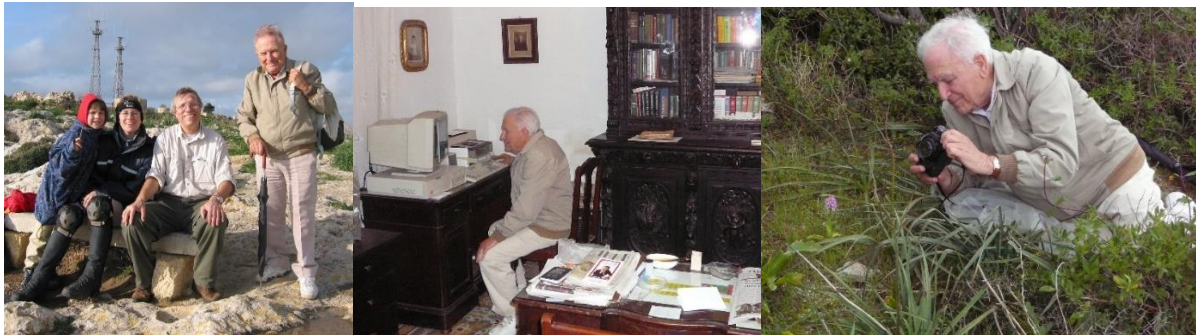
<sup>179</sup> *Ophrys basilissa* was then described by the (still) married couple C. & A. Alibertis and Hans Reinhard.

<sup>180</sup> This species is still missing today, although I have searched the locus typicus and its surroundings several times in later years.

<sup>181</sup> Here I met several times with Antonis Alibertis from Heraklion, who, together with his first wife Chryssoula, had written a booklet about the orchids of the island of Crete.

<sup>182</sup> ALIBERTIS A. (2015): Self-sown orchids of Greece. Mystis Editions, Iraklion, 624 pp.

Together with the botanist Spyros Tsiftsis, he also wrote a two-volume standard work on the orchids of Greece<sup>183</sup>. In Israel, Prof. Dr. Amots Dafni from the University of Haifa enabled us to explore the orchids of this country.



**Fig. 73: (left):** Marko, Urte and Hannes Paulus with Michael Briffa in Malta 30.12.2002. **(middle)** Michael Briffa's study in Sliema, Malta on 4.4.2007. **(right)** Michael Briffa at the age of 81 in front of the then only third specimen of *Orchis italica* in Malta: 3.4.2007 Malta, Dwejira Lines, photos: H. F. Paulus.

I would also like to mention Michael Briffa (Sliema), with whom I met on my various trips to Malta. Hans Salkowki<sup>184</sup> and I first visited him on 17.2.2000. Michael was an amiable older gentleman who described himself as a "naturalist". However, he was a well-known mushroom specialist who, among other things, had amassed an extensive collection of myxomycetes. Orchids, however, were his favorites, which he documented and mapped on his island. He took me to various places where *Ophrys* individual plants were found, which were often only found as single individuals but disappeared again after a short time. On April 7, 2007, I took him to one such individual plant, *Orchis italica*. Strangely enough, only two specimens of this otherwise widespread orchid were known from Malta: 13.3.1977 Wied Babu and 6.4.1981 Xagħra l-Hamra, both photographed by M. Briffa. As an otherwise very quiet and sober person, he was incredibly excited with joy. He let me photograph him as he was taking pictures of the plant lying on the ground. Michael, born on 17.11.1926, died on 7.2.2020 at the age of 93. This photo was used in a tribute to his achievements (<https://era.org.mt/press-releases/michael-briffa-in-memoriām/>) (Fig. 73)<sup>185</sup>.

In the course of the first fragrance analyses of the flowers and pollinator bees by the working group led by Prof. Bergström and Bertil Kullenberg in Sweden, there were numerous discussions and intensive correspondence with Bertil Kullenberg<sup>186</sup>, as they were not convinced of the specificity. However, this was mainly due to the fact that they could not find any correspondence between the scents of the bees and the scent components found in the flowers. However, since sexual attractants consist of

<sup>183</sup> ANTONOPOULOS Z. & S. TSIFTSIS (2017): Atlas of the Greek Orchids. Vol. I + II.- Mediterraneo Editions, Rethymno, Crete.

<sup>184</sup> [https://es.wikipedia.org/wiki/Hans-Erich\\_Salkowski](https://es.wikipedia.org/wiki/Hans-Erich_Salkowski). He is the author of the Maltese endemic *Ophrys melitensis* (SALKOWSKI 1992) DEVILL. & DEVILL.-TERSCHUREN 1994 and first discoverer of its pollinator *Chalicodoma sicula* and various other *Ophrys* pollinators (z. B. *Chalicodoma manicata* on *Ophrys flavicans* in Croatia).

<sup>185</sup> <https://era.org.mt/press-releases/michael-briffa-in-memoriām/>

<sup>186</sup> Bertil Kullenberg (19.3.1913-14.4.2007) was Professor of Entomology at Uppsala University from 1968-1979. In addition to his work on capsids (=Miridae, soft bugs), he began to focus on the genus *Ophrys* at the end of the 1940s. His most famous work is the comprehensive paper "Studies in *Ophrys* pollination (1961), Zool. Bidr. 34: 1-340."

[http://www.sef.nu/download/in\\_memoriām/Bertil%20Kullenberg%201913-2007%20till%20minne\(2\).pdf](http://www.sef.nu/download/in_memoriām/Bertil%20Kullenberg%201913-2007%20till%20minne(2).pdf)

a mixture of several scent components, it is a kind of scent pattern recognition and not merely a summation of individual components. As in perfumery, the mixture creates its own system property in the form of its own fragrance note. My argument in this context has always been that "in order to obtain something about the specificity of a piece of music or a passage of text, it makes little sense to break such passages down into notes or letters". The information lies, of course, in the specific sequence and combination of notes and letters used and not in the individual notes or letters themselves".

However, my research work has not only consisted of these very time-consuming and laborious field studies, but also of causal-analytical laboratory investigations. Together with my assistant Manfred Ayasse and a number of graduate students, including above all Florian Schiestl (now a zoologist and professor of botany at the University of Zurich) and Johannes Stöckl (initially at the University of Regensburg, now at the University of Hohenheim, Institute of Applied Entomology), we were able to elucidate the chemistry of the scents and their specificity of attraction experimentally with the aid of gas chromatography.



**Fig. 74 (left):** Farewell to my assistant Manfred Ayasse on 7.11.2002, as he has accepted an appointment as full professor of chemical ecology at the University of Ulm. In the background from left to right: Gertrude Rothe (TA), Ursula Hannappel (PhD student: functional morphology and phylogeny of the Scirtidae), Harald Krenn (my assistant for functional morphology of the mouthparts of flower-visiting insects), Wolfgang Eberhard (PhD student with Günther Pass), Johannes Stöckl (PhD student with me and M. Ayasse). **(right):** Florian Schiestl was our first doctoral student in Ophrys research and made a significant contribution to elucidating the specificity of scent communication between Ophrys flowers and their male pollinators. He is now a professor of botanicals at the University of Zurich (<https://archiv.ethlife.ethz.ch/images/fpschiestl-l.jpg>).

I had already been in contact with Dr. Ernst Priesner<sup>187</sup> from the Max Planck Institute of Behavioral Physiology in Seewiesen in Freiburg to initiate cooperation on pheromone studies in the genus *Ophrys*. Priesner was a recognized specialist in insect pheromones (especially in glasswinged butterflies and moths). I visited him several times in Seewiesen, where I also gave lectures on the *Ophrys* research we

<sup>187</sup> [https://www.zobodat.at/pdf/NachBIBayEnt\\_045\\_0092-0093.pdf](https://www.zobodat.at/pdf/NachBIBayEnt_045_0092-0093.pdf)

had begun. When I moved to Vienna in 1992, however, I brought Manfred Ayasse into my institute as an assistant, who then put this project of analyzing the scents of the genus *Ophrys* into practice. Incidentally, Ernst Priesner has been missing in the Garmisch-Partenkirchen mountains since July 1994. In Seewiesen I also had intensive contact with Prof. Dietrich Schneider and above all with Prof. Dr. Franz Huber (Fig. 13), who was Director of the Department of Neuroethology at the Max Planck Institute in Seewiesen. He was particularly interested in my learning experiments with bees on *Ophrys*. I have him to thank for a number of tips. He passed away on April 27, 2017 at the age of 92.



**Fig. 75:** My collaborators on the *Ophrys* project "Significance of the intraspecific variability of *Ophrys heldreichii*" in Crete (25.3.2005). From left to right: Maria Paulus, Philipp Schlüter, Johannes Spaethe, Wolfgang Moser and myself.

With Joannes Spaethe (now at the University of Würzburg) (Fig. 75) as a further assistant and doctoral students such as Martin Streinzer or Kerstin Stejskal, I was able to clarify the color perception and pattern recognition of pollinator bees of *Ophrys* flowers. In the doctoral thesis supervised by me and Prof. Tod Stuessy (Botany) by Philipp Schlüter (Fig. 75) (later assistant to Florian Schiestl in Zurich, then since 2020 as professor at the University of Hohenheim, Institute of Biochemistry of Plant Secondary Metabolism), the question of whether the *Ophrys* species are actually also genetically separate units was examined, especially in the difficult *Ophrys fusca* group in Crete and Rhodes, with the help of DNA analyses (AFLP). His results confirmed what the field observations and selection tests had long since shown, that there are indeed this high number of *Ophrys* species. Ongoing projects on evolutionary-biological and biogeographical questions on *Ophrys* species groups are in progress together with Monika Hirth (Freiburg) or Demetra Rakosy (first

in Vienna, then Helmholtz Center for Environmental Research, Institute for Community Ecology, Leipzig). In addition to the earlier regular visits to the orchid



**Fig. 76:** Hans Reinhard in Zurich on 25.12.2004. He was an enthusiastic orchid lover who, together with Peter Gölz (Winterthur), introduced objective observations of the difficult orchid groups *Dactylorhiza* and *Ophrys* for the first time, mainly by means of morphometric methods ("clade difference"). My family and I always used to visit Ruth and Hans Reinhard around Christmas (photo H. Paulus).



**Fig. 77:** Meeting for our annual "Orchid Workshops" in Eching near Munich in 2015. Participants included (from left to right): Zissis Antonopoulos (Thessaloniki), Monika Hirth (Freiburg), Helmut Presser (first Eichstätt, later Kipfenberg), Stefan Hertel (Haag), Wolfgang Wucherpfnig (Eching), Ernst Gügel (Munich), Hans-Werner Zaiss (Marloffstein) and myself. Peter Gölz from Winterthur (Switzerland) was unable to attend.



conferences in Wuppertal and Schwäbisch-Gemünd, I myself organized meetings ("workshops") once or twice a year, first in Freiburg, then in Zurich and later in Eching near Munich.

Well-known orchid researchers were invited, including Hans R. Reinhard († 2007) (Zurich)<sup>188</sup> (Fig. 77, 78) , Peter Gölz (Winterthur), Claudia Gack (Freiburg), Ernst Gügel (Munich), the Dietrich couple († 2018) and Ursula Rückbrodt (Lampertheim), later also Wolfgang Wucherpfennig (Eching), Heinz-Werner Zaiss (Marloffstein), Stefan Hertel (D-83527 Haag), Helmut Presser (initially Eichstätt, later Kipfenberg), Hannelore Spaeth († 1998) (Freiburg), Monika Hirth (Freiburg) (Fig. 78), finally also Uwe Grabner (Starnberg), Bernd Tenschert (Hohenstadt), then occasionally also Zissis Antonopoulos (Thessaloniki). In 2000 I founded a monthly meeting of the Vienna Friends of Native and Mediterranean Orchids. We met and still meet once a month in my (former) institute in Althanstrasse with lectures and social get-togethers. In 2020 and 2021 during the Covid pandemic, we continued these meetings as so-called "online zoom meetings".



**Fig. 80:** Oil painting with "*Ophrys curiosities*" by Helmut Kratochvil (Vienna, 2012). In allusion to my sporting activity as an archer, flowers are "finished off" with arrows. Otherwise, some pollination biology observations: bottom left: *Argogorytes mystaceus* during pseudocopulation with *Ophrys insectifera*, top right: *Colletes cunicularius* on *Ophrys arachnitiformis*, below bumblebee on lady's slipper; somewhat modified *Ophrys apifera*, *O. heldreichii*, *O. insectifera* and *O. speculum*.

<sup>188</sup> Hans R. Reinhard (21.4.1919-18.3.2007) was a secondary school teacher (= grammar school teacher) in Zurich, majoring in botany. Together with Peter Gölz, a mathematician from Winterthur, they very successfully established morphometric methods of orchid clade separation ("Sippendifferenz"): <http://www.reinhard-ophrys.ch/Nachrufe.htm>; H. F. Paulus dedicated a new *Ophrys* species from central and northern Greece to the Reinhard couple in 2008: *Ophrys reinhardiorum*: [https://evolutionsbiologie.univie.ac.at/fileadmin/user\\_upload/dep\\_evolutionbiologie/Paulus/Hannes\\_F.\\_PAULUS-\\_In\\_memoriam\\_Hans\\_R.\\_REINHARD\\_klein.pdf](https://evolutionsbiologie.univie.ac.at/fileadmin/user_upload/dep_evolutionbiologie/Paulus/Hannes_F._PAULUS-_In_memoriam_Hans_R._REINHARD_klein.pdf); his extensive orchid herbarium is available at <http://www.e-manuscripta.ch/>, partly digitally. See also: <https://www.e-manuscripta.ch/zut/content/titleinfo/1390918>.

In the course of the *Ophrys* studies, I discovered and described a whole series of new species. There are currently 43 and there is no end in sight. I have made a very extensive photo and video documentation of the pollination processes of numerous *Ophrys* species. While the numerous orchid enthusiasts hardly ever got to see a pseudocopulation, I owed my successes above all to my profound knowledge of the mating biology of wild bees.

When I retired in 2012, my Viennese co-worker Prof. Dr. Helmut Kratochvil gave me an oil painting of *Ophrys* curiosities that he had painted himself (Fig. 80).

## **Whereabouts of my collections**

### **Orchids**

In the course of the numerous experimental field studies on the pollination biology of the genus *Ophrys*, test material was always left over, which was collected together with flower material as an extensive alcohol flower collection. This flower collection, preserved in 70-80% denatured methyl alcohol, is now in the herbarium of the University of Vienna at the Department of Botany and Biodiversity Research, Rennweg (Herbarium WU). All *Ophrys* holotypes can also be found here. I have created a conventional herbarium of pressed plant material only to a limited extent. These few sheets are also in the WU herbarium.

### **Butterflies**

My butterfly collection compiled in the years 1960-1990 with mainly material from the greater Mainz area and Central Europe is in the collection of the Biology Center Linz.

### **Beetles and bees**

Most of my beetle collection and my bumblebee collection are in the Linz Biology Center. Remnants of the beetle collection of Hermann Jakob (Vienna)<sup>189</sup> were in my collection and are now also mainly at the Biology Center Linz. I was able to acquire these from his widow around 1980 (without the special collection Chrysomelidae). My alcohol collection of beetle larvae is in the Collection and Research Center of the Tyrolean State Museums (Hall in Tirol). A small collection of wasps and bees from the early days of my collecting activities can be found in the Natural History Museum Mainz (see RENKER & HENRICH 2009: 443).

My extensive voucher collection of pollinator bees and wasps together with the remaining collection of mainly Mediterranean bees will also be transferred to the Biology Center Linz.

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<sup>189</sup> Hermann Jakob was a specialist in the Chrysomelidae family and from 1953-1958 a member of the board of the Arbeitsgemeinschaft Österreichischer Entomologen. Published posthumously: Hermann JAKOB (1979): Part XV p: Coleoptera, Fam. Chrysomelidae - Catalogus Faunae Austriae, Vienna - XVp: 1-36.

## List of diplomas, master works and dissertations

### University of Freiburg, Germany

- 1973 JAHN B.: Sex-Pheromone bei Käfern und ihre biologische Bedeutung im Dienste des Paarungsverhaltens; 137 S. (Lit., Staatsexamen).
- 1974 MUTSCHLER G.: Funktionsmorphologie und Anatomie des Coleopteren-thorax; 116 S. (Lit., Staatsexamen).
- 1976 HIRNER S.: Vögel als Blütenbesucher und ihr Einfluss auf die Evolution der Blüte; 69 S. (Staatsexamen).
- 1976 LOHMÜLLER G.: Käfer als Blütenbesucher; 80 S. (Staatsexamen).
- 1976 LÖRCHER U.: Hymenopteren als Bestäuber von Orchideen – Anpassungen und Strategien; 134 S. (Staatsexamen).
- 1977 KRAFT Rita: Co-Evolution der Lepidopteren mit ihren Pflanzen; 119 S. (Staatsexamen).
- 1977 JAKUBOWSKY M.: Die Wechselbeziehungen zwischen Ameisen und Pflanzen mit besonderer Berücksichtigung der extrafloralen Nektarien; 100 S. (Staatsexamen).
- 1977 RENZ F.: Die Augen und cuticulären Sinnesorgane der Crustaceen und ihre Bedeutung für die Phylogenie der Arthropoda; 101 S. (Staatsexamen).
- 1977 RENZ P.: Die Augen und cuticulären Sinnesorgane der Spinnentiere und ihre Bedeutung für die Phylogenie der Arthropoda; 154 S. (Staatsexamen).
- 1977 SCHMIDT Mechthild: Vergleichend-morphologische Untersuchungen zum Bau der Stemmata bei Trichoptera und Lepidoptera; 129 S. (Diplom).
- 1977 STAMPFER T.: Dipteren als Blütenbesucher – Anpassungen und Bestäubungsstrategien; 71 S. (Staatsexamen).
- 1978 ULLRICH Renate: Zur Brutbiologie von *Anthophora acervorum*, unter besonderer Berücksichtigung der Quantifizierung des Pollensammelns (Apoidea, Anthophoridae); 125 S. (Diplom).
- 1979 BRAIG M. J.: Die Funktion der Linsenaugen der Arthropoda, eine vergleichend-funktionelle Analyse; 77 S. (Staatsexamen).
- 1979 BURCHARD M.: Zur Biologie malacophager Coleopteren, unter besonderer Berücksichtigung der Gattung *Badister* (Carabidae); 82 S. (Experiment).
- 1979 BURKARD W.: Einnischungsphänomene bei blütenbesuchenden Vögeln; 78 S. (Staatsexamen).
- 1979 HECHT Thomas: Zur Brutbiologie solitärer Apoidea, insbesondere der Halictinae; 66 S. (Staatsexamen).
- 1979 JUNKER H. P.: Die Färbung bei Schmetterlingen und ihre ökologische Bedeutung; 97 S. (Staatsexamen).
- 1979 KIEFER U.: Vergleichend-faunistisch-ökologische Untersuchungen der Carabidenfauna in Rebflächen mit unterschiedlicher Bewirtschaftung; 56 S. (Diplom).
- 1979 KURMEIER Gisela: Vergleichend-morphologische Untersuchungen zum Bau der Stemmata einiger Coleopteren; 167 S. (Diplom).
- 1979 MAYER Bodo: Blütenbesuche, Sammelgeschwindigkeiten und Konkurrenzvermeidung bei heimischen Hummeln. 88 S. (Diplom).

- 1979 LÜTZENKIRCHEN Günther: Messungen der Sammelgeschwindigkeiten an verschiedenen Blüten von Honigbienen und Hummelarten; 82 S. (Diplom).
- 1979 MÜLLER D.: Mimikry bei Pflanzen; 140 S. (Staatsexamen).
- 1980 BAUER Jürgen: Vergleichend-morphologische Untersuchungen zum Bau der Stemmata bei Dipteren; 107 S. (Diplom).
- 1980 FRITZSCHE J.: Faunistisch-ökologische Untersuchungen der epigäischen Carabiden (Coleoptera) in Rebflächen mit unterschiedlicher Bewirtschaftungsweise am Kastelberg bei Sulzburg (Süd-Baden); 73 S. (Diplom).
- 1980 FRITZSCHE R.: Faunistisch-ökologische Untersuchungen der epigäischen Staphyliniden (Coleoptera) in Rebflächen mit unterschiedlicher Bewirtschaftungsweise am Kastelberg bei Sulzburg (Süd-Baden); 73 S. (Diplom).
- 1980 KECK L.: Neuere Arbeiten zur Embryologie der Coleopteren; 79 S. (Staatsexamen).
- 1980 KEMETH H.: Die Augen der Annelida – Eine vergleichende morphologische Zusammenstellung; 77 S. (Staatsexamen).
- 1980 KIENZLER M.: Brutfürsorge und Brutpflege bei Käfern, insbesondere bei coprophagen Scarabaeidae; 75 S. (Staatsexamen).
- 1980 KOHLER A.: Untersuchungen zur Parasitierung des Einbindigen Traubenwicklers *Eupoecilia ambignella* (Lep., Tortricidae) durch den Eiparasiten *Trichogramma evanescens*; 91 S. (Diplom).
- 1980 LEHN Klaus: Vergleichend-morphologische Untersuchungen zum Bau der Stemmata der Neuropteroidea; 107 S. (Diplom).
- 1980 STRIEH B.: Die Zusammensetzung der Pollenhöschen verschiedener Hummelarten in einem Halbtrockenrasen im Kaiserstuhl; 82 S. (Experiment) (zusammen mit A. Kratochwil).
- 1981 SCHMID Klaus-Dieter: Die Lauterzeugung der Coleoptera; 110 S. (Staatsexamen).
- 1981 KLEIN Walter: Quantitative Untersuchungen zur Farbenpräferenz blütenbesuchender Insekten (Apoidea, Syrphidae) in einem Halbtrockenrasen im Kaiserstuhl; 90 S. (Staatsexamen, Experiment).
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- 1983 GEBHARDT Ingeborg: Vergleichend-morphologische und histologische Untersuchungen an Augen der Spinnentiere (Arachnida) unter besonderer

- Berücksichtigung der Pseudoscorpiones, Uropygi und Amlypygi; 126 S. (Diplom).
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- 1983 LÜTZENKIRCHEN Günther: Optimal foraging und Konkurrenzvermeidung: Labor- und Freilanduntersuchungen an Nektar sammelnden Hummeln; 126 S. (Dissertation an der Univ. Freiburg).
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- 1984 RITZHAUPT Bettina: Vergleichend-feinstrukturelle Untersuchungen zum Bau des Rüssels von Hummeln und der Honigbiene; 96 S. (Staatsexamen).
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- 1985 PLANT John: Zur Phylogenie der Bienen (Apoidea): Vergleichende Morphologie der Mundwerkzeuge; 134 S. (Diplom).
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- 1986 de WITT Michael: Thorax- und Flügelbau bei Tagfaltern und sein Bezug zum Flugverhalten; 80 S. (Staatsexamen).
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- [https://www.zobodat.at/pdf/Carolinea\\_45\\_0147-0158.pdf](https://www.zobodat.at/pdf/Carolinea_45_0147-0158.pdf)
- 1988 SOWIG Peter: Körpergröße und Rüssellänge bei Hummelarbeiterinnen: Die Rolle ihrer inter- und intraspezifischen Variabilität für die unterschiedliche Ressourcennutzung; 140 S. (Dissertation an der Univ. Freiburg).

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[https://www.zobodat.at/pdf/Neue-Entomologische-Nachrichten\\_35\\_0001-0194.pdf](https://www.zobodat.at/pdf/Neue-Entomologische-Nachrichten_35_0001-0194.pdf)
- 1989 RUPP Leo: The central European species of the genus *Volucella* (Diptera, Syrphidae) as commensals and parasitoids in the nests of bumblebees and social wasps: studies on host-finding, larval biology and mimicry; 207 S. (Dissertation an der Albert-Ludwigs University, Freiburg-im-Breisgau).  
<http://ecology.nottingham.ac.uk/~plzfg/syrphweb/Rupp1989.doc>
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- 1990 HANNAPPEL Ursula: Vergleichende Feinstrukturuntersuchungen an Mundwerkzeugen der Larven der Helodidae; 101 S. (Diplom).
- 1991 REES Patrick: Die Larven der europäischen Byrrhidae (Coleoptera). Untersuchungen zur Morphologie, Ökologie, Systematik, Entwicklung und Lebensweise; 115 S. (Diplom).
- 1992 FREITAG Urte: Spinnen auf dem Gletschervorfeld des Hornkees in den Zillertaler Alpen, Tirol; 148 S. + 30 S. Anhang (Diplom).

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- 1999 FRABERGER Rafaelo: Paarungsverhalten, Brutbiologie und chemische Kommunikation der heimischen Spiralhornbienen-Arten *Systropha planidens* und *S. curvicornis* und ihres Brutparasiten *Biastes brevicornis* (Hymenoptera,

- Halictidae und Anthophoridae); 119 pp. (Diplom, zusammen mit M. Ayasse).
- 1999 NEUMAYER Johann: Ökologie alpiner Hummelgemeinschaften – Blütenbesuch, Ressourcenaufteilung und Energiehaushalt; 283 pp. + Anhang (Dissertation).
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- 2001 KEPPERT Inge: Wespenblumen und Blumenwespen. Die Bestäubungsbiologie von *Scrophularia nodosa*, *S. umbrosa* (Scropulariaceae), *Epipactis helleborine* und *E. purpurata* (Orchidaceae); 184 S. (Diplom).
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- 2004 WILHELM Gertha: Die Lebensgeschichte von *Rhopalapion longirostre* (Coleoptera, Curculionioidea, Apionidae); 154 S. (Diplom).
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- 2006 PEHAMBERGER Elke: Eine vergleichende Strukturanalyse der Stemmata bei einigen Neuropterida; 68 S. (Diplom).
- 2008 MOSER Wolfgang: How to avoid aggressive wasps: Biology of the parasitic hover fly *Volucella pellucens*. Supervisor: H. F. PAULUS zusammen mit Johannes Spaethe, (Dissertation, nicht beendet).
- 2008 TIMELTHALER Gerald: Cameroon's Crater Lake Cichlids – Visual ecology, opsin molecular evolution and implications for a remarkable speciation in sympatry; 52 S. (Diplom, zusammen mit Johannes Spaethe).
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([http://othes.univie.ac.at/cgi/search/simple?q=Patzak%2C+Anatole&\\_action\\_search=Suche&\\_action\\_search=Suche&\\_order=bytitle&basic\\_srctype=ALL&\\_satisfyall=ALL](http://othes.univie.ac.at/cgi/search/simple?q=Patzak%2C+Anatole&_action_search=Suche&_action_search=Suche&_order=bytitle&basic_srctype=ALL&_satisfyall=ALL)).
- 2012 SCHNEIDER Sandra: UV- und Polarisations-signale bei Tagfaltern; 130 S. (Diplom).
- 2013 MORAWETZ Linde: Komplexe Mustererkennung bei Bienen. 121 S. (Dissertation, zusammen mit Johannes Spaethe).



- 2014 RAKOSY Demetra: Orchideen – Botanische Juwelen der Golfo Dulce Region Costa Rica; 125 S. (Diplom, zusammen mit Prof. Dr. Anton Weber, Botanik Univ. Wien).  
<https://orchidee.de/book-review/orchids-botanical-jewels-of-the-golfo-dulce-region-costa-rica/>
- 2016 PLANT John: Phylogeny of Apoidea – Biology and morphology (Insecta, Hymenoptera); 320 S. (Dissertation).
- 2017 SINGER Harald: Breeding Carnolian bees (*Apis mellifera carnica*) on different comb cell sizes and analyzing the effect of the different cell sizes on the *Varroa* infestation rates; 88 S. (Dissertation).
- 2017 RAKOSY Demetra: Evolution and diversification of flower traits in the sexually-deceptive genus *Ophrys* (Orchidaceae): insights from the *Eucera* pollinated *Ophrys tenthredinifera* complex. 142 S. (Dissertation).
- 2017 SCHWEIGER Silke: Molecular evolution of reptiles in Austria – Intraspecific genetic diversity, Würm glacial refuges and postglacial colonization routes of selected species; 147 S. (Dissertation, Betreuung zusammen mit Werner Mayer Nat. Hist. Museum, Wien).
- 2017 AHMAD Sohel: Adaptation to laboratory conditions, improvements in mass rearing methodologies and pre-zygotic and postzygotic isolation studies on the olivefruit fly *Bactrocera oleae* (ROSSI) (Diptera: Tephritidae) in relation with the application of the sterile insect technique (SIT) for area-wide pest management; 60 S. (Dissertation, zusammen mit IAEA Laboratories in Seibersdorf).
- 2021 BÜRGER Karoline: The Importance of Various Habitat Characteristics reflected by Population density in Dalmatian Tortoises (*Testudo hermanni hercegovinensis*); 21 S. (Masterarbeit, zusammen mit Dr. Herbert Hoi, Konrad-Lorenz-Institut für Vergleichende Verhaltensforschung, Vet.-Med. Univ., Wien).

The majority of these unpublished papers are kept in the University Library of Zoology in Vienna. Those of the examination theses at the University of Vienna are deposited in the University Library.

### Hannes F. Paulus: Excursions and trips sorted by year Excursions started from Mainz:

1961		
6.8.-28.7.1961	Ramsau am Dachstein/Salzburg	mit Annemarie Paulus
1962		
15.7.-4.8.1962	S-Kärnten (Ferlach, Waidischtal)	
1963		
21.7.-9.8.1963	S-Kärnten/Ferlach	
1964		
17.7.-20.8.1964	S-England (Kelvedon)	
1965		
4.6.-14.6.1965	Wallis/Rhonetal	mit Klaus Rose
14.7.-3.8.1965	S-Kärnten/Ferlach/Waidischtal	

<b>1966</b>		
19.4.-3.5.1966	Libanon	mit Klaus Rose
30.7.-21.8.1966	S-Tirol/Seis	
<b>1967</b>		
15.8.-22.8.1967	Stubachtal/Hohe Tauern	mit Jochen Martens, Otto von Helversen
23.8.-28.8.1967	Wallis/Rhonetal	mit Jochen Martens
30.8.-7.9.1967	Pyrenäen, N-Spanien (Kantabrisches Gebirge)	Käfer, Opiliones mit Jochen Martens
9.9.-26.9.1967		
<b>1968</b>		
5.4.-17.4.1968	Sardinien	Bot. Exkursion Univ. Mainz
10.9.-29.9.1968	Arcachon/SW-France	Meereszool. Exkursion Univ. Mainz
<b>1969</b>		
2.7.-17.7.1969	S-Kärnten/Ferlach	Käfer, Tagfalter
<b>Field trips started from Vienna:</b>		
<b>1991</b>		
27.2.-6. 3.1991	S-Portugal (Algarve), Lissabon	Urte Freitag, Josef Müller, Claudia Gack
10.8.-12.8.1991	Budapest, Trockenhänge	mit Dagmar und Otto v. Helversen, Urte Freitag
23.8.-30.8.1991	Vorarlberg (Schruns/Latschau)	mit Urte Freitag
<b>1992</b>		
29.12.91-5.1.1992	Gran Canaria	mit Urte Freitag
29.3.1992	nördl. Genua	
30.3.-23.4.1992	Sardinien	Manfred Ayasse, Claudia Gack
17.8.-21.8.1992	Totes Gebirge (Pyringer Hütte)	Alpenexkursion
21.8.-24.8.1992	Zillertaler Alpen (Berliner Hütte)	Alpenexkursion
30.8.-13.9.1992	Gran Canaria	
18.9.-19. 9.1992	Koralpe	mit Urte Freitag
<b>1993</b>		
29.3.-27.4.1993	Sardinien	Manfred Ayasse, Florian Schiestl (als Student)
28.5.-31.5.1993	Istrien (Rovinj)	mit Urte Freitag, Ludwig Freidinger
5.7.-9.7.1993	Totes Gebirge (Pühringer Hütte)	Alpenexkursion
9.7.-13.7.1993	Niedere Tauern (Preintaler Hütte)	Alpenexkursion
2.8.-9.8.1993	Montafon	mit Urte Freitag
26.9.-3.10.1993	Gran Canaria	mit Urte Freitag
<b>1994</b>		
6.2.-19.2.1994	Gran Canaria	mit Urte Paulus (geb. Freitag)
27.3.1994	nördl. Genua	Manfred Ayasse
29.3.-31.3.1994	Korsika	Manfred Ayasse
31.3.-15.4.1994	Sardinien	BBC Bristol: Film: „Geheime Leben der Pflanzen: Bestäubung“ mit David Attenborough
26.5.1994	Bily Karpathy (Tschechien)	
11.7.-19.7.1994	Hohe Tatra (Slowakei)	Alpenexkursion
28.7.-30.7.1994	Latschau (Vorarlberg)	mit Urte Paulus
<b>1995</b>		
6.4.-19.4.1995	SO-France	Claudia Gack
19.4.-23.4.1995	W-Italien: Ligurien, Toskana	Claudia Gack
24.4.-28.4.1995	SO-France	Claudia Gack
27./28.5.1995	Bily Karpathy (Tschechien)	
3.6.-9.6.1995	Istrien (Medullin)	Familie
6.8.-13.8.1995	Latschau	Familie
<b>1996</b>		
3.2.-17.2.1996	Gran Canaria	Familie
19.2.-25.2.1996	NO-Tunesien (Hammamet)	Günther Pass, Florian Schiestl (als Student)
25.3.-27.3.1996	W-Italien: Ligurien	Claudia Gack
28.3.-12.4.1996	SO-France	Claudia Gack
22.5.-29.5.1996	S-Istrien	Familie
2.7.-11.7.1996	NW-Kärnten	Alpenexkursion
<b>1997</b>		
9.2.-23.2.1997	Gran Canaria	Familie
24.3.-5.4.1997	Mallorca	BBC Bristol, Film <i>Ophrys</i> -Bestäubung
19.5.-24.5.1997	Istrien	mit Ludwig Freidinger, Urte Paulus
6.6.-8.6.1997	Illmitz	Bienenpraktikum
16.7.-18.7.1997	Dachstein (Nordseite)	Alpenexkursion
13.8.-17.8.1997	Ötztal	Alpenexkursion

<b>1998</b>		
1.2.-7.2.1998	Mallorca	Urte Paulus
19.3.-2.4.1998	NO-Tunesien (Hammamet)	Claudia Gack
6.4.-19.4.1998	S-Turkey	Familie
3.6.1998	Bily Karpathy (Tschechien und Slowakei)	
5.7.-26.7.1998	Gran Canaria	Familie
4.8.-8.8.1998	Dachstein (Simonyi-Hütte)	Alpenexkursion
8.8.-12.8.1998	Hohe Tauern (Rudolfshütte)	Alpenexkursion
<b>1999</b>		
21.2.-28.2.1999	NO-Tunesien (Bizerte)	
28.3.-11.4.1999	Rhodos	Familie, Studenten-Exkursion
4.7.-1.8.1999	Gran Canaria	Familie
<b>2000</b>		
13.2.-20.2.2000	Malta	Hans Salkowski
4.3.-11.3.2000	Korfu	Monika Hirth, Claudia Gack, Klaus Collatz
16.4.-23.4.2000	S-/M-Greece	
16./17.5.2000	Gardasee (San Zeno)	Orchideen-Tagung
9.6.-14. 6.2000	Obertraun/Salzkammergut	Familie
3.8.-31.8.2000	Gran Canaria	Familie
<b>2001</b>		
12.2.-19.2.2001	Crete	Hans Salkowski
8.4.-22.4.2001	Rhodos	Studenten-Exkursion
3.5.-9.5.2001	MittelGreece	
26.5.2001	Bily Karpathy (Tschechien)	
3.7.-13.7.2001	Gran Canaria	Familie
29.7.-4.8.2001	Montafon (Latschau)	Familie
<b>2002</b>		
1.2.-8.2.2002	Teneriffa	Familie
25.2.-3.3.2002	Kos	mit Hans Salkowski
22.3.-5.4.2002	Crete	
29.4.-4.5.2002	Crete	Exkursion
29.6.-13.7.2002	Crete	Familie
2.8.-11.8.2002	Zentralschottland	Bogenschieß-WM, Urte Paulus
<b>2003</b>		
30.12.02-5.1.2003	Malta	Familie
1. 2.-8.2.2003	Fuerteventura	Familie
28.3.-4.4.2003	Crete	
20.4.-27.4.2003	Rhodos	Philipp Schlüter, Familie
3.5.-10.5.2003	Crete	
7.6.2003	Bily Karpathy (Tschechien)	
6.7.-19.7.2003	Montafon (Latschau)	Familie
9./10.8.2003	Irrsee, Fuschlsee	Familie
15.8.-29.8.2003	West-Crete	Familie
<b>2004</b>		
28.12., 3-4.1.2004	Malta	Familie
31.1.-7.2.2004	Lanzarote	Familie
20.2.-28.2.2004	Samos	mit Monika Hirth
7.4.-14.4.2004	S-Spanien (Costa del Sol)	Familie
26.4.-3.5.2004	Crete	mit Monika Hirth
12.6.-13.6.2004	Ungarn (südl. Budapest)	
3.7.-9.7.2004	Planneralm-Ennstal	Urte Paulus (WM-Bogenschießen)
22.7.-5.8.2004	NO-Greece (Chalkidiki)	Familie
21.8.-22.8.2004	Hall – Mills Tirol	Urte Paulus (Bogenschieß-Turnier)
<b>2005</b>		
2.-12.2.2005	Fuerteventura	Familie
26.3.2005	östl. Athen	
12.3.-26.3.2005	Crete (Ost)	Johannes Spaethe, Philipp Schlüter u.a.
31.3.2005	Ithaka	mit Monika Hirth
27.3.-2.4.2005	Kephallonia	mit Monika Hirth
13. 4.-16.4.2005	Chios	Orchideentagung
7.5.-14.5.2005	Crete (West)	Studentenexkursion
11.6.2005	Ungarn (Dabas, südl. Budapest)	
10.7.-21.7.2005	Seis/Südtirol	Familie

22.7.-24.7.2005	St. Johann im Pongau	Urte Paulus (Bogenschieß-Turnier)
<b>2006</b>		
4.2.-11.2.2006	Algarve, Serra Arrabida	Familie
25.2.-3.3.2006	W-Turkey: Kusadasi	mit Monika Hirth
15.3.-18.3.2006	Lissabon, Arrabida	
27.3.-5.4.2006	Crete (Ost)	Johannes Spaethe u. a.
10.4.-16.4.2006	Rhodos	Familie, Ehepaare Peter Hubert und Karl Schebska
1.7.-4.7.2006	Großglockner-Hochalpenstation	Blüten-Projektpraktikum
7.7.-19.7.2006	Z-Portugal: Torres Novas, Serra Estrella	Urte Paulus (EM-Bogenschießen)
27.7.-8.8.2006	Süd-Finnland	Urte Paulus (WM-Bogenschießen)
<b>2007</b>		
3.2.-10.2.2007	Zypern	Familie
17.2.-24.2.2007	Rhodos	mit Monika Hirth
17.3.-24.3.2007	O-Crete	
31.3.-6.4.2007	Malta, Gozo	Familie
<b>2008</b>		
15.3.-22.3.2008	Zypern	Familie
24.3.-30.3.2008	Samos	
26.4.-3.5.2008	N-Thessalien (Olymp)	Exkursion
9.5.-13.5.2008	Istrien	Familie, Orchidgroup
21.5.-25.5.2008	London	Familie
18.7.-22.7.2008	Hohe Tauern (Hochalpenstraße)	Blütenpraktikum
25.7.-4.8.2008	Estland (Otopää)	Familie (EM-Bogenschießen)
<b>2009</b>		
20.2.-27.2.2009	Ost/SüdCrete	Monika Hirth
3.4.-10.4.2009	Mallorca	Exkursion
14.4.-17.4.2009	WestCrete	alleine
24.7.-2.8.2009	Wales (Great Britain)	Urte Paulus (EM-Bogenschießen)
<b>2010</b>		
31.1.-4.2.2010	Rom	Familie
20.2.-27.2.2010	Rhodos	Monika Hirth
28.3.-5.4.2010	Kefalonia	Familie
5.4.-10.4.2010	Samos	Monika Hirth
11.4.2010	Markopoulo (Athen-Attika)	alleine
26.4.-2.5.2010	Elassona-Olymp (Thessalien)	Exkursion
4.5.-8.5.2010	Istrien (Porec)	Urte Paulus
2.7.-4.7.2010	Ennstal: Planner Alm, Wörschacher Moor	Urte Paulus
17.-23.7.2010	Hohe Tauern (Großglockner)	Blüten-Projektpraktikum
31.7.-8.8.2010	Dahner Felsenland, Mainz	Urte, Maria Paulus (WM-Bogenschießen)
1.-4.9.2010	Venedig	Urte Paulus
<b>2011</b>		
27.2.-6.3.2011	Lesbos	mit Monika Hirth
20.4.-26.4.2011	Süd-Dalmatien (Dubrovnik)	Familie
6.5.-12.5.2011	Thessalien-Olymp	Exkursion
30.7.-8.8.2011	Lissabon-Oeiras, Cascais	Bogenschießen EFAC 2011, Familie
15.8.-18.8.2011	Venedig	Urte Paulus
30.8.-4.9.2011	Donnersbach/Ennstal diverse Moore	Urte Paulus (WM-Bogenschießen)
30.9.-3.10.2011	Rom	Urte Paulus
19.2.-26.2.2012	N-Tunesien	Familie
3.3.-10.3.2012	Rhodos	Monika Hirth
1.4.2012	Athen-Markopoulo	allein
2.4.-10.4.2012	Kos	Monika Hirth
11.4.2012	Athen-Markopoulo	
14.5.-20.5.2012	Elassona-Olymp	Studenten-Exkursion, mit Urte Paulus
14.7.-20.7.2012	Hohe Tauern (Großglocknerregion)	Studentenpraktikum
18.9.-22.9.2012	Glasgow Scotland	Urte und Maria Paulus
<b>2013</b>		
23.2.-2.3.2013	Zypern-Süd	Monika Hirth
20.3.-21.3.2013	Attika: Markopoulo-Hymmettos	Monika Hirth
22.3.-29.3.2013	Paros	Monika Hirth
29.3.-6.4.2013	Chios	Monika Hirth, Pantelis Saliaris

6.4.2013	Markopoulo-Hymmettos	
21.4.-29.4.2013	Olymp Ostseite	Urte Paulus, Monika Hirth, Studenten-Exkursion
9.6.2013	Bily Karpathy-Tschechien	Jana Jersakova (Brno), Johannes Spaethe (Würzburg), Johann Neumeier (Salzburg)
16.7.-18.7.2013	Hohe Tauern (Großglocknerregion)	Stefan Dötterl (Salzburg), Johann Neumeier,
29.7.-2.8.2013	Istrien (Porec)	Familie
9.9.-14.9.2013	Bozen, Südtirol	SIEEC-Tagung
<b>2014</b>		
14.2.-1.3.2014	Seychelles	Urte Paulus
15.3.-16.3.2014	Markopoulo	Monika Hirth
29.3.2014	Markopoulo-Koropi	Monika Hirth
16.3.-21.3.2014	Paros	Monika Hirth
21.3.-29.3.2014	Süd-Zypern	Monika Hirth
30.3.-4.4.2014	Rhodos	Monika Hirth
6.4.-13.4.2014	Süd-Turkey	Urte und Maria Paulus
21.4.-27.4.2014	Presbasee/N.Greece	Monika Hirth, student. Exkursion
20.6.-22.6.2014	Istrien	Botanikexkursion Klagenfurt
30.06.-3.7.2014	Venedig	Urte Paulus
4.9.-9.9.2014	London	Urte Paulus
<b>2015</b>		
31.1.-5.2.2015	Malta	Urte und Marko Paulus; Eva Haager
10.2.-18.2.2015	Zypern	Urte Paulus
7.3.-8.3.2015	Attika: Markopoulo, Hymmettos	Monika Hirth
8.3.-12.3.2015	Paros	Monika Hirth
13.3.-20.3.2015	Kithyra	Monika Hirth
29.3.-3.4.2015	Sizilien	Urte und Maria Paulus
6.4.-12.4.2015	Zypern	Monika Hirth
13.4.-19.4.2015	Samos	Orchid Conference
19.4.-27.4.2015	N-/NW-Greece: Grevena, Preveza	Monika Hirth
20.5.-31.5.2015	Nord-Spanien: Burgos etc	Exkursion mit Wiener Orchidfreunden
1.6.-3.6.2015	Montserrat, Barcelona	Exkursion mit Wiener Orchidfreunden
9.7.-14.7.2015	Istrien, Porec	Urte und Marko Paulus; Eva Haager
27.8.-17.9.2015	Malaysia: Borneo-Sabah	Urte und Maria Paulus
9.12.-13.12.2015	Insel Madeira	Urte und Maria Paulus
<b>2016</b>		
3.1.-8.1.2016	Dubai (Emirates)	Urte und Maria Paulus
27.1.-31.1.2016	Malta	Urte Paulus
26.2.-2.3.2016	Zypern (Süd)	Urte Paulus
9.3.-11.3.2016	Attika	Monika Hirth
11.3.-21.3.2016	Insel Skyros	Monika Hirth, Athanasios Papanikolaou
21.3.-23.3.2016	Attika	Monika Hirth
27.3.-3.4.2016	Südwest-Italien: Neapel-	Urte und Maria Paulus
5.4.-15.4.2016	Attika – Samos – Chalkidike-Presbasee - Olymp	Monika Hirth, Zissis Antonopoulos
23.4.-29.4.2016	Olympregion	alleine
25.5.-11.6.2016	Kuba	Maria Paulus
7.8.-13.08.2016	Istrien, Porec	Urte und Marko Paulus; Eva Haager
25.8.-9.9.2016	Kenia, Tanzania	Urte und Maria Paulus
<b>2017</b>		
3.3.-11.3.2017	Rhodos	alleine
22.3.-24.3.2017	London	Urte Paulus
24.3.-4.4.2017	Bali, Flores, Komodo Island	Urte und Maria Paulus
7.4.-10.4.2017	Athen-Attika	Monika Hirth
10.4.-24.4.2017	Kos	Monika Hirth
13.4.-17.4.2017	Tilos	Monika Hirth
24.4.-2.5.2017	SO-Sizilien (Grammichele)	Monika Hirth
26.5.-3.6.2017	Jordanien	Urte und Maria Paulus
20.6.-26.6.2017	Schottland (Glasgow, Edinburgh)	Urte und Maria Paulus
22.06.-24.6.2017	NW-England (Lake District)	Urte und Maria Paulus
11.7.-16.7.2017	Porec, Istrien	Marko und Urte Paulus; Eva Haager
23.11.-26.11.2017	Kitzbühel (Familientreff)	Urte und Maria Paulus
<b>2018</b>		
28.12.-6.1.2018	Ägypten (Kairo, Nilfahrt)	Urte und Maria Paulus
23.2.-7.3.2018	NW-Indien (Rajasthan)	Urte und Maria Paulus

29.3.-3.4.2018	S-Greece: Delphi, Mykene, Epidaurus, Markopoulo	Maria, Urte und Hannes Paulus, Marko Paulus und Eva Haager
04.4.-10.4.2018	Korfu	mit Monika Hirth
11.4.-13.4.2018	Lefkada	mit Monika Hirth
13.4.-20.4.2018	Kefallonia	mit Monika Hirth
21.4.-23.4.2018	SW-Peloponnes	mit Monika Hirth
23.4.-26.4.2018	SW-Greece	mit Monika Hirth
26.4.-28.4.2018	Korfu	mit Monika Hirth
10.6.-17.6.2018	Mittelitalien: Abruzzen (Maiella, Gran Sasso)	mit Wiener Orchideenfreunden
11.7.-15.7.2018	Istrien	Urte und Marko Paulus; Eva Haager
<b>2019</b>		
15.2.-17.2.2019	Serbien: Novigrad, Kikinda (Eulen)	Urte und Maria Paulus
01.3.-03.3.2019	Rumänien: Bukarest, Brasov	Urte Paulus
25.3.-26.3.2019	Attika	
27.3.-31.3.2019	Samos	Monika Hirth
01.4.-10.4.2019	Kefalonia	Monika Hirth
13.4.-20.4.2019	Ochridsee, Kosovo, Albanien	Urte und Maria Paulus
22.4.-30.4.2019	Kefalonia	Monika Hirth
04.5.-11.5.2019	Sardinien	Urte Paulus
18.5.-20.5.2019	Lettland (Riga)	Urte Paulus
02.7.-16.7.2019	Uganda (Safaris, Gorillas)	Urte und Maria Paulus
12.12.-20.12.2019	Zypern	Urte Paulus
<b>2020</b>		
06.01.-11.1.2020	S-Ägypten (Hurghada)	Urte und Maria Paulus
25.02.-10.3.2020	Marokko Rundreise	Urte Paulus
	<b>CORONA Covid19 time</b>	
05.07.-10.7.2020	Wolfgangsee	Urte Paulus
11.08.-15.8.2020	Traunsee	Akademie-Workshop
<b>2021</b>		
15.5.-30.5.2021	Nord-Greece	Monika Hirth
11.7.-18.7.2021	Istrien	Urte und Marko Paulus; Eva Haager
09.8.-15.8.2021	N-Rumänien	Urte und Maria Paulus
25.8.-29.8.2021	S-Kroatien, Bosnien, Montenegro	Urte und Maria Paulus
15.9.-19.9.2021	Zentral-Anatolien: Kappadokien	Urte und Maria Paulus
<b>2022</b>		
29.12.-10.1.2022	nördlicher Oman (Rundreise)	Urte und Maria Paulus
18.3.-21.04.2022	Attika, Kefalonia, Zakynthos, SW Peloponnes	Monika Hirth (Attika auch mit Mike Lowe)
22.5.-30.05.2022	Rundreise Republik Irland	Urte Paulus
20.9.-27.09.2022	Ägypten, Hurghada	Urte und Marko Paulus; Eva Haager
13.10.-17.10.2022	Freiburg, Kehl-Kork (Orchid-Symposium)	Monika Hirth
<b>2023</b>		
19.01.-26.01.2023	Andalusien: Fuengirola	Urte Paulus
19.2.-05.03.2023	Nordzypern	Urte Paulus
27.3.-29.03.2023	Süd-Attika	Monika Hirth
30.3.-05.04.2023	Zakynthos	Monika Hirth
05.4.-10.04.2023	SW-Peloponnes	Monika Hirth, Walter und Andrea Sterniste
11.4.-16.04.2023	Zakynthos	Monika Hirth, Mike Lowe
17.4.-19.04.2023	Süd-Attika	Monika Hirth
06.7.-17.07.2023	China-Rundreise (Peking-Xi'an, Guilin-Shanghai)	Urte und Maria Paulus

## List of taxa newly described by H. F. Paulus

### COLEOPTERA

#### Chelonariidae (Dryopoidea)

*Pseudochelonarium kalimantanense* PAULUS, 1969: Borneo

PAULUS H. F. (1969): *Pseudochelonarium (Neochelonarium) kalimantanense* nov. spec. aus Borneo, mit Bemerkungen zum System der Chelonariidae – (Col., Dryopoidea) — Z. Arbeitsgem. österr. Ent. Wien **21**: 105-109.

## Carabidae

*Cychropsis mandli* PAULUS, 1971: Nepal

*Calosoma davidis* ssp. *martensi* PAULUS, 1971: Nepal

PAULUS H. F. (1971): *Calosoma davidis martensi* nov.ssp. und *Cychropsis mandli* nov. spec. aus Nepal, mit einer Bestimmungstabelle der bisher bekannten Vertreter des Genus *Cychropsis* (Col., Carabidae). — Z. Arbeitsgem. österr. Entomol.Wien **23**: 14-24.

## Byrrhidae

*Byrrhus* (s.str.) *chinensis* PAULUS, 1970

*Curimopsis sibirica* PAULUS, 1970: O-Sibirien

*Curimopsis obenbergeri* PAULUS, 1970: O-Sibirien

*Curimopsis mongoliensis* PAULUS, 1970: Mongolei

PAULUS H. F. (1970): Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. 238. Byrrhidae (Col.) — Ann. Hist. Nat. Mus. Nat. Hung. Zool. (Budapest) **62**: 249-256.

*Asiatobyrrhus* (PAULUS, 1971): Himalaya (described as a subgenus of *Byrrhus*)

*Asiatobyrrhus tibetanus* (PAULUS, 1971): Thibet

*Asiatobyrrhus macrosetosus* (PAULUS, 1971): N-Pakistan

*Curimopsis magna* (PAULUS, 1971): N-Indien

PAULUS H. F. (1971): Neue Byrrhidae aus Asien: *Syncalypta magna* n.sp., *Byrrhus chinensis* n.sp., *B. tibetanus* n.sp., *B. macrosetosus* n.sp. mit Bemerkungen zur systematischen Stellung von *Seminolus* Muls. (Col., Byrrhidae). — Ent. Blätter (Krefeld) **66**: 163-174.

*Pedilophorus rhodopensis* PAULUS, 1972: Balkan

PAULUS H. F. (1972): Der Stand unserer Kenntnis über die Familie Byrrhidae (Col.). — Folia entomol. hungarica (Budapest) **25**: 335-348.

*Curimopsis vicentina* PAULUS, 1973: S-Alpen

*Curimopsis franzi* PAULUS, 1973: S-Tirol

*Curimopsis taurica* PAULUS, 1973: S-Turkey

*Curimopsis italica* ssp. *savoyensis* (PAULUS, 1973): France: Haute-Savoie

PAULUS H. F. (1973): Zur Systematik und Faunistik der westpaläarktischen Vertreter der Gattung *Curimopsis* (Col. Byrrhidae). — Senckenbergiana Biol. (Frankfurt) **54**: 353-367.

*Byrrhus* (s.str.) *ponticus* PAULUS, 1974: NO-Turkey: O-Pontus

*Byrrhus* (s.str.) *ponticus* ssp. *piluloformis* PAULUS, 1974: NO-Turkey: W-Pontus

*Byrrhus* (s.str.) *danieli* PAULUS, 1974: Armenien

PAULUS H. F. (1974): Studien zur Byrrhidenfauna Kleinasiens, mit Beschreibung von *Byrrhus ponticus* nov. spec. und *B. danieli* nov. spec. (Col.). — Ent. Ztschr. (Frankfurt) **84**: 213-222.

*Chrysosimplocaria* nov.gen. PAULUS, 1982: Himalaya

*Chrysosimplocaria nepalica* PAULUS, 1982: Nepal

*Morychus (Byrrhobolus) nepalensis*, PAULUS 1982: Nepal

PAULUS H. F. (1982): Zwei neue Byrrhidae (Coleoptera) aus Nepal und Sikkim: *Chrysosimplocaria nepalica* nov.gen. et nov. spec. und *Byrrhobolus nepalensis* nov. spec. — Ent. Ztschr. (Frankfurt) **92**: 319-326.

## **Elateridae, Cebrioninae**

*Escalerina serraticornis* PAULUS, 1972: S-Iran

Escalerini PAULUS, 1972. nov trib. (today Dascillidae)

Cydistinae PAULUS, 1972 new subfamily nov.

PAULUS H. F. (1972): Die systematische und phylogenetische Stellung der Karumiidae, mit einer Beschreibung von *Escalerina serraticornis* nov.spec. aus Südpersien (Col., Cantharoidea) — Senckenbergiana biol. (Frankfurt) 53: 37-54.

remark 1: *Paulusiella* MANDL, 1974: without a typ for genus and therefore invalid; later validated as: *Paulusiella* LÖBL, 2007

MANDL K. (1974): Eine neue Gattung, drei neue Arten und eine neue Unterart aus der Familie Karumiidae (Dascilloidea). — Verhandl. Naturforsch.ges. Basel **84**: 635-645. (= *Paulusiella serraticornis* (PAULUS, 1972): S-Iran)

remark 2: In the revision by KUSY D., MOTYKA M. & L. BOCAK (2023): Ontogenetic modifications produce similar phenotypes in distantly related click beetles (Coleoptera: Elateridae) - Insect Systematics and Diversity 7 (4) *Paulusiella* is treated as Elateridae, and there as a new subfamily Paulusiellinae nov.

*Cebriognathus iranicus*, PAULUS, 1981: S-Iran

*Cebriognathus arabicus* PAULUS, 1981: Saudi-Arabien

*Cebriognathinae* PAULUS, 1981 subfamily nov.

PAULUS H. F. (1981): Insects of Saudi Arabia. Coleoptera, Fam. Cebrionidae: *Cebriognathus persicus* nov.spec. und *C. arabicus* nov.spec., zwei neue Cebrionidae (*Cebriognathinae* nov. subfam.) aus dem mittleren Osten (Col., Elateroidea). — Fauna of Saudi Arabia (Basel), Bd. **3**: 257-265.

*Cebriognathus desertorum* CHOBAUT, 1899

remark: This taxon is synonymious with *Analestesa testacea* LEACH, 1824 (Monograph on the Cebrionidae, a family of insects. — Zool. Journal 1); for this with new names:

*Analestesa iranica* (PAULUS, 1981)

*Analestesa arabica* (PAULUS, 1981)



remark: In the revision by KUSY D., MOTYKA M. & L. BOČAK (2023): Ontogenetic modifications produce similar phenotypes in distantly related click beetles (Coleoptera: Elateridae) - Insect Systematics and Diversity 7 (4) *Analestesa* is assigned to the Cardiophorinae, Cebriognathini, as I already suspected in 1981, p. 264.

### **Phengodidae (Cantharoidea)**

*Penicillophorus* PAULUS, 1975 gen.nov.

*Penicillophorus ctenotarsus* PAULUS, 1975

*Penicillophorinae* PAULUS, 1975

PAULUS H. F. (1975): *Penicillophorus ctenotarsus* nov.gen. et nov. spec. aus Columbia mit einer Beschreibung einer neuen Tribus Penicilliphorini der Phengodidae (Col., Cantharoidea). — Z. Arbeitsgem. österr. Entomol.Wien **25**: 69-80.

### **Trogidae (Scarabaeoidea)**

*Trox dhaulagiri* PAULUS, 1972: Central-Nepal, Bobang, south of Dhorpatan

PAULUS H. F. (1972): *Trox dhaulagiri* nov. spec. (Col., Scarabaeidae) aus Nepal. — Senckenbergiana biol. (Frankfurt) **53**: 55-58.

### **Lucanidae**

*Platycerus pseudocaprea* PAULUS, 1971: SW-France

PAULUS H. F. (1970): Beschreibung einer neuen Lucanidae: *Platycerus pseudocaprea* nov. spec. (Col., Lamellicornia). — Ent. Ztschr. **80**: 113-116.

PAULUS H. F. (1974): *Platycerus pseudocaprea* PAULUS aus den Pyrenäen (Col., Lucanidae). — Ann.Naturhist. Wien **77**: 313-320.

### **Pyrochroidae, Ischaliidae**

*Neopyrhochroa nepalensis* PAULUS, 1972: Nepal

*Pseudohomalisus* PAULUS, 1972 subg.nov.

*Ischalia (Pseudohomalisus) nepalensis* PAULUS, 1972: Nepal

*Ischalia (Pseudohomalisus) martensi* PAULUS, 1972: Nepal

Anmerkung: *Pseudohomalisus* = synonymious with *Eupleurida* LÉCONTE, 1862 = *Ischalia (Eupleurida)*, Ischaliidae

Techmessinae PAULUS, 1972 (= Pilipalpinae ABDULLA, 1964)

PAULUS H. F. (1972): Neue Pyrochroidae aus Nepal (Col., Heteromera), mit einer Diskussion der verwandtschaftlichen Verhältnisse der Familie. — Z. Arbeitsgem. österr. Entomol. Wien **23** (1971): 75-85.

### **Lymexylidae**

*Urtea* PAULUS, 2004 gen.nov.

*Urtea graeca* PAULUS, 2004 spec.nov.: N-Greece

*Hymaloxylon aspoECKi* PAULUS, 2004: China: Yunnan China

PAULUS H. F. (2004): *Urtea graeca* nov.gen. et nov. spec., der erste Vertreter der tropischen Atractocerinae in Europa sowie eine Beschreibung von *Hymaloxylon aspoECKi* nov. spec. aus Yunnan (China) (Coleoptera, Cucujiformia, Lymexylidae, Atractocerinae nov. status). – In ASPÖCK U. (ed.): Entomologie und Parasitologie. Festschrift zum 65. Geburtstag von Horst Aspöck. Denisia (Linz) **13**: 277-290.

## LEPIDOPTERA

*Paralasa nepalica* PAULUS, 1983: N-Nepal

PAULUS H. F. (1983): *Paralasa nepalica* nov. spec., ein neuer Augenfalter aus Nepal (Lep., Satyridae, Erebiini) — Senckenbergiana biol. **63**: 337-46.

## CHELICERATA

*Euchelicerata* (=classis) WEYGOLDT & PAULUS, 1979

*Metastomata* (= subclassis) WEYGOLDT & PAULUS, 1979

WEYGOLDT P. & H. F. PAULUS (1979): Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. Teil II: Cladogramme und die Entfaltung der Chelicerata. — Z. zool. Systematik Evolutionsforsch. **17** (3): 177-200.

*Alopecosa thaleri* HEPNER & PAULUS, 2007: Gran Canaria

HEPNER M. & H. F. PAULUS (2007): *Alopecosa thaleri*, a new wolf spider from Gran Canaria (Araneae, Lycosidae). — Bull.Br. arachnol. Soc. **14** (1): 43-45.

## ORCHIDACEAE

### New species:

1. *Ophrys sitiaca* PAULUS, C. ALIBERTIS & A. ALIBERTIS 1988: Typus: Greece: O-Crete, Triphthialm  
PAULUS H. F. (1988a): Beobachtungen und Experimente zur Pseudokopulation auf *Ophrys*-Arten Cretes (II) mit einer Beschreibung von *Ophrys sitiaca* PAULUS & C. + A. ALIBERTIS nov. spec. aus dem *Ophrys fusca – omegaifera* – Formenkreis. — Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ. **20** (4): 817-882.
2. *Ophrys mesaritica* PAULUS, C. ALIBERTIS & A. ALIBERTIS 1990: Typus: Greece, S-Crete, Messara, Andiskari  
PAULUS H.F., C. & A. ALIBERTIS (1990): *Ophrys mesaritica* spec.nov. PAULUS, C. ALIBERTIS & A. ALIBERTIS aus Crete, eine neue Art aus dem *Ophrys fusca-iricolor*-Artenkreis (Orchidaceae). — Mittl. Bl. Arbeitskr. Heim. Orch. Baden-Württ. **22** (4): 772-787.
3. *Ophrys ariadnae* PAULUS 1994: Typus: Greece, O-Crete, Nikitianou (= *O. „albifrons-cretica“*):  
PAULUS H. F. (1994): Untersuchungen am *Ophrys cretica*-Komplex mit Beschreibung von *Ophrys ariadnae* spec.nov. (Orchidaceae). — Jour. Eur. Orch. **26** (3/4): 628-643.
4. *Ophrys elatior* (Gumprrecht in) PAULUS, 1996; Typus: SW-Deutschland, Istein:  
PAULUS H. F. (1996): Zur Bestäubungsbiologie und Artberechtigung von *Ophrys tetraloniae* TESCHNER 1987 und *Ophrys elatior* GUMPRECHT ex PAULUS spec.nov. (Orchidaceae). — Ber. Arbeitskr. Heim. Orchid. **13** (2): 4-13.
5. *O. cressa* PAULUS 1998: Typus: Greece, O-Crete; Thripti-Alm, 900 m,

6. *O. creberrima* PAULUS 1998: Typus: Greece, Crete, Marathos above Fodele 3.4.1985
7. *O. cretica* PAULUS 1998: Typus: Greece, O-Crete; foot of Jouchtas mountain north of Archanes
8. *O. thriptiensis* PAULUS 1998: Typus: Greece, O-Crete; Thripti-Alm, upper forest zone.
9. *O. blitopertha* PAULUS & GACK 1998: Typus: Greece, SO-Ägäis; SW-Turkey; Holotypus: Naxos, 7,5 km südl. Pirgos-Chimarou
10. *O. cinereophila* PAULUS & GACK 1998: eastmediterranean to S-Turkey; Typus: Greece, O-Crete, above Nikithianou near Neapolis  
PAULUS H. F. (1998): Der *Ophrys fusca* s.str. – Komplex auf Crete und anderer Ägäisinseln mit Beschreibungen von *O. blitopertha*, *O. creberrima*, *O. cinereophila*, *O. cressa*, *O. thriptiensis* und *O. cretica* spp.nov. (Orchidaceae). — Jour. Eur. Orch. **30** (1): 157-201
11. *Ophrys serotina* (ROLLI ex) PAULUS 2000: Typus: C-Italy (Latium), Monti Lepini, Monti sopra l'Annunziata di Carpineto verso Gorga.  
PAULUS H. F. (2000): Zur Bestäubungsbiologie einiger *Ophrys*-Arten Istriens (Kroatien) mit einer Beschreibung von *Ophrys serotina* ROLLI ex PAULUS spec.nov. aus der *Ophrys holoserica*-Artengruppe (Orchidaceae und Insecta, Apoidea). — Ber. Arbeitskrs. heim. Orchid. **17** (2): 4-33.
12. *Ophrys lyciensis* PAULUS, GÜGEL, RÜCKBRODT & RÜCKBRODT 2001: Typus: S-Turkey, Province Antalya, near Çirali.  
PAULUS H. F., GÜGEL E., RÜCKBRODT D. & U. RÜCKBRODT (2001): *Ophrys lyciensis* PAULUS & E. GÜGEL & D. RÜCKBRODT & U. RÜCKBRODT spec.nov., eine neue Art aus dem *Ophrys holoserica*-Artenkreis der S-Turkey (Orchidaceae). — Ber. Arbeitskrs. heim. Orchid. **18** (1): 19-33.
13. *Ophrys parvula* PAULUS 2001 : Typus : Greece, S-Rhodos, Prasonissi
14. *Ophrys persephona* PAULUS 2001 : Typus : Greece, Rhodos, near Epta Piges
15. *Ophrys lindia* PAULUS 2001 : Typus : Greece, S-Rhodos, Prasonissi
16. *Ophrys eptapigiensis* PAULUS 2001 : Typus : Greece, S-Rhodos, near Epta Piges
17. *Ophrys cornutula* PAULUS 2001 : Typus : Greece, S-Rhodos, Prasonissi
18. *Ophrys vernixia* subsp. *orientalis* PAULUS 2001 = *O. speculum* subsp. *orientalis* (PAULUS 2001) PAULUS & SALKOWSKI 2007: Typus: Greece, S-Thessalien, near Elassona  
PAULUS H. F. (2001): Daten zur Bestäubungsbiologie und Systematik der Gattung *Ophrys* in Rhodos (Greece) mit Beschreibung von *Ophrys parvula*, *Ophrys persephona*, *Ophrys lindia*, *Ophrys eptapigiensis* spp. nov. aus der *Ophrys fusca* s.str. Gruppe und *Ophrys cornutula* spec. nov. aus der *Ophrys oestrifera*-Gruppe (Orchidaceae und Insecta, Apoidea). — Ber. Arbeitskrs. Heim. Orchid. **18** (1): 38-86.
19. *Ophrys halia* PAULUS 2002: Typus: Greece, S-Rhodos, Plimiri  
PAULUS H. F. (2002): Daten zur Bestäubungsbiologie und Systematik der Gattung *Ophrys* in Rhodos (Greece) II. Über *Ophrys holoserica* s.lat.: *Ophrys episcopalis*, *Op. maxima* und *Ophrys halia* spec.nov. (Orchidaceae und Insecta, Apoidea). — Ber. Arbeitskrs. heim. Orchid. **18** (2): 46-63 (2001).
20. *Ophrys morio* PAULUS & KREUTZ 2002: Typus: S-Zypern, Malia

- PAULUS H. F. & K. KREUTZ (2004): *Ophrys morio* nov.spec. aus Zypern. — In: KREUTZ K., Die Orchideen von Zypern/The Orchids of Cyprus – Beschreibung, Ökologie, Verbreitung, Gefährdung, Schutz und Ikonographie. Verlag Kreutz Publishers, ISBN: 90-806626-3-1, 416 Seiten.
21. *Ophrys sabulosa* (PAULUS & GACK ex) DELFORGE 2004: Typus: Italy, N-Sizilien, Palermo, Altofonte.
22. *Ophrys fabrella* (PAULUS & AYASSE ex) DELFORGE 2004 : Typus : Spanien, Mallorca, nahe Réal.  
 DELFORGE P. (2004): Contribution à la clarification de la nomenclature dans la section *Pseudophrys* GODFERY 1928 (Orchidaceae). — Natural. Belges **85** (Orchid. 17): 110-124.
23. *Ophrys phaidra* PAULUS 2007 : Typus : Greece, Z-Crete, Kedros Berge, Spili-Gerakari
24. *Ophrys kedra* PAULUS 2007 : Typus : Greece, Z-Crete, Kedros Berge, Spili-Gerakari
25. *Ophrys pallidula* PAULUS 2007 : Typus : Greece, O-Crete, Tripti-Alm  
 PAULUS H. F. & P. SCHLÜTER (2007): Neues aus Crete und Rhodos: Bestäubungsbiologie und molekular-genetischen Trennung in der *Ophrys fusca* – Gruppe, mit Neubeschreibungen von *Ophrys phaidra* PAULUS nov.sp., *O. pallidula* PAULUS nov.sp. und *O. kedra* PAULUS nov.sp. aus Crete (Orchidaceae und Insecta, Apoidea) (News from Crete and Rhodes: Pollination biology and molecular-genetical separations in the *Ophrys fusca* group). – 13. Wuppertaler Orchideen-Tagung am 11. und 12. November 2006. — Jahresberichte des Naturwissenschaftlichen Vereins Wuppertal **60**: 101-151.
26. *Ophrys apollonae* PAULUS & HIRTH 2009: Typus: Greece, Rhodos, near Apollona;  
 PAULUS H. F. & M. HIRTH (2009): *Ophrys apollonae* spec. nov., eine neue Art der *Ophrys omegaifera*-Gruppe aus Rhodos, Samos und Chios. — J.Eur. Orch. **41** (3/4): 501-520.
27. *Ophrys saliarisii* PAULUS & HIRTH 2009 : Typus : Greece, Rhodos, Apollona  
 PAULUS. H. F. & M. HIRTH (2009): Über die Bestäubungsbiologie und Systematik der *Ophrys holoserica-episcopalis*-Gruppe: *Ophrys saliarisii* nov. spec. aus Chios und Rhodos (Orchidaceae und Insecta, Apoidea, Anthophoridae). — J. Eur. Orch. **41** (3/4): 663-680.
28. *Ophrys urteae* PAULUS 2009: Typus: S-Turkey, Taşağil, ne. Serik  
 PAULUS H. F. (2009): Bestäubungsbiologie einiger *Ophrys*-Arten der Süd-Turkey (Prov. Antalya) mit Beschreibung einer weiteren „Käfer-*fusca*“ *Ophrys urteae* spec.nov. (Orchidaceae und Coleoptera, Scarabaeidae). — Ber. Arbeitskrs. Heim. Orchid
29. *Ophrys malacitana* LOWE, PHILIPS & PAULUS 2010: Typus: S-Spanien, Malaga, Sierra Mijas, Pichon de Jarapalo  
 LOWE M. R., PHILLIPS I. & H. F. PAULUS (2010): *Ophrys malacitana* nov. spec. — In LOWE M. R. (2010): Studies in *Ophrys* L. section *Pseudophrys* GODFERY – I. *Ophrys forestieri* and *O. malacitana* spec.nov. — J. Eur. Orch. **42** (3/4): 541-562.
30. *Ophrys mycenensis* HERTEL & PAULUS 2010: Typus: S-Greece, Arkadien, Kosmas  
 HERTEL S. & H. F. PAULUS (2010): *Ophrys mycenensis* S. HERTEL & H.F. PAULUS, eine neue Art der *Ophrys oestriifera*-Gruppe in Greece. — J. Eur. Orch. **42** (3/4): 453-466.

31. *Ophrys olympiotissa* PAULUS 2011: Typus: M-Greece, Thessalien, Tsaritsani.  
 PAULUS H. F. (2011): Zur Bestäubungsbiologie einiger *Ophrys*-Arten in Nordthessalien mit Beschreibung von *Ophrys olympiotissa* aus der *Ophrys argolica – ferrum-equinum*-Gruppe (*Orchidaceae* und *Insecta, Apoidea*). — J. Eur. Orch. **43** (3): 498-526.
32. *Ophrys samiotissa* HIRTH & PAULUS, 2011: Typus: Greece, island of Samos, M. Timeo Stavrou  
 HIRTH M. & H. F. PAULUS (2011): *Ophrys samiotissa*, eine neue Art der *O. oestrifera-holosericea*-Gruppe aus Samos (*Orchidaceae*). — J. Eur. Orch. **43** (4): 863-873.
33. *Ophrys korae* PAULUS & HIRTH 2012: Typus: Greece, Rhodos, nördl. Faliraki  
 PAULUS H. F. & M. HIRTH (2012): Bestäubungsbiologie und Systematik der *Ophrys tenthredinifera*-Gruppe in der Ostägäis (*Orchidaceae* und *Insecta*). — J. Eur. Orch. **44** (3): 625-686.
34. *Ophrys penelopeae* PAULUS 2014 : Typus : Greece, S-Kefalonia, w. Argostoli
35. *Ophrys cephaloniensis* PAULUS 2014 ; Typus : Greece, Kefalonia, Mt. Rodi  
 PAULUS H. F. & M. HIRTH (2014): Zur Bestäubungsbiologie der Gattung *Ophrys* auf den Ionischen Inseln mit speziellen Bemerkungen zum Status von *O. punctulata-leucadica* sowie Beschreibungen von zwei neuen Arten aus der *O. lutea*- und *O. oestrifera*-Gruppe. — J. Eur. Orch. **46** (2): 233-304.
36. *Ophrys bilunulata* subsp. *kalirachiensis* PAULUS, HIRTH & DIMADIS 2016: Typus: N-Greece, Kalirachi near Grevena  
 PAULUS H. F. & M. HIRTH (2016): Eine neue *Ophrys fusca*-Sippe aus NordGreece: *Ophrys bilunulata* subsp. *kalirachiensis* PAULUS, HIRTH & DIMADIS subsp.nov. (*Orchidaceae* und *Insecta, Apoidea*). — J. Eur. Orch. **48** (1): 53-70.
37. *Ophrys istriensis* HERTEL, PAULUS & WEYLAND 2016: Typus: N-Croatia, Istria, near Bali  
 HERTEL S., PAULUS H. F. & H. WEYLAND (2016): *Ophrys istriensis* HERTEL, PAULUS & WEYLAND spec. nov. — Ber. Arbeitskr. Heim. Orchid. **33** (1) 78- 91.
38. *Ophrys lychnitis* HIRTH & PAULUS 2016; Typus: Greece, Island Paros, near old airport  
 HIRTH M. & H. F. PAULUS (2016): Neue Bestäuber-Beobachtungen in der *Ophrys tenthredinifera*-Artengruppe der Ägäis mit Beschreibung von *Ophrys lychnitis* aus Paros. — J. Eur. Orch. **48** (2-4): 346-388.
39. *Ophrys willingii* PAULUS & HIRTH 2017: Typus: N-Greece, Nomos Grevena, Pefkaki
40. *Ophrys prespaensis* HIRTH & PAULUS 2017; Typus: N-Greece, Prespasee, Psarades  
 PAULUS H. F. & M. HIRTH (2017): Bestäubungsbiologie und Systematik des *Ophrys mammosa*-Komplexes im östlichen Mittelmeerraum mit Neu-Beschreibungen von *Ophrys prespaensis* und *O. willingii* vom griechischen Festland. — J. Eur. Orchid. **49** (2): 219-312.
41. *Ophrys dimidiata* RAKOSY, PAULUS & HIRTH 2020 ; Typus : Greece, N-Crete, Jouchtas
42. *Ophrys eretriae* HIRTH & PAULUS 2020 ; Typus : Greece, Nomos Evia (Euböa), Ag. Lukas.

### New kombinations:

- Ophrys lusitanica* (O. & E. DANESCH 1969) PAULUS & GACK 1990 — Israel J. Botany 39: 77.  
= *O. vernixia* BROTERO 1804
- Ophrys heterochila* (RENZ & TAUBENHEIM 1980) PAULUS & GACK 1992 — Jahresber. Naturwiss. Ver. Wuppertal 43: 94.: syn. zu *heterochila* (RENZ & TAUBENHEIM 1980) DELFORGE 1991
- Ophrys parvimaculata* (O. & E. DANESCH 1975) PAULUS & GACK 1990
- Ophrys lucis* (KALTEISEN & REINHARD 1987) PAULUS & GACK 1990 — Israel J. Botany 39: 78.
- Ophrys cretensis* (BAUMANN & KÜNKELE 1986) PAULUS 1988 (= *sphegodes* subsp. *cretensis* BAUMANN & KÜNKELE 1986)
- Ophrys gortynia* (BAUMANN & KÜNKELE 1986) PAULUS 1988 (= *sphegodes* subsp. *gortynia* BAUMANN & KÜNKELE)
- Ophrys provincialis* (BAUMANN & KÜNKELE 1988) PAULUS 1988 (= *sphegodes* subsp. *provincialis* BAUMANN & KÜNKELE 1988, *sphegodes* subsp. *provincialis* NELSON 1962 nom. inval.)
- Ophrys melena* (RENZ 1928) PAULUS & GACK 1990 — Israel J. Botany 39: 79.: S-Greece
- Ophrys sicula* subsp. *galilaea* (FLEISCHMANN & BORNMÜLLER 1926) PAULUS & GACK 1990 — Jahresber. Naturwiss. Ver. Wuppertal 43: 106.
- Ophrys gracilis* (BÜEL, O. DANESCH & E. DANESCH 1972) PAULUS 1996
- Ophrys garganica* subsp. *passionis* (SENNEN ex DEVILLERS & DEVILLERS-TERSCHUREN 1994) PAULUS & GACK 1999
- Ophrys exaltata* subsp. *mateolana* (MEDAGLI et al. 1991) PAULUS & GACK 1999
- Ophrys pseudoscolopax* (MOGGRIDGE 1869) PAULUS & GACK 1999
- Ophrys spectabilis* (KREUTZ & ZELESNY 2007) PAULUS 2011
- Ophrys bilunulata* (RISSO 1844) subsp. *subfusca* (with *O. caesiella*, *O. africana*, *O. gazella* as synonyms): N-Afrika, Spanien, Portugal, SW-France, Balearen, SE-Sizilien
- Ophrys bilunulata* subsp. *punctulata* (RENZ 1928) PAULUS 2014: Ionische Inseln, S-Greece, Kythera
- Ophrys bilunulata* subsp. *sancti-isidorii* (SALIARIS, SALIARIS & ALIBERTIS 2010) PAULUS 2014: Karpathos, Rhodos, O-Ägäische Inseln, W-Turkey
- Ophrys forestieri* (REICHENB. fil. 1851) LOJACONO 1909 subsp. *laureotica* (KALOGEROPOULOS, DELIPETROU & ALIBERTIS 2011) PAULUS 2020 (p. 214)
- Neotinea aestivalis* (KÜMPEL 1988) PAULUS 2022

### Taxa named after Hannes Paulus

- Coleoptera, Cerambycidae: ***Phytoecia (Helladia) paulusi*** HOLZSCHUH, 1971: Libanon  
HOLZSCHUH C. (1971): Bemerkenswerte Käferkunde in Österreich. — Mitt. Forstl. Bundesversuchsanstalt Wien 94: 1-65.
- Coleoptera, Scarabaeidae: ***Tanyproctus paulusi*** PETROVITZ, 1980: Libanon

PETROVITZ R. (1980): Österreichisch-entomologische Expeditionen nach Persien und Afghanistan. Beiträge zur Coleopterenfauna. Teil XII. Weiteres über Lamellicornia aus Iran. – Anns. Naturhist. Museum Wien **83**: 597-638.

Coleoptera, Elateridae, Cebrioninae: genus ***Paulusiella*** (MANDL, 1974)

remark : LÖBL 2007 – MANDL K. (1974): Eine neue Gattung, drei neue Arten und eine neue Unterart aus, der Familie Karumiidae (Col., Dascilloidea). — Verh. Naturforsch. Ges. Basel **84**: 635-645. Genus name not available, as no genus type defined; this was only done by LÖBL I. (2007): Elateridae: Cebrioninae. New nomenclatorial and taxonomic acts, and comments. p.32; In: LÖBL I. & SMETANA A. (2007), Catalogue of Palaearctic Coleoptera, vol. 4. Apollo Books, Stenstrup.

Coleoptera, Byrrhidae: ***Microchaetes paulusi*** SOLERVICENS, 2016: Chile

JAIME SOLERVICENS A. (2016): Description of two new species of *Microchaetes*, *M. paulusi* nov. sp. and *M. araucanus* nov. sp. from Chile (Coleoptera, Byrrhidae, Syncalypinae). — Rev. Chilena Ent. **41**: 11-21

Araneae, Linyphiidae: ***Troglohyphantes paulusii*** K. THALER, 2002: N-Iran

THALER K. (2002): *Troglohyphantes paulusii* n.sp. (Araneae, Linyphiidae) from Iran. – Mitt. Schweiz. Entomol. Ges. **75**: 51-55.

## **Abridged version of the taxa list of newly described by Hannes Paulus:**

### **Chelicerata**

**Superklasse: Euchelicerata WEYGOLDT & PAULUS, 1979**

**Klasse Metastomata WEYGOLDT & PAULUS, 1979 (=Eurypterida+Arachnida)**

**Araneae: Lycosidae**

*Alopecosa thaleri* HEPNER & PAULUS, 2007: Gran Canaria

### **Coleoptera**

#### **Carabidae**

*Cychropsis mandli* PAULUS, 1971: Nepal

*Calosoma davidis* ssp. *martensi* PAULUS, 1971: Nepal

#### **Byrrhidae**

*Byrrhus* (s.str.) *chinensis* PAULUS, 1970: China

*Byrrhus* (s.str.) *ponticus* PAULUS, 1974: NEa: E-Pontus

*Byrrhus* (s.str.) *ponticus* ssp. *piluloformis* PAULUS, 1974: NE-Turkey: W-Pontus

*Byrrhus* (s.str.) *danieli* PAULUS, 1974: Armenien

*Asiatobyrrhus* (PAULUS, 1974): Himalaya

*Asiatobyrrhus tibetanus* (PAULUS, 1974): Thibet

*Asiatobyrrhus macrosetosus* (PAULUS, 1974): N-Pakistan

*Pedilophorus rhodopensis* PAULUS, 1972: Balkans

*Curimopsis magna* (PAULUS, 1971): N-India

*Curimopsis mongoliensis* PAULUS, 1970 : Mongolia

*Curimopsis obenbergeri* PAULUS, 1970 : East Siberia

*Curimopsis sibirica* PAULUS, 1970: East Siberia

*Curimopsis vicentina* PAULUS, 1973: S-Alps

*Curimopsis franzi* PAULUS, 1973: S-Tirol

*Curimopsis taurica* PAULUS, 1973: S.Turkey

*Curimopsis italica* ssp. *savoyensis* (PAULUS, 1973): France: Haute Savoie

*Chrysosimplocaria* PAULUS, 1982: Himalaya  
*Chrysosimplocaria nepalica* PAULUS, 1982: Nepal  
*Morychus (Byrrhobolus) nepalensis* PAULUS, 1982: Nepal

### **Elateridae, Cebrioninae**

*Paulusiella serraticornis* (PAULUS, 1972): S-Iran  
*Analestesa iranica* (PAULUS, 1981) (= *Cebriognathus iranicus* PAULUS, 1981): S-Iran  
*Analestesa arabica* (PAULUS, 1981) (= *Cebriognathus arabicus* PAULUS, 1981): Saudi-Arabia. Notice: name of the genus *Cebriognathus* is a synonym of *Analestesa*.

### **Cebriognathinae PAULUS, 1981**

#### **Phengodidae**

*Penicillophorus* PAULUS, 1975: N-Columbia  
*Penicillophorus ctenotarsus* PAULUS, 1975: N-Columbia

#### **Penicillophorini PAULUS, 1975**

#### **Cydistinae PAULUS, 1975**

#### **Scarabaeoidea**

#### **Trogidae**

*Trox dhaulagiri* PAULUS, 1972: Nepal

#### **Lucanidae**

*Platycerus pseudocaprea* PAULUS, 1971: Pyrenée

#### **Pyrochroidae/Ischaliidae**

#### **Techmessinae PAULUS, 1971**

*Ischalia (Pseudohomalisus* nov.sg.= *Eupleurida* LÉCONTE, 1862) *nepalensis* PAULUS, 1972: Nepal  
*Ischalia (Pseudohomalisus*=*Eupleurida*) *martensi* (PAULUS, 1972): Nepal  
Anmerkung: *Pseudohomalisus* was not found to be synonymous with the North American genus *Eupleurida* LÉCONTE, 1862 until 36 years later (GUSAKOV & TELNOV 2007: *Folia Heyrovskyana* **15** (1): 39-46).  
*Neopyrchochroa nepalensis* PAULUS, 1972: Nepal

#### **Chelonariidae**

*Pseudochelonarium kalimantanense* PAULUS, 1969: Borneo

#### **Lymexylidae**

*Urtea* nov.gen. PAULUS, 2004: N-Greece  
*Urtea graeca* PAULUS, 2004: N-Greece, Chalkidiki  
*Hymaloxylon aspoecki* PAULUS, 2004: China: Yunnan

#### **Lepidoptera: Nymphalidae, Erebiinae**

*Paralasa nepalica* PAULUS, 1983: N-Nepal

#### **Orchidaceae, genus *Ophrys*:**

*Ophrys apollonae* PAULUS & HIRTH: Greece: Rhodos, Samos, Chios  
*Ophrys ariadnae* PAULUS: Greece: Crete, Karpathos, Paros, Naxos, Psara  
*Ophrys blitopertha* PAULUS & GACK: Greece: eastern Ägäis  
*Ophrys cephaloniensis* PAULUS 2014: Greece: Kefalonia



*Ophrys cinereophila* PAULUS & GACK: Greece: eastern Mediterranean area  
*Ophrys cornutula* PAULUS: Greece: S-Rhodos  
*Ophrys creberrima* PAULUS: Greece: Crete  
*Ophrys cressa* PAULUS: Greece: E-Crete  
*Ophrys cretica* PAULUS: Greece: Crete  
*Ophrys elatior* (GUMPRECHT in) PAULUS: Greece, SW-Germany, W-France, SW-Svizzera  
*Ophrys eptapigiensis* PAULUS: Greece: Rhodos  
*Ophrys fabrella* (PAULUS & M. AYASSE ex) DELFORGE: Spain: Balearic Islands  
*Ophrys halia* PAULUS: Greece: Rhodos  
*Ophrys korae* HIRTH & PAULUS: Greece: Rhodos, Samos  
*Ophrys kedra* PAULUS: Greece: Crete, Kythira  
*Ophrys lindia* PAULUS: Greece: Rhodos, W-Turkey  
*Ophrys mesaritica* PAULUS & C. ALIBERTIS & A. ALIBERTIS: Greece: Crete, Kythira, Ionian Islands  
*Ophrys morio* PAULUS & KREUTZ: Cyprus  
*Ophrys mycenensis* HERTEL & PAULUS: S-Greece  
*Ophrys olympiotissa* PAULUS: NO-Greece  
*Ophrys pallidula* PAULUS: Greece: Crete  
*Ophrys parvula* PAULUS: Greece: Rhodos, Kos, Heraklia  
*Ophrys penelopeae* PAULUS 2014: Greece: Kefalonia  
*Ophrys persephona* PAULUS: Greece: Rhodos  
*Ophrys phaidra* PAULUS: Greece: Crete  
*Ophrys reinhardiorum* PAULUS (M-Greece)  
*Ophrys sabulosa* (PAULUS & GACK ex) DELFORGE: Italy: Sicily  
*Ophrys saliarisi* PAULUS & HIRTH: Greece: Rhodos, Chios  
*Ophrys samiotissa* HIRTH & PAULUS: Greece: Samos  
*Ophrys serotina* (ROLLI ex) PAULUS: M-Italien  
*Ophrys sitiaca* PAULUS, C. ALIBERTIS & A. ALIBERTIS: Greece: Crete, Karpathos, Rhodos, eastern Ägäis Islands, W-Turkey  
*Ophrys speculum* subsp. *orientalis* (PAULUS) PAULUS & SALKOWSKI 2007 : eastern Mediterranean area  
*Ophrys thriptiensis* PAULUS: Greece: Crete  
*Ophrys urteae* PAULUS: S-Turkey  
*Ophrys bilunulata* subsp. *kalirachiensis* PAULUS, HIRTH & DIMADIS, 2016: N-Greece  
*Ophrys istriensis* HERTEL, PAULUS & WEYLAND, 2016: Croatia: Istria  
*Ophrys lychnitis* HIRTH & PAULUS, 2016: Greece: Paros  
*Ophrys willingii* PAULUS & HIRTH, 2017: Greece: mainland  
*Ophrys prespaensis* HIRTH & PAULUS, 2017: N-Greece  
*Ophrys dimidiata* RAKOSY, PAULUS & HIRTH, 2020: Greece: Crete  
*Ophrys eretriae* HIRTH & PAULUS, 2020: Island: Euböa

## Lists of publications

### 1. General

- PAULUS H.F. (1966): Unser Insektenkabinett. — Z. Rhein. Naturf. Ges. Mainz **4**: 85-87.  
 PAULUS H.F. (1971): Ein durch Metathelie hervorgerufener Atavismus bei der Larve von *Mesosa curculionoides* (Col., Cerambycidae). — Zool. Anz. **186**: 217-221.  
 PAULUS H.F. (1973): Entwicklung des Individuums und Evolution. Individuum und Art im Tier- und Pflanzenreich. — Funkkolleg Biologie. – Systeme des Lebendigen Bd. **II** (4): 107-146. (Beltz Verl. Weinheim)  
 PAULUS H.F. (1976): Derselbe Titel, gekürzte Rundfunkfassung. — In: Funk-Kolleg Biologie Bd. 1, Fischer Taschenbuch Nr. 6291 (Taschentext 49), p. 67-94.  
 PAULUS H.F. (1974): Erster Nachweis von Scolopalorganen in den Gliederantennen eines entognathen Insektes (Collembola). — Z. Morphol. Tiere **77**: 245-254.  
 PAULUS H.F. (1975): Übersetzung aus dem Englischen des Buches: FOGDEN, Michael: Farbe und Verhalten im Tierreich. — Freiburg im Breisgau, Basel, Wien: Herder. 168 S. – ISBN 3-451-17361-1 Pp.



**Fig. 81:** German edition of the book by M. & P. Fogden (1971): *Animals and their colors*, translated from the English by Hannes F. Paulus (1975).

- PAULUS H.F. (1978): *Einheit und Vielfalt der Lebewesen* — Studienbriefe für Biologielehrer, Block C, Studienbrief 4. Deutsches Inst. Fernstudien Tübingen, 51 Seiten. Beltz Verl. Weinheim.
- PAULUS H.F. (1978): *Methoden der Systematik* — Studienbriefe für Biologielehrer, Block C, Brief 5. — Deutsches Inst. f. Fernstudien, Tübingen, 51 S. Beltz Verl. Weinheim.
- PAULUS H.F. (1980): *Evolution* — Biologische Grundlagen der Psychologie, Kap. 4. Versuch f. das Fernstudium im Medienverbund, Studiengang Psychologie. — Deutsches Inst. f. Fernstudien Tübingen (DIFF), 24 Seiten.
- PAULUS H.F. (1980): *Ethologie* — Biologische Grundlagen der Psychologie, Kap. 7, Versuch f. das Fernstudium im Medienverbund, Studiengang Psychologie. — Deutsches Inst. f. Fernstudien Tübingen (DIFF), 34 Seiten.
- PAULUS H.F. (1983-1987): *Herder Lexikon Biologie*, 8 Bände, Herder Verl. Freiburg. Bearbeitung der Stichwortkomplexe Morphologie der Arthropoda, Morphologie der Insekten, Biologie und Systematik der apterygoten Insekten und Käfer.
- PAULUS H.F. (1988): *Bořek Tkalců zum 60. Geburtstag*. — *Entomol. Ztschr.* **98** (6): 76-80. (Frankfurt).
- PAULUS H.F. (1988): *Festkolloquium und Symposium "Praeadaptation in der Evolution von Pflanze und Tier" zum 60. Geburtstag von Prof. Dr. Günther Osche*. — *Z. zool. Syst. Evol. forsch.* **26**: 317-319.
- PAULUS H.F. & R. ALBERT (1997) (ed.): *Ökologische Risikoabschätzung von Freisetzungen gentechnisch veränderter Organismen für die spezielle Situation in Österreich*. — Studie im Auftrag des Bundesministeriums für Gesundheit; erstellt von PASCHER K. & GOLLMANN, G., Universität Wien; *Forschungsberichte Bundeskanzleramt Sektion I*, **4/97**, 136 Seiten.
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## 6. Publikations on *Ophrys*

### 6.1. Scent communication

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<sup>191</sup> Pollinations of *Ophrys speculum*, *O. sicula*, *O. morisii*, *O. zonata*, *O. chestermanii*, *O. normanii*.

<sup>192</sup> Pollinations of *Ophrys speculum*, *O. bilunulata*, *O. balearica*, *O. dyris*.



**Abb. 82:** (left) David Thompson (from Oxford Scientific Films) made the first *Ophrys* pollination film with me in Marbella (southern Spain) in 1979. (right) Tim Shepherd (BBC Bristol) was one of the most important cameramen in the production of David Attenborough's films, including the *Ophrys* pollination films in Sardinia and Mallorca.

## 7. publications on pollination biology (without *Ophrys*)

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- PAULUS H.F. (1987): Blüten animieren ihre Bestäuber. Aus der Trickkiste der Natur. — Naturmagazin draußen Nr. **49**: Oberrhein, Kaiserstuhl: 46-57.
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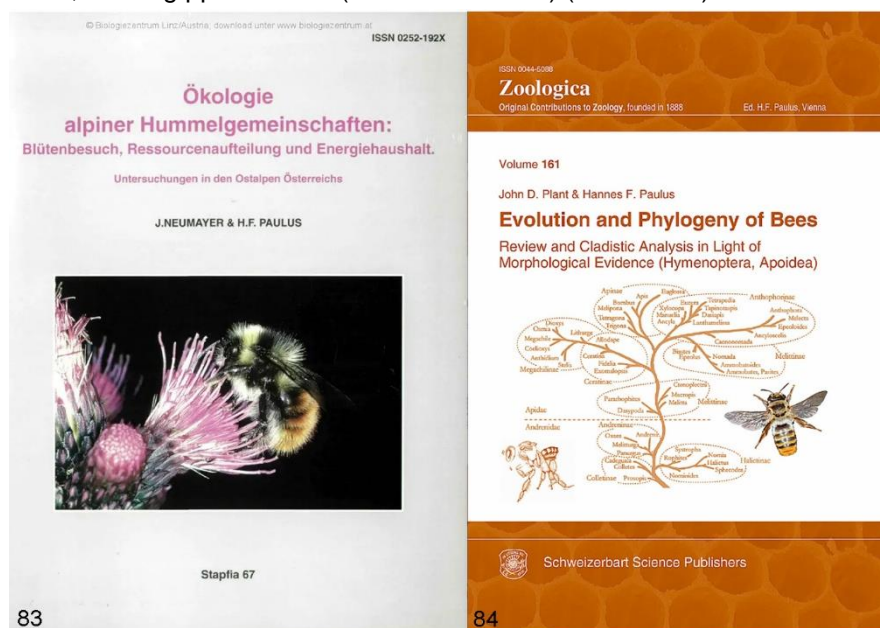
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## 9. books

- PAULUS H.F. (1983-1987): Herder Lexikon Biologie, 8 Bände, Herder Verl. Freiburg. Bearbeitung der Stichwortkomplexe Morphologie der Arthropoda, Morphologie der Insekten, Biologie und Systematik der apterygoten Insekten und Käfer.
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**Fig. 83:** Cover of our book “Ökologie alpiner Hummelgemeinschaften” (Ecology of alpine bumblebee communities) by Johann Neumeyer and Hannes F. Paulus.

**Fig. 84:** Cover of the book “Evolution and phylogeny of bees” by John D. Plant and Hannes F. Paulus.

- GLAESER G. & H.F. PAULUS (2013): Die Evolution des Auges – Ein Fotoshooting. — Springer-Spektrum Verlag, Berlin-Heidelberg, 214 S.
- GLAESER G. & H.F. PAULUS (2015): Evolution of the eye. — Springer-Spektrum Verlag, Berlin-Heidelberg, 214 S.; 2021: *chinesische Ausgabe*.
- PLANT J.D. & H.F. PAULUS (2016): Evolution and Phylogeny of Bees. Review and Cladistic Analysis in Light of Morphological Evidence (Hymenoptera, Apoidea). 364 pages, 232 figures, 49 tables. PAULUS H.F. (ed.) [Zoologica](#), vol. **161**; Schweizerbarth Verlag Stuttgart, ISBN 978-3-510-55048-7.

**Abb. 85-86: (85)** Books by Hannes Paulus (text author) together with Georg Glaeser (photographer) and Werner Nachtigall (text author) in German, English and Chinese. (86) Group photo on the GLAESER G., PAULUS H.F. & W. NACHTIGALL (2017): *Die Evolution des Fliegens – Ein Fotoshooting*. — Springer Verlag, 248 Seiten.

GLAESER G., PAULUS H.F. & W. NACHTIGALL (2017): *The Evolution of Flight*. — Springer Verlag, 248 pages.; 2021: *chinesische Ausgabe*.

**10. editions of monographs and books**

PAULUS H.F. (edit) (2011): Hans Klaus PFAU: *Functional Morphology and Evolution of the Male Secondary Copulatory Apparatus of the Anisoptera (Insecta: Odonata)*. — *Zoologica* **156**, 103 S., 65 figs.

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**Fig. 85:** Books by Hannes Paulus (text author) together with Georg Glaeser (photographer) and Werner Nachtigall (text author) in German, English and Chinese.



**Fig. 86:** 10 volumes of the journal for monographs “Zoologica”, edited by Hannes Paulus.

- PAULUS H.F. (edit) (2016): Frantisek GREGOR; Rudolf ROZKOSNY; Miroslav BARTAK; Jaromir VANHARA: Manual of Central European Muscidae (Diptera), Morphology, taxonomy, identification and distribution. — *Zoologica* **162**, 219 S., 54 Tafeln.
- PAULUS H.F. (edit) (2016): John D. PLANT & Hannes F. PAULUS: Evolution and Phylogeny of Bees. Review and Cladistic Analysis in Light of Morphological Evidence (Hymenoptera, Apoidea). — *Zoologica*, Heft **161**, 364 S., 232 figs, 49 tables,
- PAULUS H.F. (edit) (2018): Thomas BROCKHAUS: Die Eiszeitlibellen der Alten Welt. Pleistozäne Biogeographie paläarktischer Libellen. — *Zoologica* **163**, 145 S., 106 Abb. 18 Tabellen.
- PAULUS H.F. (edit) (2019): BÜSCHER T.H., GROHMANN C., BRADLER S. & S. N. GORB: Tarsal attachment pads in Phasmatodea (Hexapoda: Insecta). — *Zoologica* **164**, 94 S., 49 Abb.
- PAULUS H.F. (edit.) (2020): Prince Tarique ANWAR; Shahid Bin ZEYA; Kamalanathan VEENAKUMARI: Fairyfly genus *Camptoptera* FOERSTER (Hymenoptera: Chalcidoidea: Mymaridae) in India and Sri Lanka, with descriptions of eleven new species, 89 pages, 241 figures. — *Zoologica*, Heft **165**, ISBN 978-3-510-55052-4.

### Acting as a reviewer for international journals:

Animal Behaviour, Apidologie, Behavioral Ecology and Sociobiology, Entomologia Experimentalis et Applicata, Ethology, Evolution, Frontiers in Zoology, Insect Science, Insectes Sociaux, International Journal of Ecology, Journal of Comparative Physiology A, Journal of Experimental Biology, Journal of Insect Physiology, Nature, Naturwissenschaften, Plant Systematics Evolution, Plos One, Proceedings of the Royal Society B, Entomologia Generalis

### Memberships of scientific associations:

- Arbeitsgemeinschaft österreichischer Entomologen
- Arbeitskreis heimische Orchideen Baden-Württemberg
- Arbeitskreis heimische Orchideen Hessen
- Deutsche Zoologische Gesellschaft (DZG) (von 1969-2009)
- European Association of Coleopterology (Barcelona)



European Society of Evolutionary Biology

Gesellschaft für Biologische Systematik (GfBS)

Gesellschaft für Ökologie (GfÖ)

Internationaler Entomologischer Verein (Frankfurt) (seit 1961)

NOBIS (Network of Biological Systematics Austria)

Österreichische Entomologische Gesellschaft (ÖEG),

Österreichische Gesellschaft für Entomofaunistik (ÖGEF)

Österreichische Zoologisch-Botanische Gesellschaft (ZooBot)

Rheinische Naturforschende Gesellschaft Mainz

Société Française d'Orchidophilie (SFO) (Paris)

The Coleopterists Society (USA)

Wiener Coleopterologenverein (WCV)

Mitglied es „Wildbienen-Rates Österreichs“ ("Austrian Wild Bee Council")



**Fig. 87:** Group photo on the occasion of the Austrian Entomological Society (ÖEG) conference in Salzburg on 17.3.2018. In the center with blue checked shirt Hannes Paulus, to the right the couple Horst and Ulrike Aspöck. Photo: C. Komposch.



Fig. 88: ÖEG Colloquium 1.3.2008, University of Natural Resources and Life Sciences, Vienna. Participants at the ÖEG board meeting (Photo: Fritz Gusenleitner).



Fig. 89: General Assembly of the "Austrian Wild Bee Council" in Linz on 5.11.2021. Hannes Paulus in the middle.

### Further literature cited

RENKER C. & B. HENRICH (2009): Die entomologischen Sammlungen des Naturhistorischen Museums Mainz/Landessammlung für Naturkunde Rheinland-Pfalz. – Mainz. Naturwiss. Archiv **47**: 395-447.

## Some additional photos



**Fig. 90:** The American botanist Tod Stuessy came to Vienna in 1997 to succeed Prof. F. Ehrendorfer as full professor of the Department of Systematics and Evolutionary Botany. My family are friends with him and his family. Here on 4.4.1998, a first excursion to the Eichkogel near Mödling (Photo: Urte Paulus).

**Fig.91:** Private meeting at our home in Vienna on the occasion of my 60th birthday on October 17, 2003. Pictured from left to right: Hannes Paulus, Paty Stuessy (= Patricia Antonietta Ghivarello), Tod Stuessy, Urte Paulus and my doctoral student at the time, John Plant. Tod Stuessy retired in 2012 and went back to the USA: Columbus, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, where he continues to work in the herbarium.



**Fig. 92:** Urte and Hannes Paulus together with Bernhard and Wilma Hassenstein on February 3, 2009 on the occasion of the funeral service of Prof. Dr. G. Günther Osche in Freiburg.

**Fig. 93:** Hannes Paulus, Michael Schmitt and Klaus Hemann (all from Freiburg); in the background Ursula Hannappel. Meeting of the SW-German Beetle Friends in Beutelsbach 1987.



**Fig. 94:** A meeting of some of his former colleagues took place in Freiburg on October 5, 2019 on the occasion of the 10th anniversary of Prof. Günther Osche's death. Some of the names of the participants are shown in the picture. Mrs. Prof. Dr. Ottilie Willmanns (right) died on 29. Oktober 2023 in Freiburg.



**Fig. 95:** Some of my excursions took me to different islands of the Canary Islands. 5.2.2004 Lanzarote, SW Haria 650 m (Photo: Urte Paulus).

**Fig.96:** Maria, Hannes and Urte Paulus, excursion to Borneo Sabah in Danum Valley 11.9.2015. In this national park there are walkways running through the canopy.



**Fig. 98:** Univ.-Prof. Dr. Heinrich Römer (University of Graz) and Univ.-Prof. Dr. Hannes F. Paulus, ÖEG conference in March 2011; meeting at the University of Graz (Photo: Fritz Gusenleitner).

**Fig. 99:** Hannes Paulus and Erwin Scheuchl (Ergolding/Bavaria), Entomologist Conference Linz, November 2017. Erwin Scheuchl is one of the few experts on the bee genus *Andrena* (Photo: Fritz Gusenleitner).



**Fig. 101 (left):** Bärbel Pachinger, Karl Mazzucco, Hannes Paulus, Meeting of wild bee people and entomologist conference Linz, November 2017 (Photo: Fritz Gusenleitner).

**Fig. 102 (right):** Erwin Scheuchl (Ergolding/Bavaria) (left) is a specialist for the wild bee genus *Andrena*, Stephan Risch (Leverkusen) specializes in the long-horned bee genera *Eucera* and *Tetralonia*. Both have done valuable identification work for my pollinator findings. (Photo: H. Paulus).



**Fig. 100:** On the occasion of the expert discussion "Insects and Climate Change" of the ÖEG at the "Wasser Cluster Lunz" - Biological Station, an excursion took place nearby on October 14, 2012. 1= Prof. Dr. Reinhard Schuster (Graz) (†2023), 2= Peter Vogtenhuber (Linz), 3= Prof. Dr. Hannes Paulus (Vienna), 4= Renate Rausch (Scheibbs), 5= Prof. Dr. Ulrike Aspöck (Vienna), 6= Prof. Dr. Horst Aspöck (Vienna), 7= Julia Hüttinger (Purgstall), 8= Peter Horak (†2015), 9= unknown, 10= Hubert Rausch (Scheibbs), 11= Ernst Hüttinger (Purgstall).



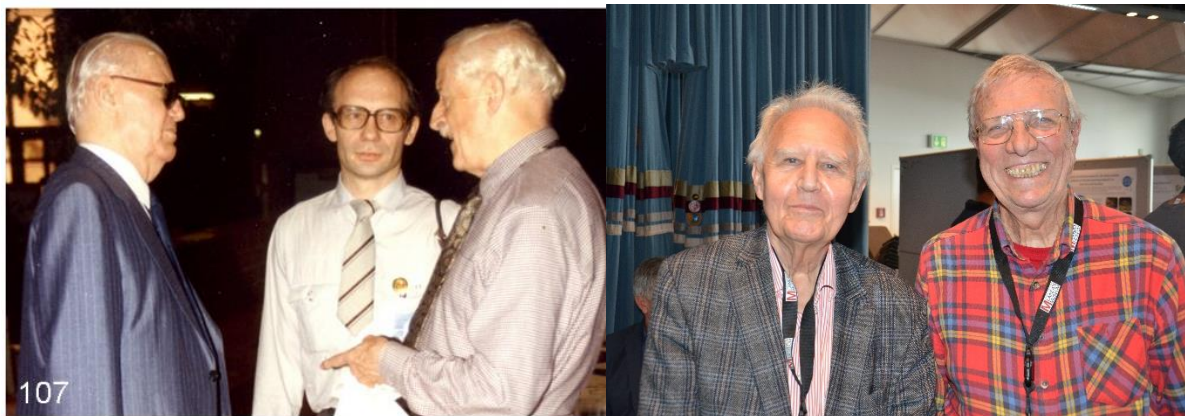
**Fig. 103:** Hannes Paulus and Dr. Ivan Löbl (Honorary Curator at the Muséum d'Histoire Naturelle of the City of Geneva, Switzerland). Ivan Löbl is one of the leading specialists in the beetle family Staphylinidae. Photo taken in Linz during the Entomologists' Conference, November 2016. In the background on the left: Prof. Dr. Horst Aspöck, on the right Father Andreas Werner Ebmer (specialist of the bee genera *Halictus* and *Lasioglossum*) (Photo: F. Gusenleitner).

**Fig. 104:** Prof. Dr. Hannes Paulus and Dr. Joachim Ziegler (Museum für Naturkunde Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin), SIEEC conference in Bolzano, September 2013. J. Ziegler is a specialist in the Diptera family Tachinidae (Photo: Fritz Gusenleitner).



**Fig.105 (left):** Prof. Dr. Holger H. Dathe (Berlin) and Prof. Dr. Hannes Paulus (Vienna), SIEEC meeting in Bolzano, September 2013 (Photo: Fritz Gusenleitner).

**Fig. 106 (right):** Follow-up session at Café Bellaria in Vienna on 21.3.2019 of the lecture by Prof. Dr. Susanne S. Renner (Prof. em., former Chair of Systematic Botany at the Ludwig-Maximilians-University Munich).



**Fig. 107 (left):** Renaud Paulian (Bordaux), Alexander Kirejshuk (St. Petersburg) and Roy Crowson (Glasgow), 1st Coleopterological Congress Barcelona 1989 (Foto: H. Paulus).

**Fig. 108 (right):** Horst Aspöck and Hannes Paulus (Entomologist Conference Linz, November 2022). Photo Fritz Gusenleitner

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