Obituary for Prof. Dr. h.c. mult. PAUL MÜLLER (1940–2010)

On May 30, 2010, Prof. Paul Müller passed away at his home in the northern Saarland, Germany. His premature death at the age of only 69 was preceded by a sudden heart attack when he was busy reorganizing the hunting gear he had used the night before. He leaves his wife Elke and four adult children. Owing to the difficulty to review Paul Müller's overwhelming scientific work and his innumerable contributions to biogeography in general, we concentrate here on his herpetological oeuvre.

Paul Müller was born on the 11th of October 1940 in Gersweiler, Saarland. When he was just about 12 years old, he looked for some butterflies in his grandmother's garden. She asked him whether catching flies might be a serious profession nowadays, and PAUL simply answered: "Yes, for sure". This childhood passion continued throughout his youth, encompassing all groups of animals and resulted in several unpublished notes, such as a work on the vertebrate fauna of the surroundings of the city of Saarbrücken from 1958. His passion for biology turned professional when he started studying zoology, palaeontology, biochemistry and geography at the University of Saarbrücken. One of the first academic teachers of Paul Müller was Gustav de Lattin, who was Professor of Zoology at the University of the Saarland at that time and who soon recognized the enormous talent of his young student. The latter finished his studies before completing the age of 24 with a synoptic work on the vertebrate fauna of a dry grassland area called Bliesgau (southeastern Saarland), which had been granted the status of a nature reserve shortly before. Because of his ability to push things straight forward and resolve problems in an unconventional manner, PAUL MÜLLER, although still being a student, was chosen by Gustav de Lattin to tackle the very responsible task of a zoological field trip to South Amer-



Figure 1. The student PAUL MÜLLER with an *Epicrates cenchria cenchria* during his first journey to Brazil in 1964 (federal state of Amazonas).

ica, for which his supervisor had secured a grant of about 10.000 Deutsch Marks (around 5000 € today).

Accompanied by the envy of some PhD students, PAUL MÜLLER started his first journey to Brazil in autumn of 1964, by ship from Le Havre (France) to Santos (Brazil). The objective of this expedition was to gain as much information as possible on the vertebrate and butterfly fauna of all of Brazil to increase the knowledge about this "megadiverse country" and infer general patterns of Neotropical biogeography. By 1970, PAUL MÜLLER had visited most of Brazil's landscape types and brought together a huge collection of amphibians, reptiles, birds, mammals and butterflies, including more than 7000 herpetological specimens and a comparably large number of representatives of the other animal groups. When he came back from this first journey, he brought his diverse collection of amphibians and reptiles to the herpetological section of the Natural History Museum Senckenberg (Frankfurt am Main) in order to compare it with the holdings stored there. He was attended by the famous herpetologist, Professor Robert Mertens, who had just retired, but was still very active. After a brief survey of the amphibian and reptile collection the young student PAUL MÜLLER had brought back from South America, Mertens put his finger on a small turtle and said: "I will need this!" MERTENS had immediately recognized the specimen as the red side-necked turtle *Phrynops rufipes*, a species considered to be extinct, as it had not been seen in nature for about 100 years. MÜLLER published this record in one of his first papers in 1966 (see Appendix) and liked to talk about the trivial circumstances of that important encounter because he made it just by chance, viz. when taking a bath in a pond in the rainforest reserve "Reserva Adolpho Ducke" near Manaus, Amazonia. Encouraged by results like this one, Müller continued his studies on the Neotropical herpetofauna in the following years, concentrating on differentiation processes of amphibians and reptiles on the islands within the 100 m-isobath off the Brazilian east coast, such as the island of Florianópolis (Santa Catarina), Campeche, or Buzios (both São Paulo). His thorough biogeographical studies on the island of São Sebastião (off the coast of the state of São Paulo) resulted in his PhD thesis finished by 1966 and published in 1968 ("The herpetofauna of the island of São Sebastião, Brazil"). The studies of island populations of the southeastern and southern Brazilian herpetofauna were a focus of PAUL MÜLLER'S earlier trips in the mid-60s (besides the Amazon region) and led to his biogeographically important publication "Vertebrate faunas of Brazilian islands as indicators of glacial and postglacial vegetational shifts" (MÜLLER 1970). His excellent field skills resulted in a large number of new distribution records for the islands mentioned above, such as the following 14 for the island of São Sebastião (names according to recent taxonomy): Ischnocnema lactea, I. guentheri (Brachycephalidae), Hylodes asper (Hylodidae), Hypsiboas albopunctatus, H. albomarginatus, Dendropsophus minutus, D. seniculus (Hylidae), Enyalius iheringi (Iguanidae), Spilotes pullatus anomalepis, Echinanthera cyanopleura, Liophis miliaris, Taeniophallus poecilopogon, Oxyrhopus doliatus, Dipsas albifrons (Colubridae). His studies on the island of Florianópolis yielded the first record of the ophiophagous snake species Clelia plumbea from this island, and the find of the slender colubrid snake Uromacerina ricardinii there turned out to be the first record of that species for the state of Santa Catarina. Another startling discovery was the record of a dried individual of a turtle, which he found in a souvenir shop in the port city of São

Sebastião that he identified as *Hydromedusa maximiliani* (Chelidae), which had been considered extinct on the island.

One of the most important results of PAUL MÜLLER'S studies, not only in the Neotropical realm but also in Europe, was that he found evidence for a much younger age of most differentiation processes than previously assumed by the majority of authors, which has been controversially discussed until today. He was convinced that many subspeciation or even speciation processes of vertebrates would not date as far back as to the Pleistocene, but should have begun or at least strongly been influenced by postglacial range shifts following repeated climatic oscillations within the last 10,000 years. These rather recent subspeciation processes led PAUL MÜLLER to describe several island subspecies of amphibians and reptiles: Tupinambis teguixin buziosensis MÜLLER, 1969, Tupinambis teguixin sebastiani MÜLLER, 1968, and Leptodactylus gracilis delattini Müller, 1968, the last being named in honour of his supervisor (MÜLLER 1968) and confirmed with regard to its validity by a subsequent researcher in 2004. For several other amphibian and reptile species, PAUL MÜLLER described slight morphological differences of island populations, e.g., the absence of a loreal scale in island populations of Clelia clelia plumbea from Florianópolis, or the striking differences in the colouration of individuals of Bothrops jararaca from the islands of Buzios and São Sebastião as compared to populations from the adjacent mainland, so that they rather resembled Bothrops insularis. However, PAUL MÜLLER did not describe all these weakly differentiated forms as new subspecies or even species as was common practice by some taxonomists, but used them mainly as "windows", facilitating expanded views into the biogeographical history of the respective islands. From 1965 onwards, PAUL MÜLLER was often accompanied to Brazil by his wife ELKE and for a longer time also by a "loyal" animal partner, a young honey bear (Potos flavus) named "Chico", who later became a housemate in PAUL MÜLLER'S home in Saarbrücken. Elke and Paul Müller loved to tell the story of Reverend Mauermann, a Jesuit priest whose hospitality they enjoyed during their stay at the island of São Sebastião: this friendly cleric seemed to be privileged by some kind of "divine protection" as he used to keep several venomous snakes in his house, such as the abundant pitviper Bothrops jararaca, in simple (open!) boxes under his bed! He treated them almost as pets and frequently handled them when praying, but was never struck by one of them.

During his research in Brazil, PAUL MÜLLER had the opportunity to meet important herpetologists such as, for example, PAULO EMILIO VANZOLINI from the Zoological Museum of the University of São Paulo, Afrânio do Amaral, the former director of the Instituto Butantan, ALPHONSO RICHARD HOGE, chairman of the herpetological collection of Butantan at that time, and THALES DE LEMA (Porto Alegre, Rio Grande do Sul). He spent time studying the most important herpetological Brazilian collections, such as the Museu Goeldi in Belém (Pará), the National Museum of Natural History in Rio de Janeiro, and the famous Instituto Butantan in São Paulo, where he collected meristic data of a large number of snake, lizard and frog specimens to obtain an overview of the morphological variability of the species he had collected in the field. It was also in São Paulo where PAUL MÜLLER first became acquainted with PAULO SAWAYA, director of the Institute of Physiology at the time, who then became a very good friend and to some degree even his "Brazilian supervisor".

PAUL MÜLLER'S work in Brazil (and basically worldwide) was influenced by the fundamental ideas of his supervisor Gustav De Lattin who had analysed dispersal centres of butterflies in the Palaearctic region. The basic ideas of this purely zoogeographical approach had already been expressed by authors he called "his scientific grandfathers", such as Cosswig, Reinig, and even before them, by the famous Russian geneticist Vavilov. Applying their methods for the first time to a region outside the Palaearctic realm, Paul Müller modified this basic approach by introducing a 3-step-method under defined conditions to infer his "centres of dispersal" (methodological steps not shown here).

In 1967, Paul Müller was appointed as a curator at the Department of Biology where he was responsible for the comprehensive zoological collection. The unexpected death of PAUL MÜLLER'S supervisor Gustav De Lattin in 1968 was followed by a sudden break in zoogeographical research at the Institute of Zoology. Paul Müller now continued his work in this discipline by cooperating with Josef Schmithüsen, who was at that time professor of plant geography at the Institute of Geography in Saarbrücken. PAUL MÜLLER completed his early investigations on Neotropical biogeography with his famous work "Dispersal Centres of Vertebrates in the Neotropical realm" published in 1973. After finishing his post-doctoral studies in 1971, he was called to head the newly founded Institute of Biogeography, which was later integrated in the "Centre of Environmental Research" (Zentrum für Umweltforschung) of the University of Saarbrücken. In the following years, PAUL MÜLLER succeeded in establishing his institute as one of the most successful departments of the entire university, with a funding volume that was sometimes larger than those of the Institute of Economic Sciences. From 1979 to 1983, he was president-elect of the University of the Saarland. While PAUL MÜLLER'S diverse duties from the 1970s onwards prohibited him from realizing comprehensive fieldwork on his own, he continued to be a very enthusiastic supervisor who supported his students by offering them access to his worldwide network of important contacts.

Paul Müller's first publications were for the greater part of herpetological content, comprising 50 original papers on amphibians and reptiles, some of which were published in the leading German herpetological journal "Salamandra". Moreover, he gave innumerable talks at national and international herpetological symposia. Over two decades and once more recently, Paul Müller organized interdisciplinary symposia on South American biogeography (together with colleagues from the Max-Planck-Institute of Limnology at Plön, Schleswig-Holstein) where he presented the results of all life science disciplines. As he always pointed out, the main purpose of his work was not to revise the taxonomy of species groups, but to use all biotic information on a species as the key to its three-dimensional range that would unlock its evolutionary history and facilitate reconstructing a model of landscape dynamics for the recent past.

Despite of him being one of the last "all-round" zoologists with an encyclopaedic knowledge of most animal groups, PAUL MÜLLER was above all an enthusiastic herpetologist. He saw himself as part of the "herpetomanic community" (cit.) and maintained close contact to many amateur reptile keepers, some of which he thought of as being more knowledgeable of biological diversity than certain scientists. In 1969, his private collection of live reptiles, consisting first of a *Boa constrictor*, a *Spilotes pullatus* and some venomous snake species, was complemented by an adult male *Geochelone carbonaria* that PAUL MÜLLER had brought back from the island of Marajó (state of Pará, Brazil). Named "Max", it became a famous "family member" over the years and was known to all friends of PAUL and ELKE.

In recent years, PAUL MÜLLER was also involved in political discussions of how the private keeping of venomous animals could be improved and more appropriately and sensibly organized. He firmly rejected an overall prohibition by law and acted as an important proponent of all serious amateur reptile keepers.

Inspired by supervising the studies of several PhD students interested in venomous snakes, PAUL MÜLLER started again to build up a very diverse collection of venomous snakes a few years ago. His focus was on the many different forms of the tropical rattle-snake *Crotalus durissus*, which forms a species complex with a range from Mexico southwards to Argentina and covering most of South America's ecoregions. His skills as an enthusiastic reptile keeper showed in an impressive breeding success of a great variety of mating combinations in his "rattlesnake community". One major question of PAUL MÜLLER's recent herpetological research was the basic, still important problem of how morphological



Figure 2. Prof. Dr. Paul Müller checking some labels of his collection in Trier, just before the move of the material to Bonn (2009). Photo: W. BÖHME.

traits are inherited in the forms of the *Crotalus durissus* complex and how basic breeding and cross-breeding experiments might contribute to a better understanding of the postglacial history of that still poorly understood species complex for which he had already proposed an evolutionary scenario in his post-doctoral thesis in 1970. In 2005, PAUL MÜLLER was invited to give the opening lecture at the rattlesnake symposium in the city of Loma Linda, California (USA).

Although representing a focus of Paul Müller's herpetological work, his investigations on amphibians and reptiles were not limited to the Neotropics. He also supervised several master theses and PhD projects on Palaearctic amphibians or reptiles, including for example, in 1972, the important work by B. Schneider on the Thyrrenian subregion of the Mediterranean realm, or some works on the postglacial biogeography of the wall lizard *Podarcis muralis* or the asp *Vipera aspis*. As to the latter, the senior author (M.M.) remembers a one-day field excursion to a place near Nancy (France) to sample individuals of this venomous snake with Paul Müller and three colleagues. It just took Paul Müller a few minutes to find the right place and catch an individual with his snake hook.

Referring to the works on the European herpetofauna mentioned above that were carried out after 2000, PAUL MÜLLER always refused to differentiate between "classic" and "modern" (for example genetic) methods in biogeography. Much rather would he make a distinction between those that provided new insights into a scientific problem or contributed to a species' evolutionary history and those that were less suitable for resolving a specific question. Thus, the "molecular era" that was arising from about the mid-1990' and offering a plethora of new methodological approaches used by PAUL MÜLLER's students, was just another "window to evidence" for him, allowing one more, but not necessarily a better view on a species' phylogenetic relationships or range dynamics.

In 1999, Paul Müller left the University in Saarbrücken and took up an offer of the new University of Trier (Rhineland-Palatinate) to establish a new biogeographical institute there. He also relocated his large herpetological collection from Saarbrücken to Trier. But when he went to retire in 2006, he felt that a university was not generally the right place for the safe long-term storing of scientific collections. He therefore, responsibly, decided to donate his important collection to a natural history museum, viz. the Museum Alexander Koenig in Bonn. The second author of this obituary (W.B.) is deeply indebted to him because he feels that this is one of the most valuable additions he ever received for that museum, and he pledges to take the greatest care of this important heritage of Paul Müller's scientific life.

Anyone who had the privilege to know Paul Müller privately and share the rare moments of rest between all his business with him, spent unforgettable moments with a very reflective, understanding and sociable man who was able to keep his friends and colleagues spellbound with an apparently endless treasure of interesting stories from his life "always on the run all over the continents". Those of us who knew Paul Müller, this fascinating personality, will miss his enthusiasm, his valuable advice, and his presence in our private and professional lives.

Acknowledgements

We are deeply indebted to ELKE MÜLLER for her patience and for providing photos, unpublished information, and sharing memories to complete this portrait.

Appendix

Herpetological and herpetology-based publications by Paul Müller

BÖHLER, E. & P. MÜLLER (1971): Bemerkungen zur Variabilität und Terra typica von *Anops kingi* (Bell 1833). – Aquaterra, **9(4)**: 39–41.

MÜLLER, P. (1966): Doppelschwanzbildung beim Teju (*Tupinambis teguixin*). – Natur und Museum, **96(4)**: 151–154.

MÜLLER, P. (1966): Studien zur Wirbeltierfauna der Insel São Sebastião (23°50'S/45°20'W). – Inaugural-Dissertation, Universität Saarbrücken, 1–348.

MÜLLER, P. (1966): Ein Wiederfund der Roten Krötenkopf-Schildkröte (*Phrynops rufipes*). – DATZ, **19(12)**: 373–374.

MÜLLER, P. (1967): Beitrag zur Herpetofauna von Montecristo (42°20'N/10°9'O). – DATZ, **20(10)**: 315–318.

MÜLLER, P. (1968): Einige Bemerkungen zur südamerikanischen Krötenart *Bufo granulosus* Spix 1824. – DATZ, **21(8)**: 248–251.

MÜLLER, P. (1968): Zur Verbreitung der Mauereidechse Lacerta muralis (Laurenti, 1768) im Saarland. – Faunistisch-Floristische Notizen aus dem Saarland, 1: 5–6.

MÜLLER, P. (1968): Zur Verbreitung der Gattung *Hydromedusa* (Testudines, Chelidae) auf den südostbrasilianischen Inseln. – Salamandra, 4: 16–26.

MÜLLER, P. (1968): Über die Schlangenarten des Saarlandes. – Faunistisch-Floristische Notizen aus dem Saarland, 2: 9–12.

MÜLLER, P. (1968): Bemerkungen zu den beiden südamerikanischen Natternarten Spilotes pullatus und Pseustes sulphureus. – Aquaterra, 5(12):

MÜLLER, P. (1968): Die Herpetofauna der Insel von São Sebastião (Brasilien). – Verlag Saarbrücker Zeitung, 1-82, Saarbrücken.

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MÜLLER, P. (1969): Zur Verbreitung der Gattung *Chironius* (Serpentes, Colubridae) auf den südbrasilianischen Inseln. – Senckenbergiana biologica, **50(3/4)**: 133–141.

MÜLLER, P. (1969): Herpetologische Beobachtungen auf der Insel Marajó (Amazonasdelta). – DATZ, 22(4): 117–121.

MÜLLER, P. (1969): Über die nördliche Arealgrenze von *Lystrophis semi*cinctus (Dumeril, Bibron und Dumeril). – Aquaterra, **6(8)**: 96–99.

MÜLLER, P. (1969): Über den Subspezies-Status südbrasilianischer *Bufo ictericus*-Populationen. – DATZ, **22(11)**: 340–342.

MÜLLER, P. (1969): Über eine neue Subspezies von Teju, *Tupinambis teguixin buziosensis* n. ssp. – Salamandra, **5(1/2)**: 32–35.

MÜLLER, P. (1969): Einige Bemerkungen zur Verbreitung von *Vipera aspis* (Serpentes, Viperidae) in Spanien. – Salamandra, **5(1/2)**: 57–62.

- MÜLLER, P. (1969): Über die Krötenarten (Salientia, Bufonidae) des Saarlandes. Faunistisch-Floristische Notizen aus dem Saarland, **2(2)**: 17–20.
- MÜLLER, P. (1970): Durch den Menschen bedingte Arealveränderungen brasilianischer Wirbeltiere. Natur und Museum, 100(1): 37-68.
- MÜLLER, P. (1970): Merkwürdige Doppelschwanzbildung bei einer südamerikanischen Schienenechse (*Teius teius*). Aquaterra, **7(2)**: 22–24.
- MÜLLER, P. (1970): Das Beutespektrum von *Philodryas pseudoserra*. DATZ, **23(2)**: 33–37.
- MÜLLER, P. (1970): Die saarlandnächsten Fundorte von Vipera aspis. Faunistisch-Floristische Notizen aus dem Saarland, **3(4)**: 25–27.
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- MÜLLER, P. (1971): Beobachtungen an brasilianischen *Geochelone carbonaria.* Aquaterra, **6**: 73–75.
- MÜLLER, P. (1971): Erstnachweis von *Dermochelys coriacea* (L. 1766) für die Insel von São Sebastião (Brasilien). Salamandra, **7(2)**: 86.
- MÜLLER, P. (1971): Ausbreitungszentren und Evolution in der Neotropis.

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- MÜLLER, P. (1975): Zum Vorkommen von *Liolaemus occipitalis* im Staat von Santa Catarina (Brasilien) (Sauria, Iguanidae). Salamandra, 11(1): 57–59.
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