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OBITUARY

On the love of detail and the search for grand connections: a tribute to Reinhard Rieger, 10th May 1943 to 11th October 2006

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Reinhard Rieger was born in 1943, in Linz (Oberösterreich) and grew up in Hartberg, in the hilly eastern part of the Steiermark, where the Alps give way to the openness of the Hungarian plains. Both his parents were high school teachers. From his father Othmar Rieger, a poet whose work was quite well known in this area after World War II, he inherited the impulsive joy about everything new and beautiful, and above all the imagination that would give wings to his ideas concerning phylogeny and evolutionary biology. This imagination was fed by a love of observing the details of the objects he was studying. At first, he found plenty of objects in the bucolic neighborhood of his home. In the investigation of details, he was helped along by friends of his parents, notably by a naturalist, by a histologist, and by a chemist/philosopher. By the time he began to study biology at the University of Vienna in the fall of 1961, he had familiarized himself with the use of a complex microscope, with standard histological techniques and also with Kant's Kategorien. After the botanist Friedrich Ehrendorfer had recommended that he attend Ruppert Riedl's lecture about "Die Bedeutung der Niederen Würmer für die Verwandtschaftsforschung der Metazoa", the young student soon found himself in Riedl's working group, investigating macrostomid turbellarians from the Adriatic and the Red Sea. In 1969 he completed a morphological–taxonomic dissertation on 60 mostly new species of the newly erected taxon Dolichomacrostomidae (only 14 of which, unfortunately, have so far been published). The extraordinarily painstaking descriptions and line drawings of these animals (Fig. 1), which were characteristic of him from then on, immediately made him a member of the elite group of Scandinavian/German/Austrian systematists who ruled turbellarian taxonomy at that time. And he remained one of the leading representatives of this scene until his death—still an impressive person to observe at the last International Platyhelminthes Congress in August 2006 in Innsbruck and it filled him with pride to be mentioned together with the great Austrian scholars of Turbellaria Reisinger and Steinböck.

Nevertheless, Reinhard never regarded himself as a genuine taxonomist, even though he was to continue to describe significant taxa during his entire scientific career. This was, because he loved to look through the dissecting stereomicroscope into a petri dish containing all kinds of living creatures from the interstitial sand fauna. His talent for uncommonly subtle observation enabled him to distinguish these animals by their specific shape and movement, thus repeatedly arriving at spectacular discoveries of which only a few will be cited here. After the Dolichomacrostomidae of his doctoral studies, at the beginning of the 1970s it was the family Retronectidae that he and Wolfgang Sterrer discovered and described: Platyhelminthes of relatively basic organisation belonging to the Catenulida, most of which living in the ecologically highly interesting anoxic sulfide system of coastal sediments. Among all the many turbellarian species, which are themselves very similar to one another, he detected two forms which looked like turbellarians but actually were quite distant species: *Lobatocerebrum psammicola* Rieger, 1980 and *Jennaria pulchra* Rieger, 1991 were considered by him as belonging to two different annelid-like taxa, possibly evolved by progenesis. The structural description and the phylogenetic positioning of the two species constituted the subject of his habilitation at the University of Vienna in 1984. A remarkable aspect here was his wise restraint in the creation of higher taxa for the

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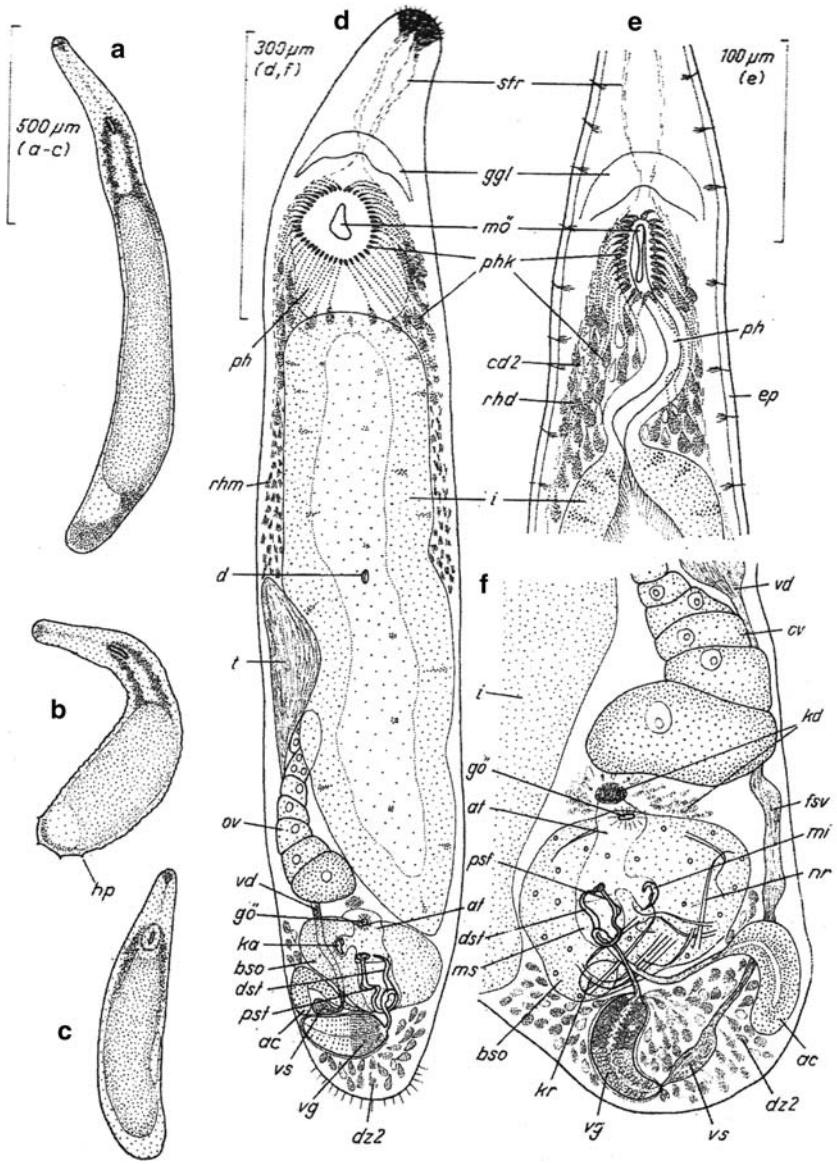

Fig. 1 Facsimile reproduction of Fig. 2l, *Paramalostomum atratum* Rieger, 1971. From: Rieger R (1971) Die Familie Dolichomacrostomidae Rieger (Turbellaria–Macrostomida). II. Teil Dolichomacrostomidae Rieger. Zool Jb Syst 98:569–703

two still enigmatic worms. Finally, in laboratory cultures of *Macrostomum pusillum* originating from the Adriatic Sea, he found a few specimens of another macrostomid which could soon be established as one of the best-growing laboratory turbellarians. It was described as *Macrostomum lignano* Ladurner et al., 2005 and is now increasingly being used in various labs (e.g., in Basel by Lukas Schärer, in Hasselt by T. Artois, in Los Angeles by Volker Hartenstein), for a number of developmental and evolutionary studies, thus becoming a highly welcome model organism among the lower Bilateria.

Around his doctoral professor Riedl, during the 1960s an Austrian centre for marine biology had formed, initially with a traditional faunistic-taxonomic orientation. Because the interest also focused on the meiofauna ("Sandlückenfauna"), this group became a kind of antipode of the school with this subject already established by Adolf Remane in Kiel. The Viennese at first probably less broadly based than the people in Kiel and in Peter Ax's group in Göttingen, which had developed from them nevertheless recognized first as early as the end of the 1960s the unique possibilities of transmission electron microscopy (which had just become available for laboratory use) for working on these tiny metazoans and Reinhard Rieger was at the centre of this development. He was really the one, who initiated comparative morphological studies at the EM level at a time when others still seemed to suspect that structures at this level would be too uniform to have any significance for comparative morphology.

For him, with his devotion to detailed observation, this new technique must have been particularly fascinating, given all the possibilities it offered for peering deeper into the structures. From now on he was motivated by nothing less than to use this new depth of characteristics to test the

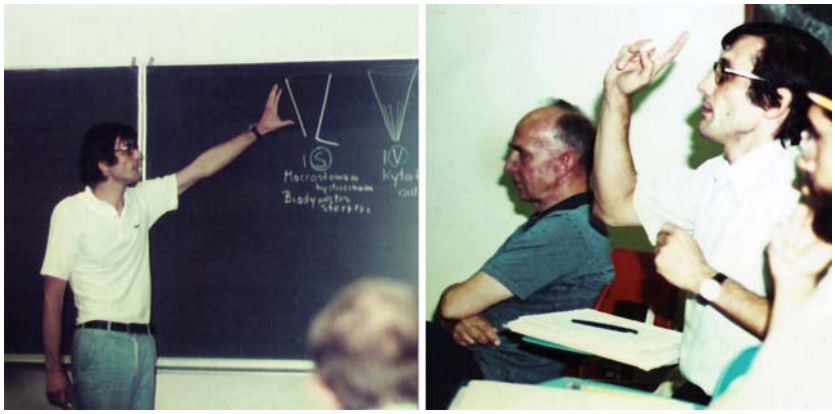

Fig. 2 Reinhard Rieger in his unmistakable way giving a lecture and entering into the discussion. Both photos taken during the Meiofauna Symposium at the Bermuda Biological Station (1975)

entire large-scale phylogeny of the Metazoa and provide a new foundation for it. In fact, with his great enthusiasm for the meiofauna, his unlimited ambition and his restless way of working, within only a few years he had catapulted himself up to the front line of comparative research on the ultrastructure of invertebrates. To this was added his unique sense of mission, which made a very convincing and sympathetic impression as he explained his ideas, made them widely known and established their validity. He "burned" for his work, as Peter Ax once expressed it at a meeting.

Several fortunate circumstances favored this development, as follows: as early as 1969 Riedl accepted an invitation to become Kenan Professor for Zoology and Marine Sciences at the University of North Carolina, Chapel Hill. Reinhard was one of the students who accompanied him to the USA and were supposed to support the morphological scene of US east coast zoology. Although this was fully intended by the initiators of the Riedl appointment, it also caused some US colleagues to express not only acknowledgment but also mistrust by characterizing them as the "Austrian mafia". Another, probably the most fortunate circumstance in this period for his early career was his marriage to Dr. Gunde Reinwald shortly before moving to the USA. Having obtained her degree under Wilhelm Marinelli in Vienna, with a study on the anatomy of lampreys, she then relinquished a career of her own and became his congenial coworker, his conscience regarding publication style, being responsible primarily for the technical–methodological fundamentals of his TEM analyses. In Chapel Hill the couple found a modern TEM laboratory awaiting, along with intelligent students. When Riedl soon returned to Vienna, in 1971, the two Riegers made use of their new methodological knowledge to set up a corresponding TEM laboratory (together with Waltraud Klepal) at the Viennese institute, but did not comply with Riedl's urging that they permanently return to Vienna. At this time not even the offer issued by Ernst Mayr to come to Harvard made Reinhard leave Chapel Hill. He had meanwhile become an Assistant Professor in this very active and idyllic university town, and he had found an excellent personal and professional environment and a number of very good students. Among the latter were some doctoral students who stayed on after Riedl left, and their studies were successfully concluded under Reinhard's guidance: Rick Farris (systematics and ecology of Gnathostomulida from North Carolina and Bermuda), Michael Creezé (Solenofilomorphidae, Turbellaria) and Ed Ruppert (Xenotrichulidae, Gastrotricha). By now he had acquired just as much competence for Gnathostomulida and Gastrotricha as for the Turbellaria; frequent trips to the Atlantic coast and close collaboration with his friends and fellow doctoral students, above all Wolfgang Sterrer and Jörg Ott, likewise expanded his taxonomic, methodological and also ecological expertise. A lifelong close friendship and fruitful scientific collaboration began in Chapel Hill with his first student from start to finish, Seth Tyler. His outstanding dissertation on the duo-gland-adhesive system (1975) became an example of the TEM-based functional–morphological and phylogenetic work propagated by Reinhard. This first major ultrastructure comparison in the zoological literature carefully analyzed the general structure of these organs, comprising anchor cell, releasing cell and viscid cell, in various meiofaunal taxa, which thus proved to be one of the most characteristic convergently evolved features ("Lebensformmerkmale") of the interstitial fauna. Many other comparative studies followed, funded by the National Science Foundation and concerning ecology and ultrastructure, which either were carried out by Reinhard and his wife or were the subjects of doctoral dissertations and master theses. The latter included, e.g., studies on spatial and migration pattern for *Tetranchyroderma* species (David Nixon 1975), sulfide stress in interstitial metazoans (Eric Powell 1975), investigations of the pharynx simplex in Turbellaria (David Doe 1978), fine structure of the polychaete *Owenia fusiformis* (Steven Gardiner 1979), the filospermoidean Gnathostomulida (Beth Knauss 1979), coelomic organisation in Polychaeta (Margret Franzen 1980), dispersal of meiofauna (George Hagerman 1981), anatomy of acoelan Turbellaria (Julian Smith 1981),

body cavity lining in secondary acoelomates (Peter R. Smith 1983), sediment reworking by Enteropneusta (Bruce Duncan 1984), coelomic lining in echinoderm podia (Julian Lombardi 1984) and macrofauna–meiofauna interactions (Steven Fegley 1985).

And his work did not fail to exert a broader influence. His studies left unmissable traces in the picture of zoological taxonomy, morphology and phylogenetics. Many of the facts discovered by him rapidly became textbook knowledge, and his hypotheses formed part of the general discussion about the evolution of the Metazoa. Rieger's description of the ultrastructure of the monociliary cell in, e.g., Gnathostomulida, Gastrotricha and Oweniidae, has become the classical example of the significance of ultrastructural features for determining the reading direction of alternative characters in phylogenetic analyses.

Regarding the question of evolution of the integument in invertebrates, he succeeded in formulating an illustrative and convincing hypothesis: starting from cuticular structures in Eumetazoa that arose by multiple convergence, from simple glycocalyx depositions on apical–epidermal cell membranes or between epidermal microvilli, the multilayered fibre lattices in true exoskeletons developed by incorporation of a few collagen fibres into the extracellular matrix.

With another convincing series of characters (in Annelida and Echinodermata) he was able to derive the evolution of the somatic fibrous muscle cells of coelomate Bilateria, situated below the basal epidermal matrix, from simple epithelial muscle cells by way of myoepithelial cells. Closely related to these results were frequent ultrastructural studies giving rise to inferences about the structure of the coelomic lining, coelomogenesis and the origin of coelomate body plans—a theme running like a golden thread through his scientific work, beginning with the first papers on the subject by his student Margret Franzen. Here he frequently complains about the lack of more ultrastructural facts with which he could really clarify the reading direction and evolution of these key structures for the Bilateria. On the other hand, he comes to a crowning conclusion (together with Seth Tyler, Julian Smith and Gunde Rieger) about the ultrastructural picture of the turbellarian Platyhelminthes, with the nearly encyclopedic treatment in the microscopic anatomy of invertebrates (1991). Another observation of small details, but one with considerable phylogenetic significance, is the homology in ultrastructure (TEM) between the jaws of gnathostomulids and rotifers, with which he was the first (with Seth Tyler) to recognize the crucial morphological synapomorphy for the recently established taxon Gnathifera.

Rieger's scientific work is too multifaceted for all the focal points of his thoughts and actions to be given credit here. However, his attitude towards Hennig's phylogenetic systematics should not remain unmentioned. For a long time he confronted this new methodological approach with scepticism, almost with incomprehension. Attempts to make it more acceptable to him were sure to end in arguments; he disliked the schematics and oversimplifications of cladistic analyses, ignoring, in his estimation, the details by errors in coding and misunderstanding of their connections, and he could be seriously enraged by the frequently expressed disdain for a comprehensive homology estimation before characters were evaluated, as well as rejection of the significance also of plesiomorphic character complexes for kinship research—a common subject of passionately presented discussion contributions, which many participants at such meetings can probably still remember. And naturally "Turbellaria" was not an undesirable word to him, even though he did not doubt the paraphyly of the group. In particular, he regarded cladistics as representing a dismissal and neglect of Adolf Remane's ideas and principles, and Remane was (along with Lybbie Hyman) his most respected "hero". He admired his detailed treatment (similar to his own meticulous way of working) of, e.g., the rotifers and gastrotrichs as well as his theoretical work. For a long time while in the USA he intended to translate into English Remane's book on "Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik" (1952). His 1979 publication with Seth Tyler on "The homology theorem in ultrastructural research" is paying tribute to Remane's homology criteria while simultaneously proceeding further ("The homology theorem is the heart of systematic research in that it provides the means by which characters relevant to systematics and phylogeny can be identified. It is the foundation, in particular, of biological structural research and can, we believe, be applied at all levels of structural hierarchy, from the macroscopic to the ultrastructural"). Primarily influenced by the newly discovered characters at the ultrastructural level, both authors place special emphasis on the three "helping criteria" of Remane, and formulate them as an important last step of the homology analysis, in which the distribution of one homologue is traced in a group of organisms and compared to the distribution of other homologues in the same group. The significance of a homology countercheck is likewise enhanced by an analogy evaluation, for which the authors explicitly presented five criteria of their own.

In a collaborative publication about the systematisation of three cryptic *Microphthalmus* species (1987), Reinhard and I finally at the end of many vigorous but mutually illuminating discussions which I remember with special fondness worked out, for example, a Remane-type hierarchy of homologues and a Hennig-type estimation of primitive versus derived characters that were not incompatible. We were able to demonstrate that the two procedures led to the same result, and are actually two parts of one single method for

phylogenetic reconstruction. However, the homology hierarchy offers the advantage of providing a better visual representation of the level of probability of homology, i.e. synapomorphy. The need for such an evaluation, in which the probability of synapomorphy is carefully weighed against the probability of convergence, was indeed one of Reinhard's beliefs (see above) of which he was rightly firmly convinced and which he did not see generally being followed in many cladistic analyses.

One idea that will forever link the name Rieger to the discussions of the theory of large-scale metazoan phylogeny is his progenesis concept for the origin and radiation of the Metazoa and Bilateria, in particular. Ronald Jenner (2004, PalAss Newsletter 56:50–59) called it "an ingenious solution by construction a beautiful synthesis of evidence garnered from comparative morphology, embryology, life history, and ecology"). The starting point of his concept certainly not new at all is the assumption of a biphasic life cycle with a larva and an adult for the metazoan stem species. His hypothetical early adult, however, is a clonal cell colony of flagellates of macroscopic size producing microscopic larvae with ciliary locomotion, so that the life cycle alternates between non-motile and motile stages (Fig. 3). Selective pressures acting independently on the two phases led to the origin of the different metazoan tissue types; the sponges in parallel with the eumetazoan taxa (coelenterates and bilaterians), both originally originating from food-capturing modules within cell colonies. The different bilaterian taxa originated either (1) through transformation of polypoid feeding structures of such adult colonies into bilaterally symmetrical colonial forms such as Bryozoa and Pterobranchia and freely motile individual forms such as Enteropneusta and Annelida, or (2) by the evolution of microscopic larvae of these colonies into trochophora-like and dipleurula-like larval types. By progenesis these larvae developed into various protostomian and deuterostomian groups. I see the ingenious nucleus of this concept less in the idea of clonal cell colonies being the stem species of both Metazoa and Bilateria than in his insight about the significance of both the non-coelomate (larvae) and the coelomate type of body organisation (adults) within a single life cycle. Thus, non-coelomate and coelomate groups could be derived

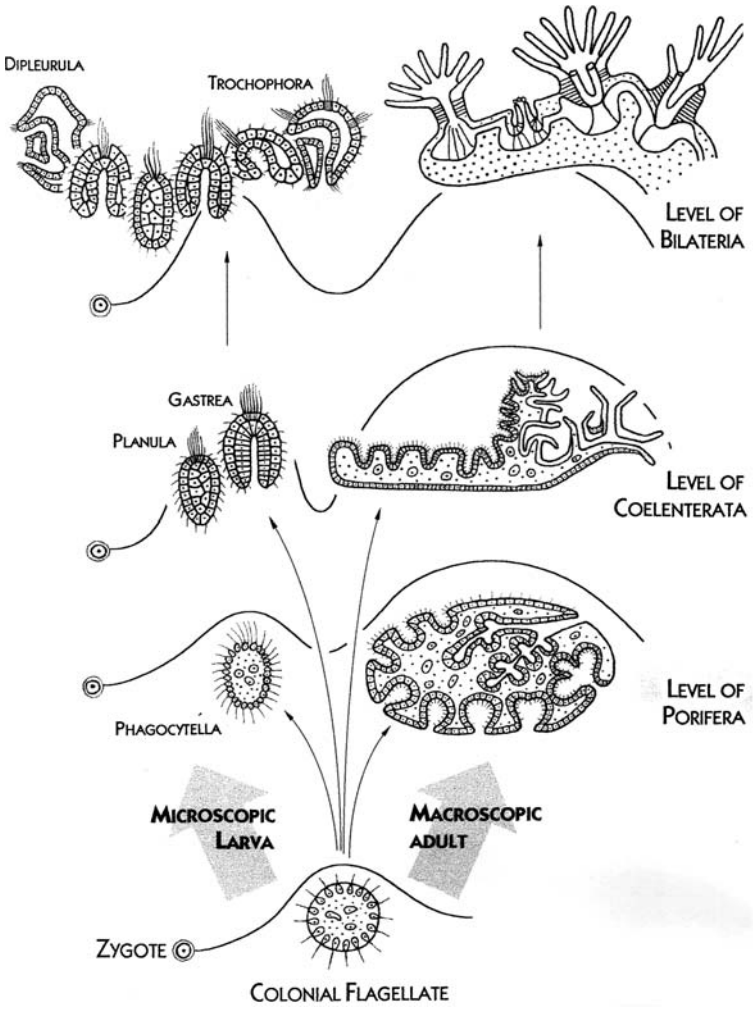

Fig. 3 Schematic presentation of Rieger's ideas of the early metazoan radiation. From: The biphasic life cycle—a central theme of metazoan evolution. Am Zool 34: 484–491 (1994)

from the same level of organisation without assuming, e.g., difficult explanations for the reduction of coelomic cavities. His expertise in metazoan phylogeny caused him various honourable invitations, e.g., to the Nobel-Symposium "Early life on earth" in Sweden 1992.

In 1976/1977 I spent almost a year in his laboratory in Chapel Hill, probably the most productive and happiest time of my life, in which I experienced him as a colleague and teacher who filled me with enthusiasm, and came to regard him as a lifelong friend of my family and myself. Hence it was a matter of course for me to convince him to join me when in 1992 the Gustav Fischer publishers in Stuttgart asked me to be responsible for the new edition of Siewing's textbook of systematics. At first we both underestimated the demands this project would make, in that we had to invest an unexpectedly large amount of time, but in the process each of us benefited in a quite unusual way from the strengths of the other (1st volume, 1996: "Einzeller und Wirbellose Tiere"; 2nd volume, 2004: "Schädel- oder Wirbeltiere"). No other undertaking made such demands, kept us so busy and enthusiastic, and finally brought us so close together as did the publication of this textbook and the collaboration with its authors. We worked on the second, extensively altered edition of volume 1 together up to the final correction, but when the finished book appeared in November 2006 (now published by Spektrum/Elsevier, Heidelberg), Reinhard was no longer able to receive it. It is consoling that this textbook will keep Reinhard Rieger's name alive also in zoological teaching.

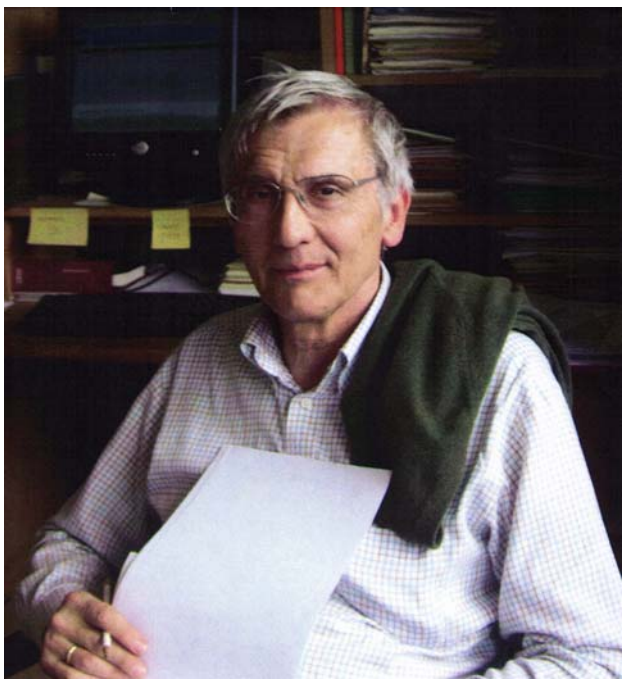

Fig. 4 Reinhard Rieger in his office of the biological department of the University of Innsbruck, 2005

For everyone who experienced him as teacher, colleague or friend he will in any case remain in memory as an original, wonderful personality. He was characterized especially by two things: he loved to approach other people, and people in his vicinity were never indifferent to him. In a charming, often surprising and funny way he was able to open up to others and entrust them with his thoughts. These people could be his students in a lecture, whom he surprised with a personal admission, or the dairy farmer in his Tyrolean home village, to whom he explained our textbook when collecting the evening's milk. His compassion was awakened for everyone, and his active caring encompassed everyone he regarded as disadvantaged—the student who was at risk of losing time when the threat of military service loomed, the colleague who seemed to be unjustly criticised in a discussion, the friend whose private life he feared might be endangered—he never failed to help, to console, to find a way out of trouble, very often in very long telephone calls. So he also thought it necessary in all kind of discussions to employ his expertise in support of other colleagues and their ideas, in order to assist the young ones and to ensure that the achievements of the older ones were adequately appreciated. For this he was loved. Few things could make him so emotional even in public as a failure to cite the facts and ideas associated with elderly or deceased colleagues; his enormous knowledge of the literature enabled him almost always to detect such omissions.

Reinhard's career was uninterrupted. In 1981 he became Full Professor in Zoology and Marine Sciences at the University of North Carolina, and in 1981/1982 he spent a year as a Humboldt scholar in the institute of Peter Ax in Göttingen. Finally, in 1985, he accepted the professorship at the University of Innsbruck (Fig. 4). It never became quite clear to me why he left the permanent position in Chapel Hill and became successor to the soil zoologist Heinz Janetschek in Innsbruck. His family situation (e.g., his ailing mother and the mother of his wife) played a role here as did the opportunity to see his son Roland (now an ophthalmologist in the Charité, Berlin) grow up in Austria, but it was certainly also the pleasure at being summoned back to his homeland, as an internationally acknowledged Professor. Despite his demonstrative openness to the world and an especially high esteem for the American university and scientific systems, in which he felt appreciated and well accommodated, he was nevertheless always a profoundly committed Austrian patriot. Conspicuous to everyone on the door of his office in Chapel Hill was the sticker "Styria—the green heart of Austria"! For him it was also the heart of the world.

The first years in Innsbruck were certainly not easy. He served as chairman of the Institute for Zoology and Limnology for many years, getting lumbered with an enormous load of all sorts of commitments, besides a heavy teaching

schedule. From the start he felt committed to convincing the administrators in the Austrian university system of the tenure track system he had benefited from in Chapel Hill. At the administrative level this was of course unsuccessful. Within his own working group, however, assistant professors brought new methodologies and new points of view to the laboratory, but were pursueing their careers in their own specialties. Two of them soon moved on to full professorships, albeit at other universities: Gerhard Haszprunar, working on mollusc phylogeny, is now Professor at the University of Munich; Christian Sturmbauer, working on the evolution of cichlids with molecular methods, became Professor of Zoology at the University of Graz.

In Innsbruck it soon became apparent that the continuation of the line of research from Chapel Hill would not be possible without further development of his ultrastructural–morphological evolutionary biology. It was, therefore, quite logical to incorporate molecular methods into the comparative framework he had already developed. After he was able to gather around him an active group of talented, highly promising young people (among them Johannes Achatz, Bernhard Egger, Robert Gschwentner, Peter Ladurner, Gunnar Maier, Bert Hobmayer, Dietmar Reiter, Willibald Salvenmoser) his work was ultimately focussed on two main points: (1) the problem of the transition between diploblastic and triploblastic organization in the evolution of Metazoa, which was approached by subtle cytological and molecular investigations of the development of the complex body-wall muscle grid in Platyhelminthes, and the development of body-axes in basal turbellarians, (2) working out, by structural, evolutionary and genetic analyses, regulatory systems for the formation of tissues and organs in lower Metazoa with emphasis on the totipotent stem cells (neoblasts) of the Platyhelminthes. This unique system of cells, from which all cell types including germ cells can differentiate, are responsible for the long-term renewal of cells and tissues and form the basis for the extraordinary regeneration abilities in this taxon. He regarded knowledge about them as crucial for understanding the stem-cell systems in other groups of organisms. At the same time, he saw in the stem cells the most important synapomorphic character complex for Acoelomorpha and other Platyhelminthes, i.e., a key character in one of the most important controversies in the current phylogenetic discussion.

The 10th International Platyhelminthes Conference can almost be regarded as a kind of summary of this work and the many successfully published papers of recent years in Innsbruck, and their international acknowledgment; organized by him and his coworkers and held in Innsbruck in August 2006, this was the last occasion before his death when many colleagues, students and friends gathered around him there. Reinhard Rieger departed this life on 11 October 2006 in Birgitz/Tirol. It had been a rich, vibrant and in science uncommonly fruitful life, leaving an extraordinary inheritance for our zoology and a lively memory of a lovable human.

Acknowledgments I am very grateful to Dr. Gunde Rieger, Birgitz/Tirol, Prof. Dr. Seth Tyler, Orono, Maine, and Prof. Dr. Bert Hobmayer, Innsbruck, for data, information and helpful advice. Andrea Noël, Osnabrück, kindly typed the manuscript.

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