In memoriam

Professor Günther Osche (1926 – 2009) and his scientific legacy

Günther Osche died on February 2, 2009, in Freiburg (Southern Germany) at the age of 82 after a period of illness. He leaves behind his wife, three children and two grandchildren. He was born on the 7th of August, 1926, in Haardt near Neustadt (Weinstraße) in Southwest Germany as the only child of a bank officer and his wife. A short time later, his family moved to Nürnberg (Bavaria). There, he spent his childhood and developed his early interest in natural history as a bird watcher, which continued throughout his life. The world war took its toll when he became a soldier in 1944; he was deployed in France where he was seriously injured the same year. He came back from war captivity in 1946 with a stiff knee and entered Erlangen University to study Natural Sciences with zoology as principal subject. There, under the supervision of the distinguished zoologist Hans-Jürgen Stammer he obtained his Dr. rer. nat. in 1951 with his famous treatise on the systematics, phylogeny and ecology of *Rhabditis* [1, 2]. As a scientific assistant he was able to perform research in the nematology group of Stammer, who initiated a large-scale investigation of parasites of small mammals in Germany. Osche's task was to identify the parasitic nematodes. However, in addition he used these specimens, which could be studied alive, to elaborate his own topics of more general significance. In 1963 he received the *venia legendi* in zoology with a *habilitation* thesis on the embryology and comparative morpholgy of Pentastomida and became a *private* lecturer at the University in Erlangen. From 1967 until his retirement in 1988 at age 62 he was *ordinary* professor at the University of Freiburg in Breisgau and in this capacity he was responsible for teaching systematic zoology, comparative morphology, ecology, and evolutionary biology. Over the years there, he led a successful research group in evolutionary biology, systematics and ecology, from which five professors can trace their academic lineage. He authored many research papers and text books in evolutionary biology, parasitology and ecology.

In his original work and as an author of reviews and textbooks, Günther Osche was a highly succesful scientist in five very different fields: systematics of nematodes, parasitology, evolutionary biology, human biology and flower biology, thus demonstrating his wide-ranging interest in natural sciences. Throughout his scientific work he sought for historical-narrative explanations [3]. Here, "only" his contributions on morphology, phylogeny, systematics, ecology, preparasitic associations, life cycles and the evolution of free-living and parasitic nematodes including coevolution with vertebrate hosts will be recognised. He authored about 20 outstanding articles with about 650 pages on nematodes, starting with Rhabditidae, of which more than half dealt with parasitic groups (Acuaridae, Ascaridae, Rhigonematidae, Strongylidae), always focusing on a subject of general interest to biology. Topics of Osche's contributions included: *i*) evolutionary change by paedomorphosis (which he called fetalisation), which he proposed could be used to understand the origin of sexual dimorphism; *ii*) cryptotypic characters – which are genetically maintained but not phenotypically expressed – as one source of character evolution (something he termed "latent potential"); *iii*) the evolution of complex and synorganised structures; and *iv*) parasite-host coevolution. In different groups, he observed recapitulations in the morphogenesis of structures and used them as Ariadne's thread for a rough outline of the phylogeny of that particular group. Taxonomy played only a small part in his publications insofar as he had to clarify the objects of his investigations, although he discovered and described some new species and created some genera names like *Caenorhabditis, Matthesonema* and *Stammerinema*.

Günther Osche was a scientist with an eye for biological detail and a view of the broader context. By recognising a diversity of minute structures on the glottoid apparatus of the stoma of 65 investigated species of *Rhabditis sensu lato,* which he used for systematisation in his doctoral thesis, he set the cornerstone for understanding the phylogeny of the "Rhabditidae" [1]. His comprehensive revision of this group was the foundation for 25 years. In this publication, he gave new names for six taxa of the genus group, from which *Caenorhabditis* is the most famous, and he described three new species. It has been little recognised that, in this paper, he debated about possible modes of speciation without separation (sympatric speciation) in rhabditids, assuming that all the species were cosmopolitan (today we know that this is not the case). He took up this subject again and dealt with it in greater detail in his trailblazing paper on sibling species and "complementary species" [4], the latter differing in their mode of reproduction (gonochoristic *versus* autogamous hermaphroditic). For groups of three such species he developed the idea that a new gonochoristic nematode species could evolve *via* a detour through an intermediate hermaphroditic offshoot. After a certain period of evolution and ecological differentiation from the gonochoristic complementary species, the hermaphroditic one would revert to gonochorism, likely to be ecologically and genetically incompatible to its sibling species. The occurrence of such a possible mode of speciation with both events occurring sympatrically is still an open question. His discussions were based on crossing experiments between the sibling species and comprehensive studies on the variability of morphological structures and aberrations to bridge the gap between the species. In this context, he redefined the term "cryptotype" (K. Saller) as complexes of the genotype maintained for features that usually are not realised phenotypically. The most impressive example in nematodes of such a latent character harboured for a very long time were the three tips (one dorsal, two subventral; comparable to the caudal glands of "Adenophorea") on the tail observed in a rhabditid (*Pellioditis papillosa*), which he interpreted as atavistic and found in the same arrangement as "reanimated" characters of species disjunctively distributed in mostly parasitic groups. Thus, it was a cryptic part of the bauplan, at least of the Secernentea (for him all nematodes), that could reemerge independently [5, 6]. In an evolutionary scenario, Osche connected this plesiomorphic "triply pointed" tail to the behaviour of aquatic nematodes that adhere to the substratum by secretions of the caudal glands; specifically, such nematodes display an oscillating body motion, from which he derived the "waving" of dauer and infective larvae of the terrestrial Secernentea by "change of function" [7].

Günther Osche [8] first observed waving "in a tube" in unrelated rhabditid species. His preliminary results on the genetics of waving behaviour of dauer larvae from crossing experiments between a waving and a non-waving strain of *Rhabditoides inermis* [2] were cited in many textbooks. He also discovered some interesting associations, like *Rhabditella typhae* (as we now call it) living in the frass of the caterpillar of *Nonagria typhae* [1], or *Matthesonema tylosum* existing entoecic in the gill chamber between the pleopods of the isopod *Tylos latreillei* [9], a phenomenon which should be reinvestigated. He discovered that third-stage juveniles of a saprobiontic nematode (*Rhabditis* "*strongyloides*") could invade the skin or the conjunctival sac of small rodents and were morphologically distinguishable according to the source. This phenomenon could be resolved 30 years later by his scientific "grandson" Franz Schulte. Schulte showed that instead of one species with different behaviours, a complex of ecologically different species exists, namely *Pelodera strongyloides, P. cutanea* and *P. orbitalis*, the last two living in nests of rodents and using the hosts for transport and nourishment [10]. The premature statement by Osche [11, 12] that the juveniles in a rodent possibly were waiting to develop on the decaying cadaver turned out to be wrong, but was unfortunately perpetuated in recent literature [13].

As mentioned before, in his morphological investigations of different parasitic nematode groups ontogenetic changes that could be interpreted as recapitulations played an important part and suggested ideas about evolutionary transformation. For example, the cuticular cordons at the anterior end of *Stammerinema soricis* (Acuariidae) pass through different stages, which are known from the adults of related taxa (stages like the terminal characters in *Paracuaria* → *Acuaria* → *Dispharynx* → *Synhimantus*) [14]. The various cordon types were organismically explained as a result of heterochrony of different growth processes. In Ascaridoidea [15] the morphogenesis of the lip complex of *Porrocaecum ensicaudatum* passes through stages that are characteristic for adults of five different ascarid taxa (*Acanthocheilus* → *Contracaecum* → *Stomachus* → *Amplicaecum* → *Ophidascaris*). Hypothesising this as a recapitulatory development, Osche proposed a guideline for ordering the groups in a phylogenetic sequence, which was supported by the host-range ("*Wirtskreis*") and the life cycles of the nematodes (primarily heteroxenous, secondarily monoxenous). For him, a strong argument for this sequence and his phylogenetic hypothesis was the coevolution of the ascarids with the phylogeny of jawed vertebrates nearly from their beginning (cartilaginous fishes → bony fishes → amphibians/reptiles → birds/mammals). The main exception of this parallel evolution (not cospeciation!) of parasitic groups and host groups are the Stomachinae, which could be explained as multiple transfers from teleosts as primarily definitve hosts to fish-eating marine mammals (whales and seals), birds (gulls, petrels, penguins etc.), and turtles with the ancestral hosts becoming intermediate hosts [15, 16]. This "host-range expansion" ("*Wirtskreiserweiterung*": Osche) of primarily "fish parasites" was facilitated because the ancestral (autochthonous) ascarids in these taxa (e.g. whales) were lost when entering the marine environment in the course of evolution.

The conclusions of this article on ascarids, which Osche regarded as his best publication on nematodes [3], are hard to accept from an eco-evolutionary point of view. As parasitic lineages within Secernentea originated terrestrially, "it is difficult to accept any scheme that jumps from terrestrial free-living bacterial feeders to the marine environment and sharks" [17: p. 250]. To resolve this problem, a new approach combining data from morphology, life-cycles and host-range with a phylogenetic tree generated from molecular data is required.

On a broad scale of parasitic taxa, Osche investigated the different modes of host shifting [18]. With good arguments, he assumed earthworms as primary intermediate hosts of the ascarids *Porrocaecum*, whereas predators of earthworms like shrews and moles were added later as second intermediate hosts, which made possible a host switch to birds of prey as definitive hosts. By contrast, a host switch to herbivores was possible by abandoning the intermediate host, so that *Parascaris* and others became secondarily monoxenous, with a complex migration in the host that recapitulates the behaviour in an earlier intermediate host before (ontogenetically) the same host becomes the definitive host. In the heteroxenous Acuariidae (arthropods as intermediate hosts and birds feeding on arthropods as definitive hosts) a host switch to birds of prey or owls and herons was achieved *via* small vertebrates (shrews, frogs, fishes) as paratenic hosts, whereupon in the further course of evolution *Stammerinema* succeeded in capturing former paratenic hosts (shrews) as definitive hosts.

Other comparative morphological studies helped in understanding the origin of complex, synorganised structures like the lip complex of *Paraspidodera uncinata* (Heterakidae) by interdigitation of three lips, each with different processes, while individual preconditions for this closing device were found in related groups and in aberrations [19]. The study of aberrations, a theme for Osche from the beginning of his scientific career, to demonstrate the evolutionary potentialities for transformations within a group, was exemplified with the bursal rays of Strongylida by investigating thousands of unfixed specimens and considering a vast literature [6]. Since that time, we are clear that strongylids are closely related to rhabditids. Not knowing about ray-like phasmids in males of rhabditids he wrongly assumed ten pairs of rays as typical and (based on some aberrations) suggested the loss of one ray by fusion of rays nos. 7 and 8, thus forming the externodorsal ray in Strongylida. This fusion of two rays cannot be accepted. The bursa of Strongylida is formed by nine pairs of rays with nos. 4 and 7 pointing dorsally (d), the others ventrally (v), and terminal phasmids (ph). In our formula it reads: v1(v2,v3)/[ad(v4,v5)]pd(v6,v7,ph).

In the only article resulting from his profound research on parasito-phylety and biogeography of Rhigonematidae (parasites of the hind gut of subtropical and tropical diplopods), Osche concentrated on sexual dimorphic structures of the buccal cavity and the pharynx [20]. The pronounced sexual dimorphism in these organs – as different as in two genera – results by prolongation of development in females or an arrest in males at an earlier ontogenetic and evolutionary stage (paedomorphosis). Osche wondered about the selective value for structures concerned with nutrition, but at that time did not yet think of different partial econiches of the sexes [21]. The phylogenetic significance of his analysis of the terminal bulb that exhibits five levels of valves has still to be established. In *Brumptaemilius* he discovered four rows of special sense organs in the vulva region and suggested a stimulatory effect of two rows of cuticularised male papillae precloacal and a spiny area postcloacal (*area rugosa*) during courtship behaviour. His attempt to use the ancient Rhigonematidae as an auxiliary means of research on the historical biogeography of the hosts (Diplopoda) got stuck in its infancy. This was not only due to the onset of his extensive teaching as Professor in Freiburg, but because dozens of new species would first have to have been described, and Osche was not thrilled to do so extensive a taxonomic study. In addition, anticipated biological observations on special rhigonematids like spermatophores [pers. comm. 1970; 22: p. 54] or giant sperms remained unpublished. Osche only casually documented observations about *Rhigonema* feeding on filiform fungi (Eccrinidales) attached on the wall of the hindgut of the host [23: p. 101]. He also documented an undescribed species of rhigonematids with a voluminous buccal cavity carnivorous on other endozooic nematodes [23: p. 115], which he thought emerged from an ancestor grazing on such fungi that also settled on the cuticle of nematodes. The evolution of nematophagous nematodes in the alimentary tract of a host would not have been possible if the ancestors were real parasites and certain substances of the host were indispensable for them. Not until decades later were all these facts discovered and published by other authors. In contrast to most scientists, Osche was not very much interested to claim credit because of priority of observation or thinking; rather, he was delighted if he was confirmed by others coming to the same conclusions. In the same vein, he generously bestowed a cornucopia of new ideas to those close to him.

Günther Osche developed a convincing scenario for the transition of nematodes from free-living to zooparasitic ones. His “preadaptation concept” states that adaptations, successively evolved in saprobiontic nematodes (like rhabditids) living as bacteria-feeders in ephemeral biochores of decaying organic matter and using other organisms initially for transport (phoresy), at least served as a complex of preadaptations for a transition to parasitism in animals [24, 11, 16]. Parasites originated in multiple lineages of Secernentea and in different geological periods, so that very old and relatively young parasitic groups exist side by side. Phoretic and pre-parasitic species are “models” demonstrating, respectively, the successive steps in which parasitism evolved in the past. The “rule of the infective third stage” in parasitic Secernentea, due to the infective larva being a transformation of the phoretic dauer larva, is just as much part of this concept as is the "void in the sea", i.e., the situation that marine invertebrates are nearly free from parasitic "Adenophorea" because the pre-adaptive plateau was not achieved in this paraphyletic group [12]. (Benthimermithidae and Marimermithida are rare exceptions.) This vacancy demonstrates that there exist no “empty niches” to be “occupied”; moreover the animals offer “ecological licences” (redefined by Osche) that cannot be exploited until the organisms first evolved necessary preadaptations (“organismic licences”, coined by Osche) to establish a new econiche.

One reason that Osche was so succesful in discovering new and phylogenetically relevant structures and aberrations was that both in free-living and in parasitic nematodes he could always study ample numbers of live specimens, where many structures are more clearly recognisable. Besides A. G. Chabaud and W. G. Inglis, he was certainly *the* authority in understanding the phylogeny of parasitic nematodes at that time. His articles are an endless source of ideas for scientists even today. Asking a wide range of questions, he approached a subject from every possible angle. By considering the variety of organisms and structures, his aim was to develop a coherent image of evolution of a group, synthesising facts from very different branches of biology to allow predictions. He was a master of such syntheses, resulting in a rounded overall picture. Although he had read the publications of Willi Hennig from the beginning (cited already in his 1952 article [1]) he never in his studies on phylogeny of nematodes employed cladistic methods to reconstruct cladograms or to find apomorphies to establish monophyletic groups, which is the benchmark for all such discussions today. His main interest was anagenesis, not cladogenesis, for which he pursued a strictly gradualistic approach. Among colleages giving talks or plenary discussions that involve gradualistic transformation series and require continuous functionality to cope with daily life, Osche's most-cited statement is that, in contrast to the possibilities that can occur during ontogeny, "evolving organisms cannot close in order to rebuild".

As a professor, Osche had a huge impact on the thinking of students and prospective schoolteachers by his comprehensive and stimulating lectures. He was an exceptionally gifted speaker, who could “explain complex subjects in such a clear way that even non-biologists could follow and could understand the issues” [25]. His excellent lecture on the special zoology of invertebrates, refreshed every year over two decades, nearly attained cult status. At one time he intended to publish a textbook on this topic, but he gave up the idea, among other reasons possibly because he was afraid to satisfy the growing expectations of cladistics in the early seventies. Also brilliant were his many lectures at various societies and symposia, which covered all the domains mentioned at the beginning of this article. He was an enthusiastic participant in scientific debates, where he often clarified discussions with convincing arguments based on his excellent memory and enormous background knowledge in all fields of biology. Whether it was in a greater audience or in a small circle, he enjoyed discussing all aspects of natural history, and during such discussions and dialogues he developed novel ideas by establishing new connections between facts. We owe to him many hypotheses on evolution that accompanied us during our research. Many scientists from different disciplines consulted him, as they appreciated his stimulating enthusiasm and open-minded discussion on their questions and results. He was a supervisor of many student theses and served as editor of several high-class German scientific journals [25], where he altruistically put much work into improving submitted papers. He was beloved, as he was a person of highest integrity, fighting for a matter or a friend, not for his personal gain. His profound knowledge in very different fields of his wide interests and pleasing colourful explanations were admired, and therefore his dominant part in discussion circles was respected.

Prof. Osche was a great scientist and a major figure in German evolutionary biology and zoology. He was a member of many visiting groups and national committees and served as president of the Deutsche Zoologische Gesellschaft (1973–74). His reputation from his nematological work was international, although with two exceptions he published only in German and participated only on two international symposia: 1957 in Neuchatel (Switzerland) on host specificity among parasites of vertebrates and 1960 in Asilomar (California) on comparative biology and phylogeny [16]. Since 1979, he was made a fellow of the Deutsche Akademie der Naturforscher Leopoldina (Halle). In recognition of his outstanding contributions to zoology and evolutionary biology he was awarded the Dr. *honoris causa* at the University of Bonn in 2001. He is honoured in some species names of protists, gastropods and arthropods and the nematode names *Diplolaimelloides oschei* Meyl, 1954 (Monhysteridae), *Parasitylenchus* (*Metaparasitylenchus*) *oschei* Rühm, 1956 (Allantonematidae), *Macdonaldius oschei* Chabaud & Frank, 1961 (Onchocercidae), *Brumptaemilius oschei* Dollfus, 1964 (Rhigonematidae), and the "Rhabditidae" *Oscheius* Andrássy, 1976, *Rhabditis* (*Mesorhabditis*) *oschei* Körner, 1954 and *Rhabditis (Oscheius) guentheri* Sudhaus & Hooper, 1994. Günther Osche maintains a significant presence in his pioneering publications and concepts pointing to the routes for prolific research, and he lives in the memories and hearts of his friends and his alumni.

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