SYNECOLOGY AND EVOLUTION – GERD VON WAHLERT'S APPROACH TO EVOLUTIONARY BIOLOGY

Edited by
Michael Schmitt

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Front cover vignette:
Latimeria chalumnae J. L. B. Smith, 1939 (from VON WAHLERT 1968)

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Against all early prophesies of doom, evolutionary biology, founded on Charles DARWIN's theories of descent with modification based on natural selection, provides an explanatory frame for countless questions in biology. These theories have been tested to date in unimaginably many cases and can, therefore, be regarded extremely well corroborated. The Modern Evolutionary Synthesis has been completed in the early 1950s. Its outcome, however, has been further developed and extended again and again, which is normal for all scientific theories. Gerd VON WAHLERT's contribution has been an essential further development. He focussed on the interdependences of all organisms; his approach is consequently a "synecological" analysis of evolutionary history.

In ecology, it is not an open question but basic understanding that no species of organisms can exist in isolation from all others. However, in phylogenetics it is by

Gerd VON WAHLERT, cutting the marzipan cake model of *La~~s~~timeria chal~~l~~umnae*, served at the symposion dinner on 30th of September, 2000 (left: Hartmut GREVEN; right: Gabriele VON WAHLERT; Axel GOLDAU phot.).

far unclear whether any feature can be modified independently of all others. Charles DARWIN was well aware of the importance of the mutual relations between organisms for evolution. However, until the present time it is common usage to talk about the "phylogeny of the canine" or the "evolution of social grooming". Against this habit stand Gerd VON WAHLERT's statements that life is participation („Leben ist Teilhabe") and all evolution is co-evolution („Co-Evolution herrscht überall").

We, a group of scientific colleagues who hold Gerd VON WAHLERT's ideas in high regard and who apply them ourselves in research and in university teaching, used his 75th birthday (on 26th of August, 2000) as an opportunity to hold a symposium on 30 September 2000 at the Zoologisches Forschungsinstitut und Museum Alexander Koenig in Bonn. Here, we examined the diverse fields of biology in which Gerd VON WAHLERT's ideas bore fruit for a deeper and clearer understanding of evolutionary theory and of the evolutionary history of organisms.

Since Gerd VON WAHLERT never held a full professorship and, therefore, did not found his own "school" at a university, one could get the impression that he did not have an importatn role as an innovator and teacher in evolutionary biology. But even if Gerd VON WAHLERT did not have a university career, this did not lessen the broad impact of his evolutionary ideas. His synecological approach made numerous exciting and extraordinary insights and perspectives accessible to students of evolutionary biology, leading to a far better understanding of the history of living organisms.

The present volume contains the elaborated versions of seven oral contributions presented at the symposium and of one lecture that was planned but could not be given due to unexpected obligations of the author (H. SCHUHMACHER). I wish to thank all authors for their cooperation, and especially Walter J. BOCK (New York) for his willingness to undertake the final English editing of all manuscripts.

It is a pleasure to dedicate this volume to Gerd VON WAHLERT and his wife Adelheid VON WAHLERT. They gave us not only a fresh and stimulating perspective in evolutionary biology, but also demonstrated how this could be achieved by a scientific couple of which the female part may be less mentioned publicly, but is by no means less important.

Michael SCHMITT

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Gerd VON WAHLERT and the German Evolutionary Biology from 1950 to 1970 – a Companion's Perspective

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This symposium on the occasion of Gerd VON WAHLERT's 75th birthday gives me the opportunity to evaluate his achievements as one of the pioneers of German evolutionary biology and evolutionary ecology of the first 20 years after WWII. It was his aim to reach a causal explanation of phylogenetic processes through a synthesis of functional morphology, ethology and ecology, i.e. to render possible an "explanatory natural history" (VON WAHLERT 1968).

Since Ernst HAECKEL's „Systematische Phylogenie" (1894/95), evolution research in Germany was primarily phylogenetics in the sense of analysis of the history of organisms or pure descent without further causal explanation, i.e. search for phylogenetic trees. The first little textbook that had been published in the time Gerd and I studied biology in the late 1940's, written by Gerhard HEBERER (1949), had the significant title „Allgemeine Abstammungslehre" (General Theory of Descent). This theory of descent based mainly on morphology, seen as homology research which yielded the basis for a nested system of organisms and the construction of phylogenetic trees by working out body plans and homology circles. Adolf REMANE described comprehensively methods and theoretical background of this approach in his book „Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik" (1952). This book, too, focussed predominately on the detection of phylogenetic relationships. In contrast, Gerd VON WAHLERT did not consider as fundamental the phylogenetic descent of organisms, instead he was interested in how the major animal groups evolved, and what were the prerequisites for their evolution. He wanted to understand and show the course of the phylogenetic history along with its causation. Thereby he started from the conviction that changes in the relations between the organisms and their environment were the crucial process in evolution. Consequently, he stated (1977: 36): „Die Geschichte der Lebewesen (Stammesgeschichte) muß als Geschichte ihrer Lebensweisen erforscht und dargestellt werden" (The history of the organisms (phylogeny) has to be investigated and described as history of their modes of life) and „Die ökologische Betrachtung der Stammesgeschichte gilt gerade auch für die Hauptlinien der großen Gruppen der Pflanzen und Tiere" (The ecological perspective on phylogeny holds true also for the major lineages of plants and animals) (VON WAHLERT 1981: 10). Such an enterprise requires an incorporation of behaviour and ecology of the organisms into a comparative and synthetic view. In this way Gerd VON WAHLERT strived to establish ecological approaches to evolutionary biology and to the analysis of the evolutionary history of organisms. Through his approach he saw the chance to explain phylogenetic processes causally, and to work out an "explanatory natural history". It was important for him to introduce principles of causality into the exploration of macroevolution (VON WAHLERT 1968). He outlined what he saw as the explanation of the phylogenetic change of a group of organisms: „Ein Evolutionsschritt wird als erklärt angesehen, wenn die Entstehung einer Gruppe aus einer älteren durch eine Änderung der Lebensweise gedeutet werden kann und die dann erfolgten morphologischen Änderungen als Anpassung an die Änderung der Lebensweise dargestellt werden können" (An evolutionary history is regarded explained if the emergence of one group of organisms from an older one can be interpreted as a change in the mode of life, and the morphological transformations can be shown to be adaptations to this change in the mode of life; 1968: 115). To Gerd VON WAHLERT, it always mattered to understand the evolution of a group of organisms as a true historical process for which a narrative explanation based on underlying causal mechanisms is essential. Therefore, he did not hesitate to add the subtitle "An explanatory natural history of vertebrates ... told by Gerd VON WAHLERT" to the book „Das Schädelkabinett" which he jointly authored with Eva HÜLSMANN (1972).

Other contributions to this volume treat Gerd VON WAHLERT's scientific achievements, i.e. results obtained through a combination of field work and laboratory studies. My aim is to sketch briefly the situation of evolutionary biology in Germany during the period between 1950 and 1970 in order to shed some light on the background and the environment against and in which Gerd VON WAHLERT developed and improved his approach.

Only one year younger than Gerd VON WAHLERT, I lived in the same time as he and can, therefore, report as a contemporary. The two of us received our doctoral degree in 1951 with dissertations in the broad field of evolutionary biology: Gerd VON WAHLERT, supervised by Wolf HERRE at Kiel University, presented his thesis on „Eileiter, Laich und Kloake der Salamandriden" (Oviduct, spawn and cloaca of the salamandrids) which was partly published as a comparative explanatory natural history of urodeles (1953). I was supervised by Hans-Jürgen STAMMER at Erlangen, working on "Systematics and phylogeny of the genus *Rhabditis* (Nematoda)". Just the titles of our dissertations demonstrate how close our aims were. Gerd VON WAHLERT adhered to the vertebrates through the following 20 years, I to the invertebrates, and throughout our lifetime we were concerned with evolutionary biology. Thus, we experienced as fellow travellers the period between 1950 and 1970 which HOSSFELD (1999) called the Golden Age of the evolutionary synthesis, we met at the regular meetings of the German Zoological Society (DZG) and at the [North German] Phylogenetic Symposia (KRAUS & HOSSFELD 1998), where we discussed and "slandered" a lot, we corresponded much and underwent many a "reciprocal illumination".

Let me report firstly as a *contemporary*.

What was the time like when we studied and received our degrees? One year after the end of that terrible war, close to the "hour zero", the German universities reopened their gates in 1946. It was a miserable time when everything was short, not just food, clothing and dwelling, but to us students especially text books (during the first semesters we had to rely completely on our notes of the lectures) and later, during our work on our dissertations, international scientific literature and equipment were also scarce. Many university teachers were killed during WWII, others were still in captivity or not yet reinstalled. The German Zoological Society (DZG) had suspended up by the occupying powers, and its re-establishment was not achieved before 1949. The re-founding document of the DZG bears the signature of the unforgettable mayor of West-Berlin, Ernst REUTER (this and all other information on the first DZG meetings from GEUS & QUERNER 1990). In the years before this re-establishment of the DZG, Berthold KLATT, Adolf REMANE and Wolf HERRE initiated a first "unofficial" meeting of the German zoologists at Kiel (where Gerd VON WAHLERT studied at this time). This meeting was attended by 186 zoologists who had to be asked with the invitation letters to be certain that they brought bedding with them. In August, 1949, the German zoologists met in Mainz for a second time immediately before the re-establishment of the DZG. At this time 262 participants were recorded who learned the shocking news that during the war years between 1939 and 1945, 341 members of the DZG had been killed or died (HOSSFELD 1998). The first official annual DZG meeting after WWII was held at Marburg in August, 1950, hosted by Wulf Emmo ANKEL. Werner ULRICH (Berlin) gave an invited lecture on „Vorschläge zu einer Revision der Großeinteilung des Tierreichs" (Proposals for a Revision of the Major Divisions of the Animal Kingdom), purely descriptive and lacking any evolutionary biological approach. Apparently, the organizers were not quite satisfied by the congress since immediately afterwards W.E. ANKEL wrote to B. KLATT: „Ich bin ebenso, wie Sie der Meinung, daß man als Referenten künftig mehr die junge Generation heranziehen sollte. Natürlich nicht gerade die Blastulae, sondern, sagen wir, die Metatrochophorae! Aber wen?" (I agree with you that we should in the future recruit the invited speakers more from the younger generation. Of course, not just the blastulae but more, let's say, the metatrochophorae! But whom?). Gerd VON WAHLERT and I were still "blastulae" at that time, but few years later, at the Freiburg meeting in 1953, Gerd VON WAHLERT reported on his results on „Verlauf und Wesen der stammesgeschichtlichen Entwicklung der Schwanzlurche" (Course and nature of the phylogenetic development of the urodeles), and in 1955, when the DZG met at Erlangen, I could discuss on „Die Präadaptation freilebender Nematoden an den Parasitismus" (The preadaptation of free living nematodes for parasitism).

What did the relaunch of evolutionary biology in Germany after WWII look like? During the Nazi times since 1933, and especially during war times (1939–1945), Germany was isolated from international research, in the beginning only

partially but later totally. Into this period fall the years of the synthetic theory of evolution (1937–1950) in the USA and Britain during which the central books of the Modern Synthesis of evolution were published; namely:
1937 Theodosius DOBZHANSKY: Genetics and the Origin of Species
1942 Ernst MAYR: Systematics and the Origin of Species
1942 Julian HUXLEY: Evolution. The Modern Synthesis
1944 George Gaylord SIMPSON: Tempo and Mode in Evolution.

None of these basic works were accessible to most German biologists during this time. This circumstance became shockingly evident when, 11 years after the end of WWII, the first phylogenetic symposium was held at Hamburg in 1956. Its topic was „Genetik und Evolutionsforschung“ (genetics and evolutionary research) which had attracted a series of prominent biologists, e.g., Kurt KOSSWIG (Hamburg, the organizer), Adolf REMANE and Wolf HERRE (both from Kiel and academic teachers of Gerd VON WAHLERT), and further on, amongst others, Gerhard HEBERER (Göttingen) and Dietrch STARCK (Frankfurt am Main). There were hardly any "metatrochophorae" on this first meeting. As a guest speaker, Ernst MAYR introduced the principles of the evolutionary synthesis. On the occasion of a workshop on the question „Gab es eine Moderne Synthese in der deutschen Evolutionsbiologie“ (Has there been a Modern Synthesis in German evolutionary biology) in December of 1996 (JUNKER & ENGELS 1999), Ernst MAYR remembered the discussions of the Hamburg meeting in 1956: "Virtually all attending argued against the synthesis" … "There simply was no sense to argue with people who (except for de Lattin) did not know population genetics. So I stopped arguing". Erwin STRESEMANN, who had heard through Erna MOHR (curator of mammalogy at Hamburg museum) of Ernst MAYR's "capitulation", wrote his student and friend Ernst MAYR highly stunned: "Ernst, this doesn't sound like you. I am sure you would have argued to the bitter end" (MAYR 1999). It becomes clear why just Erwin STRESEMANN was so surprised by this situation if one knows that he was one of the crystallization centres within the just beginning synthesis of systematics, population genetics and biogeography in Germany. The roots of population genetics lay in the early 1920's in Moscow, where Sergey CHETVERIKOV began his investigations on the population genetics of *Drosophila* (1926). Shortly thereafter, he published his ideas in German (1928), in a paper entitled „Die genetische Beschaffenheit wilder Populationen“(The genetic constitution of free living populations). Two of his students, Theodosius DOBZHANSKY and Nicolaj Vladimirovich TIMOFÉEFF-RESSOVSKY, continued CHETVERIKOV's approach in the USA and in Germany, respectively. When Oskar VOGT, at that time director of the Kaiser-Wilhelm-Institute of Brain Research in Berlin, was in Moscow in 1924 (in order to undertake research on Lenin's brain), he invited Nicolaj TIMOFÉEFF-RESSOVSKY and his wife Elena, who also worked on population genetics, to join the team at the Berlin institute. The TIMOFÉEFF-RESSOVSKYS did extremely successful research for 20 years at Berlin until Nicolaj was arrested by the Soviets in 1945. He was sentenced to prison camps in Siberia because he had refused to return to the USSR in 1937 (HAFFER et al 2000;

SATZINGER & VOIGT 2001). N. TIMOFÉEFF-RESSOVSKY laid the foundations for the German population genetics during his years in Berlin.

N. TIMOFÉEFF-RESSOVSKY regularly held a colloquium on evolution at his department in Berlin-Buch, which often was attended by Bernhard RENSCH and William Friedrich REINIG. Especially important to German evolutionary biology was the cooperation between N. TIMOFÉEFF-RESSOVSKY and Erwin STRESEMANN who was head of the bird department at the Berlin Museum of Natural History since 1921. The two of them were primarily concerned with the geographic differentiation within species, and with the emergence of geographical „Formenkreise" (roughly: superspecies), i.e. with the evolution of subspecies and with speciation. From this cooperation, a joint paper resulted but could only be published in 1947 on the „Formenkreis" of *Larus argentatus-cachinnans-fuscus*. It was then cited in many textbooks of zoology (detailed descriptions of the cooperation between these two scientists can be found in HAFFER 1999 and HAFFER et al 2000).

The most renowned learned society of Germany, the Deutsche Akademie der Naturforscher Leopoldina, elected N. TIMOFÉEFF-RESSOVSKY as a member in 1940, on nomination of Alfred KÜHN, and acknowledged his achievements by awarding him the Darwin-plaquette in 1959 and the Mendel-medal in 1970 (PATHIER 2001).

With STRESEMANN and N. TIMOFÉEFF-RESSOVSKY forming the nucleus in Berlin, a series of scientists gathered together who worked on a synthesis of population genetics and systematics, and who strove after a "physiological definition" of the species that could form the basis of the biological species concept. Included was Bernhard RENSCH, from 1922 to 1924 co-worker of Erwin STRESEMANN, from October, 1925, assistant at Berlin Zoological Museum, where he later became head of the department of molluscs and in 1929 wrote his book on „Das Prinzip der geographischen Rassenkreise und das Problem der Artbildung" (The principle of geographic Rassenkreise and the problem of speciation). Ernst MAYR worked here as a doctoral student (PhD in 1926), supervised by Erwin STRESEMANN, he was an assistant from 1926 until 1932 at the Zoological Museum and regarded himself later as STRESEMANN's "younger brother". He has pointed out several times that STRESEMANN had the biological species concept long before himself (RUTSCHKE 2000). In 1999, Ernst MAYR paid tribute to his teacher's preparatory work writing that "virtually everything in MAYR's 1942 book was somewhat based on STRESEMANN's earlier publications". Therefore, it is not astonishing that in this atmosphere the plan arose in Berlin in 1938 – stimulated by N. TIMOFÉEFF-RESSOVSKY – to found a "working group for experimental and biogeographical evolution research" within the Prussian Academy of Sciences. William Friedrich REINIG, who these times intensively analyzed the formation of geographical subspecies, the meaning of "elemination" (= genetic drift) and other factors of evolution, was intended to become head of this working group.

How close STRESEMANN also came to those evolutionary problems which were in the focus of Gerd VON WAHLERT's later research, is shown by a manuscript only now published by HAFFER et al (2000: 343), resulting from a series of lectures given by STRESEMANN to American museums and universities, entitled "On the relation of structure to function". Here, STRESEMANN emphasized that in the first period following DARWIN, the main aim of morphology was to reveal the relations of descent between the organisms by evidence of homologies. In contrast, STRESEMANN's "biological morphology proceeds to study the animal connection with its surroundings, regarding both as an indivisible whole ..." and "in this way morphology becomes intimately connected with ecology, physiology, ethology, and finally also psychology".

The attempts to establish the "working group for experimental and biogeographical evolution research" failed in the end. Also failed was a department of ecological research which was planned within this "working group". The beginning of WWII brought the end to all those plans. It can hardly be imagined what such a "working group" could have meant to the development of an evolutionary synthesis in Germany. Anyway, right in the middle of the war Gerhard HEBERER, friend to Bernhard RENSCH since school days and participant in his expedition to the Smaller Sunda Islands in 1927, dared to publish an attempt of a synthesis. In the work that HEBERER edited on „Die Evolution der Organismen und Probleme der Abstammungslehre“ (The evolution of organisms and prob-lems of the theory of descent) in 1943, several authors (amongst them Bernhard RENSCH, Nicolaj TIMOFÉEFF-RESSOVSKY, Konrad LORENZ) were offered the opportunity to present contributions from their field of expertise. The first edition was sold out quickly, within five months. Two further editions (1959 and 1974) with further cooperation of some new authors (e.g., Adolf REMANE, Wolfgang WICKLER) yielded substantial additions.

Written in the last years of WWII but published in 1947 was Bernhard RENSCH's „Neuere Probleme der Abstammungslehre – die transspezifische Evolution“ (the English translation was entitled "Evolution Above the Species Level", 1959). This book immediately became most important for the further development of evolutionary biology in Germany. RENSCH sought to demonstrate that „... die Faktoren der Rassen- und Artbildung d.h. Mutation, Genkombination, Genausbreitung, Selektion und Isolation, genügen können, auch den Ablauf der transspezifischen Evolution zu erklären.“ (...the factors forming subspecies and species, i.e. mutation, gene combination, gene dispersion, selection and isolation, are sufficient to explain also the course of transspecific evolution.) (from the preface to the 3rd edition in 1972). Only after the first edition was printed, did RENSCH acquire access to the most important books of HUXLEY (1942), MAYR (1942) and SIMPSON (1944), a consequence of the above mentioned isolation of the German research through many years. After reading these books, RENSCH could realize with satisfaction that „... die geistige Gesamthaltung .. (ihrer) rein kausalistischen Erklärungsweisen“ (... the total intellectual attitude in their purely causalistic modes of explanation) coincided entirely with his ideas. He found especially high affinities to the ideas advocated by the paleontologist SIMP-

SON. The relationship between macroevolution (RENSCH's "transspecific evolution") and microevolution (RENSCH's "infraspecific evolution") was object of a lively debate in the 1950s.

Since Gerd VON WAHLERT's interest was primarily directed at "The Role of Ecological Factors in the Origin of Higher Levels of Organization" (1965), I briefly outline the opposite opinion. Three years after the comprehensive account by RENSCH, and during our student days, the Tübingen-based paleontologist Otto SCHINDEWOLF published in 1950 his „Grundfragen der Paläontologie, geologische Zeitmessung, organische Stammesentwicklung, biologische Systematik" (Basic problems in paleontology, measuring geological time, organic phylogenetic development, biological systematics). SCHINDEWOLF was a typologist, like many of his contemporary paleontological colleagues and biologists in Germany. He demanded "type saltations" (Typensprünge) and also proper "macromutations" to explain macroevolution, and he emphasized the episodic nature of the course of evolution. He described a sequence of a relatively rapid "typogenesis," followed by a much longer and stable phase of "typostasis," which was said to merge into "typolysis" which led into extinction and thereby completed the whole "typostrophe." This idea, that evolution does not proceed gradually, in small steps, but in "saltations," i.e. in leaps, has arisen several times in the history of evolutionary biology. In 1933 and in 1940 it was brought up by Richard GOLDSCHMIDT, and in 1972 by Niles ELDREDGE and Stephen Jay GOULD, whose theory of "punctuated equilibria" and at the same time disapproval of the idea of gradual evolution is to a great degree reminiscent of SCHINDEWOLF's concepts.

In 1938, even before RENSCH and SCHINDEWOLF, the Tübingen-based botanist Walter ZIMMERMANN had stated that he believed that the same factors operated in macroevolution as in microevolution, and he described this conclusion in more detail in his book on „Grundfragen der Evolution" (Basic problems in evolution) in 1948. Also Gerhard HEBERER had argued emphatically in favour of a gradual view on evolution, for the first time on the unofficial zoologists' meeting at Kiel in 1948. There, he presented his concept of "additive typogenesis" which he explained more extensively in the 2nd edition of his „Evolution der Organismen" in 1959. According to this concept, new "types" arise by a sequence of small steps through addition of mutationally produced changes within a wide „Übergangsfeld" (transitional field). The continuity of evolutionary processes from microevolution to macroevolution was stated most insistently by Walter ZIMMERMANN in his contributions to HEBERER's „Evolution der Organismen" (1959, 1967). He pointed out that evolutionary change must take place in an continuous chain of ontogenies from one level of organisation to the next which he termed "hologenesis". He wrote concisely: „Die Abwandlung der Ontogenien im Verlaufe einer Hologenie ist eben das, was wir Phylogenie oder Evolution nennen" (The change of ontogenies in the course of a hologenesis is just what we call phylogeny or evolution). „Unter Hologenie verstehe ich die Gesamtheit der Organismenänderungen in Gestalt und Lebensweise" (By hologenesis I mean the whole of organismic change in form and mode of life; 1967: 88). This concept of hologenesis does not ask for "descent" in the first place, but rather looks at the change of properties (of forms and modes of life!) in the series of generations, i.e. after the concrete process of evolution.

This is evolutionary history, and this is Gerd VON WAHLERT's subject. He aims at explaining evolutionary history, and he wishes to tell its story. In order to do this, the synthetic theory of evolution, as it was at that time, had to be broadened. In the 1950s, the evolutionary synthesis sought mainly for the factors of evolution, its main subject was speciation, the "origin of species," a phrase which significantly appears in the titles of DOBZHANSKY's (1937) as well as MAYR's (1942) books, following DARWIN (1859). The analysis of the evolutionary history, i.e. the course of evolution, as intended by Gerd VON WAHLERT, required besides morphology and systematics, the inclusion of ethology and ecology as elements of a synthetic consideration. Therefore, I will consider briefly the state of the discussion in these fields and their connections to evolutionary biology in Germany between 1950 and 1970. This is done to illustrate the background of the developing evolutionary ecology and Gerd VON WAHLERT's approach.

a) Morphology in those times was primarily search for homologies. „Morphologie als Homologienforschung" (Morphology as homology research) was the title of a lecture given by Adolf REMANE to the DZG meeting at Tübingen in 1954. Wilhelm TROLL, at these times Germany's leading plant morphologist, was – like the paleontologist Otto SCHINDEWOLF – a follower of idealistic morphology and regarded biomorphology and biosystematics as typological science (as he entitled an essay in 1955 – „Biomorphologie und Biosystematik als typologische Wissenschaft").

To Gerd VON WAHLERT rather a functional than a comparative morphology mattered. He was interested in an approach to understand a functioning structure and its role in the interaction with the environment (or rather Umwelt, BOCK & VON WAHLERT 1965). Such a perspective was in Germany mainly introduced by vertebrate anatomist Hans BÖKER who investigated the functions of structures in the natural environment of organisms, in order to grasp their adaptational nature. This enterprise led already in 1924 to a „Begründung einer Biologischen Morphologie" (Foundation of a Biological Morphology) and was extensively outlined in his two volume work of 1935/37 „Einführung in die Vergleichende biologische Anatomie" (Introduction to Comparative Biological Anatomy). Regrettably, he explained the adaptation of the structures under consideration by means of direct environmental influence, i.e. he was a Lamarckist. However, this was not unusual these days. Even STRESEMANN, RENSCH and Ernst MAYR adhered to the idea of inheritance of acquired characters until the early 1930's, i.e. they, too, were Lamarckists (MAYR 1999: 22).

Already Charles DARWIN (1859) attempted to show that organs can change their function or role in the course of evolution using swim-bladder and lung as a model. Anton DOHRN presented substantial evidence in his book „Der Ursprung der Wirbeltiere und das Prinzip des Funktionswechsels", 1875 (The origin of the vertebrates and the principle of change of function). However, Gerd VON WAHLERT developed the most important foundations of this approach himself, jointly with Walter BOCK in a seminal paper on "Adaptation and the form-function complex" (BOCK & VON WAHLERT 1965). Here, the authors clearly distinguish between "function" and "biological role" of a feature. The former is subject to functional morphology, the latter can only be studied by looking on live organisms in their natural environment. Through change of roles (by change of behaviour) a feature can become a "morphological key character" opening up new modes of life, new environmental and functional relationships and, therefore, new ecological niches. In this way, new selective factors enter the game, leading to evolutionary change. In this context it became important to ask for the prerequisites for such an opening of new modes of life and new biotopes, i.e. for the special preadaptations (= predispositions) or the complex "preadaptive plateau." This subject was discussed by Walter BOCK (1959) as well as myself (1955, 1961).

Transferring of existing (preadaptive) structures to new functions and roles requires changes in behaviour and implies, therefore, inclusion of an additional discipline into the synthetic view.

b) Ethology was – within a phylogenetic framework – as "comparative behaviour research" originally oriented to homologize modes of behaviour and make them useful to systematics. Under these auspices Charles O. WHITMAN (1919) investigated "the behavior of pigeons", O. ANTONIUS (1937) studied the behaviour of horses, and Oskar HEINROTH (1911) and Konrad LORENZ (1941) the behaviour of anatids.

To Gerd VON WAHLERT, the taxonomic meaning of behavioral homologies was not the only area of interest. Rather he wanted to know the role of behaviour and its evolutionary modifications as "ethological key character" and consequently as the pacemaker in the establishment of new ecological niches and zones. Likewise, Wolfgang WICKLER saw „Die ökologische Anpassung als ethologisches Problem" (the ecological adaptation as an ethological problem; 1959) and chose as heading of one of the chapters in his contribution to HEBERER's „Evolution der Organismen" (1967) „Verhaltenseigenschaften als Schrittmacher der Evolution" (Behavioral features as pacemakers in evolution). In this chapter, Wickler referred to Gerd VON WAHLERT „Verhaltensweisen gehen in der Evolution voran, weil sie das im Dienst der Anpassung variabelste Element sind" (Modes of behaviour lead the way in evolution because they are the most variable element serving adaptation).

c) Ecology plays the crucial part in Gerd VON WAHLERT's approach. The term ècology' was coined by Ernst HAECKEL and introduced to science in his basic work „Generelle Morphologie der Organismen" (1866, vol. 1: 238, vol. 2: 286). There, he defined the term in a way it made this new discipline useful to evolutionary biology: ecology is „... die gesammte Wissenschaft von den Beziehungen des

Organismus zur umgebenden Außenwelt, wohin wir im weiteren Sinne alle ‚Existenz-Bedingungen' rechnen können. Diese sind theils organischer, theils anorganischer Natur; sowohl diese als jene sind ... von der grössten Bedeutung für die Form der Organismen, weil sie dieselben zwingen sich ihnen anzupassen" (...the whole science of the relations between the organism and the surrounding exterior world, whereto we can count in a wider sense all conditions of existence. These are partly an organic, partly an inorganic nature; these as well as those are ... most important to the form of the organisms since they force the latter to adapt to them) (1866: 286). While HAECKEL especially emphasized the impact of exterior factors on relationships between organism and environment, Jacob Baron VON UEXKÜLL first emphasized the behaviour of animals towards their environment. In his books „Theoretische Biologie" (1920) and „Umwelt und Innenwelt der Tiere" (1921), he developed his „Umweltlehre" (theory of Umwelt – roughly: environment, see BOCK & VON WAHLERT 1965) and observed the relations of organisms and their Umwelt in their different „Funktionskreise" (roughly: functional contexts). Thereby he distinguished between „Umwelt" and „Umgebung". Animals perceive certain elements of their „Umgebung" (= physical environment), depending on their species-specific sensory equipment. Through perception, these elements become part of their „Sinneswelt" (sensory world) or „Merkwelt" (perceived world). They interact only to certain elements of their „Merkwelt" and make them elements of their „Wirkwelt" (action world). „Merkwelt" plus „Wirkwelt" make up the „Umwelt" of a species. VON UEXKÜLL therefore defined ‚Umwelt' as the whole of all environmental factors which are relevant to the members of a species. A consequence of this view is the possibility that different species could establish different „Umwelten" within the same „Umgebung" (or 'biotope', in modern terms). By this refinement of the concept of environment, VON UEXKÜLL came very close the concept of "ecological niche" as introduced by Charles ELTON in 1927. VON UEXKÜLL's considerations have been perceived as extremely stimulating by some biologists in the 1930s. Thus, Erwin STRESEMANN wrote to Ernst MAYR in 1934 that VON UEXKÜLL's book „Umwelt und Innenwelt der Tiere" had impressed him „fast so ..., wie die Paulusbriefe den Augustinermönch Luther ..." (nearly that much as the Epistles of St. Paul did on the Augustine monk Luther ..); and he urgently recommended to his friend to read this book (cited from HAFFER et al. 2000: 264). In any case, VON UEXKÜLL's ideas did not succeed in those days since he was a typologist and adherent of holism, and therefore disproved of phylogenetic interpretations (POTTHAST 1999). In total contrast, Charles ELTON referred explicitly to evolutionary biology when defining 'ecological niche' in his book on "Animal Ecology" in 1927, which led to broad international acceptance. In ELTON's concept, the biotope (VON UEXKÜLL's „Umgebung") played the role of the "address" of a species, while the ecological niche was a species' "profession".

However, the niche concept became important to Gerd VON WAHLERT only in its new and much stricter version as advocated by Klaus GÜNTHER (1950). GÜNTHER defined 'ecological niche' as a network of interaction of "autozoic" (i.e. pertaining to the organism) and "oecic" (i.e. offered by the „Umgebung") constituents. Only this interaction constitutes the ecological niche. The importance of GÜNTHER's concept of ecological niche to evolutionary biology differs markedly from ELTON's. According to GÜNTHER, unoccupied (empty) niches cannot exist by definition, in contrast to ELTON. Besides the redefinition of `niche', GÜNTHER (1950) likewise refined SIMPSON's concept of adaptational zones, a concept especially important for transspecific evolution. GÜNTHER considered an adaptational zone to be a dynamic system of interaction between organisms and environment, and consequently broadened this concept into the "ecological zone" which is – like the niche – defined in terms of ecological interaction (for detailed discussions of GÜNTHER's role in evolutionary biology see SCHMITT 1987, 1991; SUDHAUS 1996).

The ecological niche and the ecological zone in the dynamic version of GÜNTHER (1950) were the concepts on which were based Gerd VON WAHLERT's evolutionary-ecological approach. RENSCH (1947) assumed as a prerequisite for the evolution beyond species level the origin of novel biotopes devoid of competition because of geological events, or even the existence of biotopes occupied by significantly inferior competitors („stark konkurrenzunterlegenen Typen"). In VON WAHLERT's view the opening of a biotope not inhabited before is made possible by a change in mode of life of a species and permits the establishment of ecological niches and zones not existing before. It is not at all necessary that by the establishment of new niches, existing organisms became "out-competed" and went extinct, rather the result could be an „Überschichtung" (self-layering), and consequently an increase in different modes of life and new organismic forms (VON WAHLERT 1977, 1978). To demonstrate this view by concrete case studies is, in VON WAHLERT's opinion, an "ecological description of phylogeny".

d) Systematics is the last discipline that has to be included into Gerd VON WAHLERT's approach. Here, the arising controversies can be shown in full clarity. Especially the difference between phylogenetics in the sense of theory of descent or search for trees and Gerd VON WAHLERT's attempt to reveal the unique evolutionary history becomes evident. Classical systematics is based on a search for homologies which enables the grouping of the diversity of species together according to „Homologie-Kreise" (homology rings; REMANE 1952: 105). These result in a classification possessing "lower" and "higher" categories, i.e. a nested system making it possible to master this diversity. "System" was comprehended originally in a purely typological way. After DARWIN's explanation of homology as the result of genealogical relationship, "typological" systems could be turned into "natural" ones, representing real kinship relations. These could be presented as phylogenetic trees, as shown extensively by HAECKEL in his „Systematische Phylogenie" (1894/95). Half a century later, the entomologist Willi HENNIG worked out the first version of his book „Grundzüge einer Theorie der phyogenetischen Systematik" during his time as a prisoner of war in Italy in 1945. This book was published only in 1950, right when Gerd VON WAHLERT and I worked on our doctoral dissertations. This book revolutionized systematics and provoked discussions lasting until the present day (for more on Willi HENNIG and his work see SCHLEE 1978 and SCHMITT 1996, 2001).

HENNIG's method requires making systematic work definitely more precise and aims at a substantiated and therefore criticizable outline of proposed genealogical relations. It is based on the process of speciation. According to HENNIG, by "splitting" of one stem species two new species (daughter species, which are then sister species) evolve, while the stem species goes extinct obligatorily. Through continued splitting events sister groups evolve which are characterized by the fact that they can be traced back to a stem species associated exclusively (!) to them. HENNIG states that hypotheses on "monophyly" can be substantiated in this way only. And only taxa that are monophyletic in this sense are admitted in his phylogenetic system. Monophyly of a taxon can be recognized and substantiated if one is able to show that all possible members of a monophyletic taxon have at least one apomorph (derived) character in common that had been acquired as an evolutionary novelty in the last common ancestor (SUDHAUS & REHFELD 1992). Only apomorph characters as commonly inherited features (synapomorphies) can support a hypothesis on sister-group relationship. Primitive characters, so-called plesiomorphies, are not considered when constructing a phylogenetic system sensu HENNIG. Sister-group relations can be represented unequivocally in cladograms, thus offering a subject to critical discussion.

Although Gerd VON WAHLERT worked from 1962 for 12 years at the same institution as Willi HENNIG – the Stuttgart Museum of Natural History at Ludwigsburg – HENNIG was quite skeptically disposed towards considering evolutionary-ecological aspects when constructing a phylogenetic system. HENNIG's „Stammesgeschichte der Insekten" (1969) contains a chapter on „Stammesgeschichtsforschung und Evolutionsökologie" (Phylogenetic research and evolutionary ecology, p. 41). However, the main aim of this chapter is to criticize that evolutionary-ecological statements do not take into account the apomorphies he demanded and therefore often remain non-committal remarks („im Unverbindlichen steckenbleiben," p. 43) and give a story tale impression (p. 42). Hence, HENNIG concludes „All diese Schwierigkeiten haben uns bestimmt, in der folgenden Darstellung evolutionsbiologischen Erörterungen nur einen bescheidenen Raum beizumessen." ("All these difficulties have made us attach only modest space to evolutionary-biological disputations", p.45). HENNIG's skeptical attitude becomes understandable if one knows what he considers phylogenetic research to be. He wrote (1969: 33): „Stammesgeschichtsforschung ist ein wesentlich systematisches Problem. ... Ihre Ergebnisse beruhen darauf, daß rezente Arten zu Gruppen zusammengefaßt werden und daß Fossilien ... diesen rezenten Gruppen zugeordnet werden." (Phylogenetic research is essentially a systematic problem ... its results come from grouping recent species and attaching fossils to these groups). Obviously, HENNIG did not discriminate here between descent and phylogeny. His concepts allowed for recognizing degrees of commonality of descent ("genealogical relationship") and to represent it in a phylogenetic system and/or a cladogram – neither more nor less. HENNIG's reservation towards considering the results of evolutionary biology sensu Gerd VON WAHLERT becomes clear if one knows that HENNIG was a museum entomologist who analyzed preserved recent organisms and – mainly amber – fossils to obtain phylogenetic characters, i.e. he did not work on live organisms in their natural habitats. In such an approach is no space for an evolutionary ecology that requires the observation of the behaviour of animals in their natural environment.

In contrast, Gerd VON WAHLERT emphasizes explicitly that the genealogical relationships of a taxon under consideration have to be settled before one attempts at an evolutionary-ecological "explanation". However, cladograms are in this context just a skeleton waiting to be filled with life. Gerd VON WAHLERT expresses this clearly when writing (1981: 29) „Die gesamte Evolution geht mit Artentrennung einher .... Das besagt natürlich nicht, daß wir mit dem Verständnis der Artentstehung auch schon die gesamte Evolution verstehen. Diese lange gehegte Ansicht hat sich als vorschnelle und unzutreffende Verallgemeinerung erwiesen." (The whole of evolution is accompanied by splitting of species ... Naturally, this does not mean that we understand the whole of evolution if we understand speciation. This long held opinion has proved to be a premature and inappropriate generalization). In 1971, Gerd VON WAHLERT again made clear: „Anders als die Phylogenetik geht die Evolutionsbiologie den kausalen Zusammenhängen der Stammesgeschichte nach – dazu gehört die Untersuchung der Lebensweisen und ihr Vergleich." (Different from phylogenetics, evolutionary biology traces the causal interrelations in phylogeny – investigation on modes of life and their comparison is necessary).

I see the main causes of the problems HENNIG faced in considering evolutionary-biological and evolutionary-ecological discoveries when constructing the phylogenetic system of a group of organisms in the following three aspects:

- As already mentioned, evolutionary biology sensu VON WAHLERT can only be done on live animals in the wild, not on museum material.
- The evolutionary novelties (apomorphies) on which hypotheses on monophyly and sister-group relations are based are rarely those key innovations which made possible the establishment of a new ecological niche by a species or a new ecological zone by a group. Thus, HENNIG lists as the only synapomorphy uniting cockroaches and termites constituting the Blattodea the lack of the anterior ocellus of their frontal eyes. As the apomorphies constituting the Crustacea he gives the fact that the frontal eyes have approached each other, thus forming a nauplius eye, and the restriction of excretory organs to two head segments (1969). In both cases, these were certainly not the novelties which facilitated the origin and radiation of these two taxa.
- Similar reservations apply to the majority of characters regarded crucial by phylogenetic systematics. On the other hand, preadaptations important for the formation of new ecological zones are, as a rule, offered by plesiomorphies (e.g., fish lungs as prerequisites for acquiring a terrestrial mode of life and, consequently, for the radiation of the tetrapods). However, plesiomorphies are meaningless for detecting genealogical relationships.

– In phylogenetic systematics, only the splitting of species into sister-taxa – the cladogenesis – matters, but not the transformation of features or characters during the succession of generations without splitting, termed anagenesis or phyletic evolution. Precisely in the course of anagenesis, however, the real evolutionary transformation of characters takes place, untouched by all species splitting, and within the continuity of hologenesis (ZIMMERMANN). Within this hologenesis, the evolutionary species (SIMPSON 1961) forms an "evolutionary lineage in time" (SUDHAUS & REHFELD 1992), it is "on the way through its phylogenetic history," as it were. Particularly during this anagenesis it comes to "additive typogenesis" (HEBERER), just here the "phyletic sequences" (VON WAHLERT) are realized. These "phyletic sequences" in total result finally in the new Bauplan or the constituting ground pattern which enables the subsequent adaptive radiation of a – perhaps speciose – new group of organisms. But this ground pattern is made up by both apomorphies and plesiomorphies (SUDHAUS & REHFELD 1992). In the different assessment and consideration of cladogenesis and anagenesis lies the essential root of the controversies between "consequent phylogenetic systematics" sensu HENNIG and the so-called "evolutionary classification" as advocated by Ernst MAYR in his "Principles of Zoological Systematics" (1969). He wishes to express in his system not just cladogenesis but also anagenesis (see the chapter on "cladistic contra evolutionary systematics" in MAYR 1976: 435).

This is the end of my cursorily and certainly subjective survey of the situation in different disciplines of zoology, as far as they provide background and milieu of Gerd VON WAHLERT's ideas and research. A proceedings volume edited by JUNKER & ENGELS (1999) contains a much broader and deeper analysis of the role the disciplines mentioned here played in the development of the evolutionary synthesis between 1930 and 1950. The most important foundations of a biological-ecological analysis of the process of evolution to which Gerd VON WAHLERT contributed were completed and published in the mid 60's and were, therefore, already treated properly in the handbook chapter on „Grundzüge der allgemeinen Phylogenetik" (Principles of general phylogenetics) (OSCHE 1966), where the state of the evolutionary biology of that time is reviewed.

Gerd VON WAHLERT's advocation of an "explanatory natural history" (VON WAHLERT 1968) received recognition and consideration. In his great work on "The growth of biological thought" (1982), Ernst MAYR acknowledges VON WAHLERT's achievements, writing that Gerd VON WAHLERT is "... among the pioneers in this new evolutionary morphology". And MAYR continues that "their approach built a bridge between morphology and ecology, leading to the establishment of a new borderline field which is still in its youth and on the threshold of further interesting developments" (p. 613). There is nothing to add.

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The urodele oviduct and its secretions in and after G. von Wahlert's doctoral thesis „Eileiter, Laich und Kloake der Salamandriden"

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Abstract. After a short historical introduction, a survey is given on the structure and function of the urodele oviduct and its secretory products. The selection of topics is determined at least partly by statements in G. von Wahlert's doctoral thesis which are used as starting points. The paired oviducts begin anteriorly with the ostium (infundibulum) and a short straight segment (*pars recta*) each. They continue with a convoluted part (*pars convoluta*) that can be easily divided in three main portions. This part is followed by the most posterior uterine portion, often considered as segment of the convoluted part. Each oviduct opens separately into the cloaca posteriorly. Subdivisions of the convoluted part, probably taxon-specific, can be identified in histological sections, particularly when stained for mucopolysaccharides. However, uniform criteria for subdividing the oviduct and careful comparative studies are missing as yet. Appearance of the oviduct clearly depends on the mode of reproduction (oviparity *versus* viviparity) and the reproductive cycle. A considerable part of the monolayered epithelium lining the oviductal lumen, above all that of the *pars convoluta*, is differentiated into large columnar gland cells and/or tubular glands and contains ciliated cells. The columnar secretory epithelium and tubular glands reflect two different structural types of oviduct organisation. In some species smaller secretory cells occur at the mouth of tubular glands. Secretory cells discharge neutral and acid mucopolysaccharides and proteins that encase the eggs with various jelly layers. In all species investigated so far the anterior part of the *pars convoluta* secretes highly acidic and often sulfated mucopolysaccharides that later form the egg's capsular fluid. Biochemical analyses show a variety of sugars (hexoses) and hexosamines in all oviductal segments as well as proteins including lectins that are at least partly species-specific. Location of lectins within the *pars convoluta* differs among species. The uterine portion of oviparous species may contain columnar gland cells in some species, but is never provided with tubular glands. The same holds for the *pars recta* equipped mostly with less differentiated secretory as well as ciliated cells. The uterine epithelium of viviparous species lacks ciliated cells. Its cuboidal or flat cells secrete some sulfated mucopolysaccharides. Activity of membrane-bound Na^+-K^+-ATPase, a fair number of mitochondria, tortuos and widened intercellular spaces as well as a negative potential difference across the uterus wall demonstrated in *Salamandra salamandra* reveal the uterine lining as a transporting epithelium. It is involved in maintaining a suitable intrauterine environment. Beyond that, the uterus of *Salamandra atra* possesses a cranial zone (*zona trophica*), whose epithelial cells proliferate in the presence of a certain larval stage. Trophic cells are scraped off by properly positioned larvae, or are detached by necroses and/or apoptosis. Detached cells are continuously replaced. The eggs of urodeles are covered with several discrete jelly layers formed by the components secreted along the oviduct. Their number varies among species and does not always correspond with the number of the identified highly secretory oviductal subdivisions. Jelly layers have a variety of functions depending on the habitat of species and the mode of reproduction. Certain components facilitate fertilization (e.g. sialic acids), prevent excessive polyspermy (e.g. lectins) and may be relevant to gamete recognition (species-specific carbohydrate moieties such as O-linked oligosaccharides). However, the taxon-specific variability of egg jelly layers, their possible relations to the oviposition site, their anchoraging and antipredator effects as well as their significance for respiration are insufficiently understood as yet. In most urodeles fertilization takes place in the cloaca, but at least in *Salamandra salamandra* eggs become fertilized in the oviduct. A generally accepted definition of viviparity exists neither for Urodela nor for other live-bearing organisms. Widely used are the terms lecithotropy (energy requirements of the fetuses exclusively yolk dependent) and matrotrophy (transfer of energy by the female during development) that also work in viviparous salamanders. It is suggested, however, to use the terms oviparity for egg-laying, larviparity for larvae-bearing salamanders and pueriparity for salamanders giving birth to metamorphosed young.

Key words. Urodele oviduct, egg jelly layers, histology, histochemistry, ultrastructure, biochemistry, fertilization, oviparity, viviparity.

1. Introduction

Knowledge about the oviducts of the Urodela developing from the Mullerian ducts during embryogenesis have a fairly long history. An early, though surely not the first picture of these organs (Fig. 1a) was shown by Johann Jacob Wurffbain. In 1683 he published his revised thesis titled "Salamandrologia, i.e. descriptio historico-philologico-philosophico medica salamandrae, quae vulgo in igne vivere creditur". From today's view this booklet is one of the first empirical studies on the biology of the Urodela, in particular of the Fire Salamander, *Salamandra salamandra*, and a critical compilation of what was believed and written on this species in the previous centuries. Furthermore, it shows that practice of scientists has not changed over time: Wurffbain wrote that he dissected several specimens of the Fire Salamander, but took the figure of the oviducts from Jacobaeus (1677). He commented on this picture as follows: "sub intestinis, Ovula rotunda …. in duas partes divisa collacabantur, quibus Uterus bifurcatus succedebat, cuius Tubae varios anfractus efformantes, ad pedum anteriorum tegionem ascendebant, & utraque extremitate jungebantur, prout hoc Fig. III. A Jacobaeo mutuata, eleganter est expressum" (underneath the intestine the round 'ovula' divided into two portions are situated ... followed by a bifurcate uterus with many convolutions. They rise at the height of the anterior legs and are connected at both ends, as illustrated elegantly in fig. III taken from Jacobaeus, Wurffbainus 1683; Cap. VIII 2, p. 68). The word 'ovula' clearly means the ovaries. For obvious reasons he named the oviducts 'uterus' as the Fire Salamander is live-bearing, a fact known earlier to Belon (1553). According to Steno (1673, cited after Francis 1934) oviducts are not connected at both ends. This study appeared to be unknown to Wurffbain. Moreover, Jacobaeus (l.c.) described and illustrated the oviduct of a *Triturus*-species, i.e. an oviparous urodele, which he named salamander as was common for that time. A drawing of the oviduct of the live-bearing Alpine Salamander, *Salamandra atra*, from 1840 demonstrates that the oviduct of viviparous salamanders, in particular its most posterior portion (van der Hoeven 1840), looks quite different (Fig. 1b). Spengel (1876) has explicitly stressed the anatomical differences between the oviduct of viviparous and oviparous urodeles. Later investigations complete the macroscopic aspect of the urodele oviduct adding the ostium at its cranial end (also seen in the drawing of van der Hoeven) and the cloaca at its caudal end.

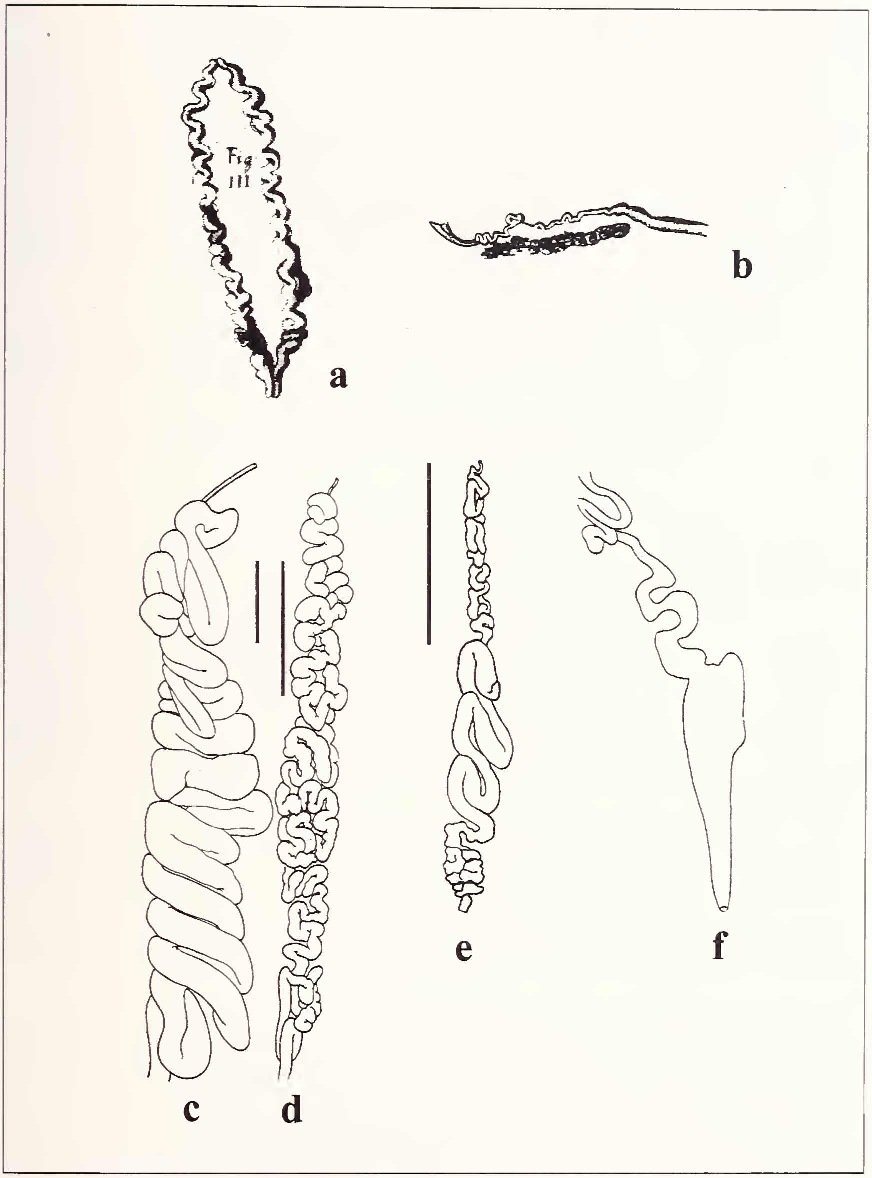

Fig. 1 a-f. a Woodcut of the salamander oviduct pictured by Wurffbainus (1683). **b** Oviduct of the viviparous Alpine Salamander (from van der Hoeven 1840). Note the large ostium (left side), the convoluted middle part and the caudal uterus (right side). **c** Oviduct of *Ambystoma maculatum*. **d** Oviduct of *Triturus alpestris*. **e** Oviduct of *Notophthalmus viridescens*. **f** Oviduct of *Batrachuperus pinchonii* (c-f from von Wahlert 1953). Bar 1 cm.

Stüve (1889) was one of the first, who cut hardened, non identified segments of the oviduct of the Fire Salamander, at that time still *Salamandra maculata*, and the oviparous *Triton* (= *Triturus*) *palmatus*. Considering previous literature he concluded altogether: „Die Eileiter der Amphibien sind lange, schlauchförmige Organe, welche vielfach gewunden in der Bauchhöhle liegen, und dazu dienen, die Eier der Thiere mit einer Hülle zu versehen“ (The oviducts of Amphibia are long tubular and highly convoluted organs located in the abdominal cavity. They serve to provide the eggs with a covering, Stüve 1889, p. 123). Stüve's statement as well as his observations that the diameter of the oviduct and development of its glands depend largely on the reproduction cycle still apply.

In the following period only selected portions of the urodele oviduct were investigated, above all the most posterior uterus of the viviparous *Salamandra*-species (Wiedersheim 1890; Schwalbe 1896). More than twenty years later Stieve (1918) analysed the *pars convoluta* (considered as one region) and the uterine portion of *Salamandra maculosa*, *Salamandra atra*, *Triturus alpestris* and *Proteus anguinus* histologically.

The review of van den Van den Brock (1933) did not contain any new information apart from a cross section of the oviduct of the Axolotl (probably *Ambystoma mexicanum*, see von Wahlert 1953). This overview as well as following investigations ignored the study of McCurdy (1931). The authoress subdivided the oviduct of *Triton torosus* (= *Taricha torosa*) into four different segments including the caudal "uterine" division. Subdividing was based on diameter, colouring, position and different histological stainings but did not consider the most cranial, very short straight portion (see her fig. 1). Subdivisions were said to be lined by a single-layered columnar epithelium of secretory and ciliated cells.

In the time thereafter no investigation analysed the mature urodele oviduct in its full lenghth on the basis of histological sections. That holds true also for studies dealing with the development of the urodele oviduct (see also McCurdy 1931). In one of these investigations the authors distinguished a convoluted portion with tubular glands and a uterine portion lined with a prismatic epithelium (Rodgers & Risley 1938) in the oviduct of mature females of *Ambystoma tigrinum*.

In this environment G. von Wahlert's thesis was published. This study was supervised by the late W. Herre (1909–1997) who also wrote some papers on salamanders and their phylogeny, primarily on the Salamandridae (see among others Herre 1935), before he turned to the study of domestic animals. It was published with the goal „Unterschiede im Bau der Eileiter, der Form des Laichs und der Ausbildung der weiblichen Kloake der Salamandriden zu erfassen und in ihren Zusammenhängen zu klären“ (to recognize differences in the structure of the oviduct, in the appearance of the spawn and the structure of the female cloaca of the Salamandridae and to clarify their relations, von Wahlert 1953, p. 227).

Apart from inspecting an extensive material macroscopically, partly from museum collections, he selected different portions of the oviducts of 10 species from seven genera and cut them serially (VON WAHLERT, personal information 2000). In his paper he discussed the results of the macroscopic inspection first, then those of the microscopic investigation and afterwards the properties of the oviduct of oviparous and viviparous salamandrids. Then he dealt with the egg jelly layers and the cloaca. The final discussion culminated in the phylogeny of the Salamandridae, which essentially acknowledged the view of HERRE (1935).

In the present outline, that is by no means an exhaustive sample, I will try to keep structuring and train of thought of VON WAHLERT's thesis, wherever possible. I will leave the cloaca and will not cover the hormonal regulation of the urodele oviduct. Also I will treat the remainder subjectively and selectively, since the oviduct of salamandrids and other amphibians has been reviewed recently (GREVEN 1998; WAKE & DICKIE 1998).

2. Macroscopic and microscopic anatomy of the oviduct

2.1. Macroscopic anatomy

Along the oviduct VON WAHLERT distinguished the *pars recta*, a short relatively straight cranial portion that begins with the ostium, and the *pars convoluta* including the most posterior "uterine" portion (Fig. 1). The latter opens into the cloaca. Further, he recognized two structural types, which he called the *Ambystoma*- and the *Triturus*-type. The former is characterized by a thick *pars convoluta* with large loops taking almost the entire width of the body cavity (Fig. 1c); it is found also in the salamandrids *Pleurodeles waltl* and *Taricha granulosa*. The latter has thinner and more convoluted loops using not the width of the body cavity (Figs. 1d, 2). In *Notophthalmus viridescens* the anterior and posterior part of the *pars convoluta* are organized as the Triturus-type, the middle part, however, is organized as the *Ambystoma*-type (Fig. 1e). In his sketch of the hynobiid oviduct (Fig. 1f) the *pars convoluta* appears less convoluted showing probably an oviduct after oviposition. Here the most caudal portion of the oviduct forms the ovisac. *Situs*-preparations of *Hynobius retardatus* (MAKINO 1934) and *Hynobius nigrescens* (HASUMI 1996a, b) show a more convoluted oviduct during reproduction.

As already mentioned oviducts of viviparous species are modified. Live-bearers are the species and subspecies of the genus *Salamandra* (essentially only findings on *S. salamandra salamandra*, *S. salamandra terrestris* and *S. salamandra fastuosa* and *S. atra* are available) and *Mertensiella*, with the exception of *Mertensiella caucasica*, which is oviparous (for review see GREVEN & THIESMEIER 1994). Compared with oviparous species the *pars convoluta* here appears less convoluted and is reduced in length in favour of the uterus (see the reviews by GREVEN 1998; GREVEN & GUEX 1994; GUEX & GREVEN 1994). Especially the structure of the large uterus of *Salamandra*-species and its microscopic anatomy was known since the late 19th century (WIEDERSHEIM 1890; SCHWALBE 1896; for review see FRANCIS 1937). VON WAHLERT suggested that the more convoluted and longer oviducts of the oviparous species lacking a "typical" uterus are correlated with the high number of eggs generally laid by these species as numerous eggs need a larger amount of secretions to form a complete set of egg jelly layers (see section 5).

In the *pars convoluta* there can be generally distinguished three main portions, an anterior, a middle and a posterior one (see Fig. 11 and Jego et al. 1986). In his preserved material von Wahlert distinguished at least two portions that differed in colour and consistency. That suggests a „tiefergehenden anatomischen und physiologischen Unterschied zwischen den beiden Abschnitten der *Pars convoluta*" (fundamental anatomical and physiological difference between the two portions of the *pars convoluta*, von Wahlert 1953, p. 81). In brief, the macroscopic view shows that each of the both oviducts of the Urodela begins with the ostium and continues in a convoluted part that can be easily divided in three main portions and the "uterine" portion. Degree of convolutions and their thickness are taxon-specific, but also depend on the reproductive cycle.

Fig. 2. Dissected female of *Triturus alpestris* during ovulation. Note the convoluted, thickened oviduct and the eggs in the most posterior uterine portion.

2.2. Microscopic anatomy

2.2.1. Light microscopy. The fully differentiated urodele oviduct is covered externally by the thin peritoneal epithelium; it is followed by a muscle layer, loose vascularized connective tissue and the oviductal lining. The muscle layer becomes thicker and may be differentiated in longitudinal and circular muscles (e.g. Stieve 1918), particularly in the uterus of viviparous species. Also density of blood vessels in the connective tissue increases in the uterine portion (e.g. Boisseau 1980). In the uterus of a medium sized pregnant female of *Salamandra salamandra* the total length of capillaries amounts to approximately 38 m (Greven & Guex 1994) (Fig. 3).

The wall of the oviduct forms longitudinal folds of different length protruding in the oviductal lumen (e.g. Stieve 1918; Greven & Rüterbories 1984). Folds are covered by a monolayered epithelium, most strikingly differentiated in large secretory cells in the *pars convoluta*. The distribution and structure of these cells (columnar secretory cells and/or tubular glands) as well as the histochemical reactions of their secretory products allowed a more detailed specification of subdivisions (see below). How sharply subdivisions may be separated from each other is shown in Figures 4a, b, 5a.

Often, however, boundaries are less conspicuous (Fig. 5b) and visible only after specific stains. In *Ambystoma mexicanum* (Uribe et al. 1989) and several plethodontids (Ehmcke et al. submitted) putative subdivisions intergrade structurally after general stainings such as hematoxilin-eosin or the more specific combination of Alcian-blue (AB) and the Periodic-Acid-Schiff (PAS) reaction (Fig. 5b).

Generally the *pars recta* is provided with small, less differentiated secretory cells and ciliated cells. Occasionally gland cells occur, e.g. in its posterior part (possibly already *pars convoluta*?) as in *Ambystoma mexicanum* (= posterior infundibulum according to Uribe et al.1989). In this species the authors distinguished an infundibulum, a convoluted part with several subdivisions considered as one region and a caudal glandless segment, which contains higly prismatic secretory cells. Examinations of the figures in this paper reveal four or five subdivisions, but reexamination seems necessary.

Ciliated cells are scatterered among the entire epithelium (see above). Their number is low during the preovulatory and high during the postovulatory period, and decreases when gland cells recover secretory activity (*Triturus cristatus carnifex*, Fasolo & Franzoni 1970). Such changes in the course of the reproductive cycle are a general phenomenon in the female genital tract of vertebrates, but more detailed investigations in the Urodela are lacking. The uterus of the viviparous species does not possess ciliated cells nor glands. It is lined by a simple cuboidal or flat epithelium that secretes some sulfated mucopolysaccharides (e.g. Lostanlen et al. 1976; Greven 1977 and the literature cited above).

Von Wahlert (1953, p. 282) claimed that in species having an oviduct of the *Ambystoma*-type „die Zellen in mehreren Schichten übereinander gelagert und mit ihrer oberen Fläche radiär um Lumina gestellt sind, die in das Eileiterlumen

Fig. 3. Transparency of an area of the uterus of a pregnant female of *Salamandra salamandra* showing the dense network of blood vessels (whole mount preparation, Indian ink injection).

münden. Es entsteht so eine wabenartige Anordnung von Zellgruppen" (the cells lie on top of each other and are arranged with their upper surface radially surrounding lumina, that are continuous with the lumen of the oviduct. Thus, secretory units form a honeycomb pattern). He continued „Die eng geschlängelten, als *Triturus*-Typ bezeichneten Eileiter weisen den einfachen Epitheltyp auf" (in the narrowly convoluted oviducts of the *Triturus*-type, the simple type of epithelium is present) and concluded „Die Bauart des Eileiterepithels wirkt sich auf die Wandstärke und damit auf den Durchmesser des Eileiters aus, der seinerseits wieder die Art der Schlängelung bestimmt" (the kind of organisation of the oviductal epithelium influences thickness of the wall and, thus, the oviductal diameter, which determines the form of convolution). Interestingly enough according to him and previous studies *Salamandra salamandra* has the "honeycomb" epithelium in the *pars convoluta*, most clearly seen in the middle part (Fig. 4c), whereas *Salamandra atra* is said to have the simple columnar type (Fig. 4d; see also STIEVE 1918; VILTER 1967b; NIEDERL 1981). The simple columnar epithelium was shown also to be present in the oviduct of *Proteus anguinus* (Proteidae) (STIEVE 1918) and more recently in plethodontids (EHMCKE et al., submitted; see also VILTER & THORN 1967; WAKE & DICKIE 1998).

Glandular units in the urodele oviduct showing the "honeycomb" pattern are named differently in literature. More recent papers use the term tubular glands. I follow this terminology here, as the clutch of cells that constitute the glandular unit are tubular in shape and the tubules are surrounded by a thin layer of connective tissue (Fig. 4c). Unlike typical exocrine, tubular glands (e.g. HAM 1974) the oviductal glands in Urodela are not provided with ducts that are lined by less highly differentiated cells.

Our serial sections of the oviduct of *Triturus vulgaris* immediately before ovulation confirm the presence of a monolayered columnar epithelium (Fig. 5a-d; see VILTER 1966). In *Salamandra atra* the arrangement of gland cells is more complex and groups of large gland cells in some subdivisions were taken for tubular glands in a previous paper (GREVEN 1998; see Fig. 4d); a careful reexamination of specimens in different stages of the reproductive cycle would be helpful. In all species investigated as yet, tubular glands are absent in the *pars recta* and the uterine portion.

Oviductal tubular glands and/or columnar secretory cells and their arrangement on folds were pictured repeatedly since 1953 (summarized by GREVEN 1980a). According to my knowledge, however, nobody explicitly considered them as two perhaps fundamentally different structural types of the oviductal epithelium in the Urodela. VON WAHLERT believed that these differences are of phylogenetic relevance at least in the Salamandridae and that the simple columnar secretory epithelium is a derived feature. According to the view of HERRE (1935) who considered a set of different characters, the genera *Cynops*, *Triturus*, *Trituroides*, *Neurergus* and *Hypselotriton* form a unit (Fig. 6a). These genera appear to be

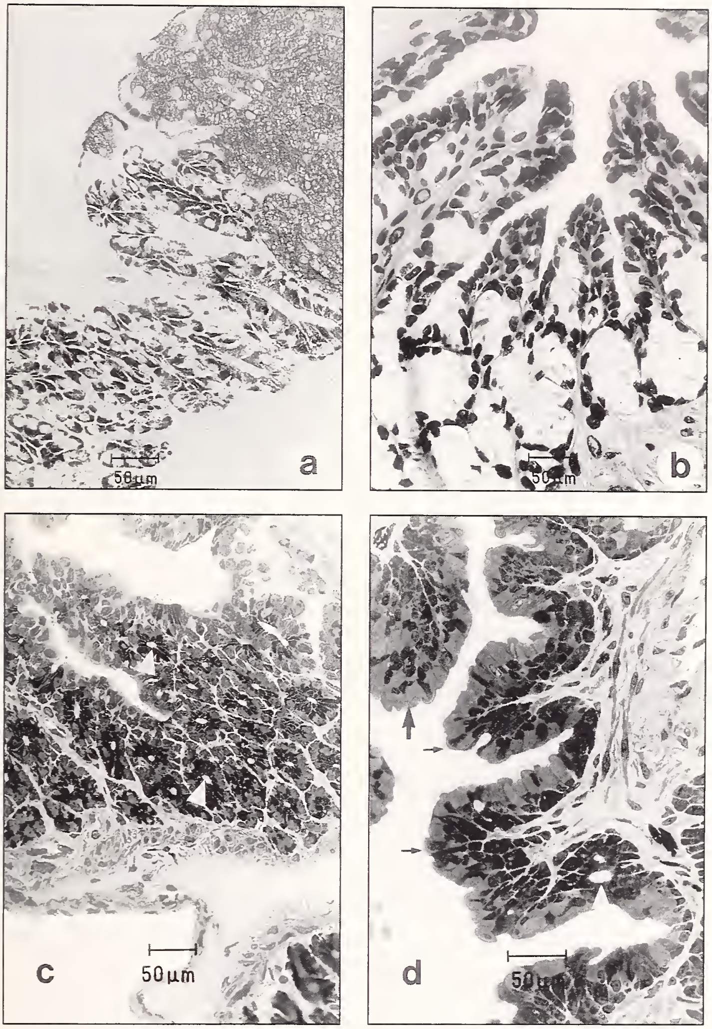

Fig. 4 a-d. The oviduct of *Salamandra*. **a** Abrupt transition from the anterior (on the top) to the middle (below) part of the *pars convoluta* in *Salamandra salamandra*. Note the different size of glands, the aspect of secretory products of the two subdivisions and the cross sectioned tubular glands in the middle part (Paraplast section, AB-PAS-staining). **b** Transition from the posterior glandular part of the *pars convoluta* (below) to the aglandular uterus (on the top) in *Salamandra salamandra* (Paraplast section, Trichrom Goldner). **c** Tubular glands (arrowheads) in the middle part of the *pars convoluta* in *Salamandra salamandra* (1 µm semithin-section, Toluidine blue-borax). **d** Middle part of the *pars convoluta* in *Salamandra atra*. Note the more simple arrangment of gland cells; lumen of a tubular gland (arrowhead). Smaller secretory cells (arrow), ciliated cells (small arrows) (1 µm semithin-section, Toluidine blue-borax).

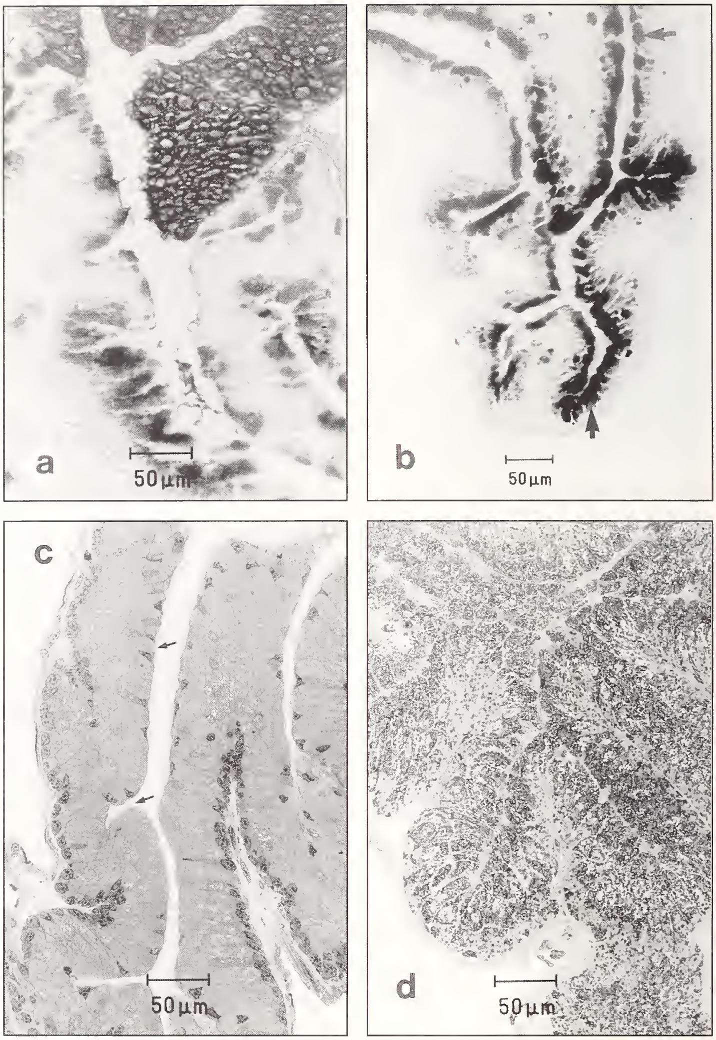

Fig. 5 a-d. The oviduct of *Triturus alpestris*. **a** Abrupt transition from the first (on the top) to the second (below) subdivision of the *pars convoluta*. Both subdivisions are stained blue. Note different size of gland cells (Paraplast section, AB-PAS-staining). **b** Transition of the second (left side, stained blue) to the third (right side, stained more red) subdivision of the *pars convoluta*. Subdivisions are distinguishable mainly by their staining. Transition is not very abrupt as lighter (blue stained) cells can be found also in the more dark (red stained) subdivision (arrows) (Paraplast section, AB-PAS-staining). **c** Epithelium of the *pars convoluta* showing exclusively large columnar gland cells with basally located nuclei and ciliated cells (arrows) (1 µm semithin section, Toluidine blue-borax). **d** The columnar epithelial cells of the uterine portion secrete a scleroprotein seen as distinct granules (1 µm semithin section, Toluidine blue-borax).

characterized by the simple oviductal epithelium. The grouping *Pleurodeles*, *Tylotriton* and *Salamandrina* possesses tubular glands in their oviducts. The same is valid for the grouping *Mertensiella*, *Chioglossa* and *Salamandra* with the exception of *S. atra*. VON WAHLERT speculated that in this species the simple epithelium evolved independently. However, it might be a secondary reduction, particularly if the assumption of the higher complexity of its organization is correct.

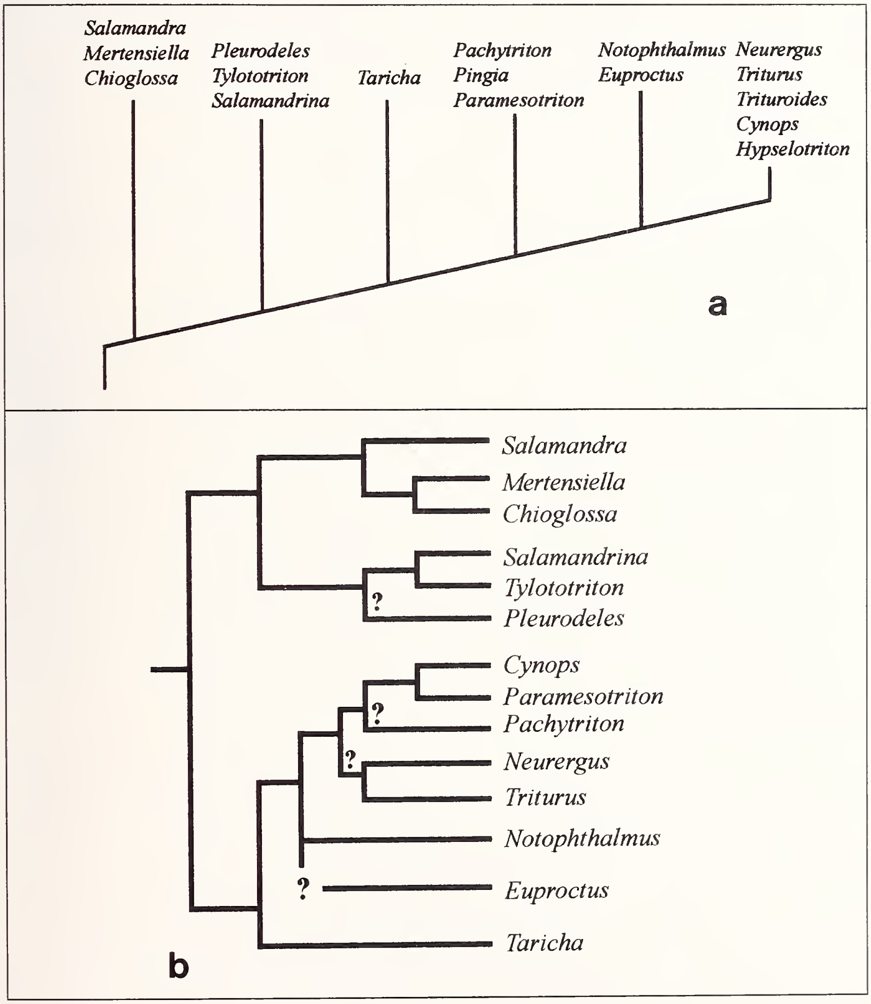

Fig. 6 a, b. Phylogenetic relations of Salamandridae according (**a**) to HERRE (1935) and VON WAHLERT (1953) and (**b**) to SCHOLZ (1995) (modified).

Comparing the results of a cladistic analysis, that considered courtship behaviour and external as well as skeleton features of 15 species of the Salamandridae (Scholz 1995) with the views of Herre and von Wahlert, the two latter groupings form a monophylum each (Fig. 6b). The second group, the "true" salamanders, includes the viviparous species (for further detailed views on the phylogeny of the Salamandridae based on molecular, morphological and reproductive data see among others Titus & Larson 1995).

Overall similarity could be attributed to the fact that all Urodela use the same "substrate", i.e. the Mullerian duct, for egg jelly production and, if present, intrauterine care of young. Even in the viviparous taxa it could not be excluded that viviparity has evolved several times independently as structural and functional aspects of this reproduction mode differ considerably between species (Veith et al. 1998). Papers published after von Wahlert's thesis have never considered the structure of the oviduct as a reliable character for phylogenetic speculations. Its basic structure and function, reactions to hormones, secretory capacity, etc. are very similar within the Amphibia. Therefore, distinction of possible homologies from homoiologies turns out to be difficult. However, future comparative studies are welcome.

Only a few mature oviducts, predominantly of members of the Salamandridae, of the about 360 living species of Urodela that partly show quite different modes of reproduction (Duellman & Trueb 1986), have been analyzed more or less thoroughly employing histological techniques. With respect to other families some data are available from *Ambystoma mexicanum* (Ambystomatidae), *Siren intermedia* (Sirenidae) and from several species of Plethodontidae depositing eggs in terrestrial sites (Tab. 1).

These investigations showed that oviductal gland cells or tubular glands – the latter were most clearly seen in the middle main portion of the *pars convoluta* – and in some cases smaller secretory cells partly located at the mouth of the tubular glands discharge acidic (sulphated and carboxylated) and neutral mucopolysaccharides. The microscopic anatomy of the epithelium and histochemical reactions of its secretory products allowed to subdivide the oviduct, in particular the three main portions of the *pars convoluta* (see above) into a variety of segments (Tab. 1).

The oviducts of the oviparous *Pleurodeles waltl* and the viviparous *Salamandra salamandra* should be treated here in a more detailed manner. Careful investigations of the oviduct of *Pleurodeles waltl* revealed five main portions (*pars recta*, anterior, middle and posterior convoluted part, uterine portion) (see also Fig. 11). Using mainly carbohydrate specific stainings the anterior oviduct was subdivided in two, the posterior oviduct, however, in three segments (Boisseau & Joly 1972; Boisseau & Jego 1972). Therefore strictly spoken, altogether eight subdivisions could be identified along the oviduct with six in the *pars convoluta* (Tab. 1). However, authors defined only five in the convoluted part as secretions of the two subdivisions of the anterior portion mix after being discharged forming the innermost layer of the egg jelly (see section 5). According to Boisseau (1979)

Tab. 1: Number of subdivisions in the oviduct of several urodele species seen after general histological or specific histochemical stainings (Arabic numerals) and number of subdivisions equipped with secretory units (more or less columnar gland cells or tubular glands), partly present also in the *pars recta* and in the "uterine division" of oviparous species (Roman numerals) as well as number of egg jelly layers (Roman numerals) shown in histological sections. The table includes only those species, whose entire oviducts have been studied at least roughly and of which data on the egg jelly layers were available. *(V/VI) the sixth egg jelly layer is amalgamated with the fifth; ** despite the identical number of glandular subdivisions no congruence; [a]probably without the innermost layer as gastrulae or later stages were investigated; [b]perhaps a very short aglandular *pars recta* not identified as yet or presence of a glandular *pars recta*; [c]authors distinguished six main layers further subdivided by histochemical tests.

Family and Species	Number of subdivisions, total and with glands ()	Source	Number of egg jelly layers	Source
Sirenidae				
Siren intermedia/ lacertina	3 (?)	Sever et al. 1996	V	Salthe 1963
Ambystomatidae				
Ambystoma mexicanum	6 (IV-V)	Uribe et al. 1989	V IV*	Salthe 1953 Caroll et al. 1992
Salamendridae				
Salamandra atra	6 (IV)	Vilter 1967b; Niederl 1981		
	5 (III)	Guex & Greven 1994; Greven 1998		
Salamandra salamandra	5 (III)	Greven 1980a, 1998	II[a]	Lostanlen et al. 1978
Mertensiella luschani	5 (III)	Polymeni & Greven 1992		
Triturus alpestris	7 (VI)	Vilter 1966, 1968	VI	Vilter 1967
Triturus vulgaris	5 (IV)	von Wahlert 1953	IV	von Wahlert 1953;
			V (VI)*	Salthe 1963
Triturus helveticus	5 (IV)	von Wahlert 1953	IV	von Wahlert 1953
Triturus cristatus	7 (VI)	Andreozzi et al. 1970		
Taricha torosa	5 (IV)	Mc Curdy 1931	VI	Salthe 1963
	7 (VII)	Wake & Dickie 1998		
Pleurodeles walti	8 (VI)	Boisseau & Joly 1972; Boisseau & Jego 1972	V	Boisseau et al. 1974; Picheral 1977
Notophthalmus viridescens	6 (V)**	Adams 1940	V (VI)*	Salthe 1963
	6 (V)**	Humphries & Hughes 1959	V	Humphries 1966; McLaughlin & Humphries 1978
Cynops pyrrhogaster	5 (IV)	Kambara 1957	IV	Nadamitsu 1957
	8 (VI-VII)	Okimura et al. 2001	VI-VII	Onitake et al. 2000; Okimura et al. 2001
Plethodontidae				
Hydromantes genei	6 (VI)[b]	Vilter & Thorn 1967	VI (VIII)[c]	Vilter & Durand 1970
Hydromantes italicus				
Ensatina eschscholtzii	4 (III)	Wake & Dickie 1998		
Bolitoglossa subpalmata	4 (III)	Wake & Dickie 1998		
(= pesrubra)	6 (IV)	Ehmcke et al. submitted		
Bolitoglossa schizodactyla	6 (IV)	ibidem		
Bolitoglossa dofleini	7 (V)	ibidem		
Bolitoglossa marmorea	7 (V)	ibidem		
Oedipina uniformis	7 (V)	ibidem		

also in *Triturus marmoratus* two subdivisions of the anterior *pars convoluta* can be distinguished, whereas in *Salamandra salamandra*, *S. atra*, *Euproctus asper*, *Taricha granulosa*, *Trituris alpestris* and *T. cristatus* the anterior portion is more uniform.

The *pars recta* of *Pleurodeles waltl* is lined by less differentiated secretory cells and ciliated cells. The same holds for the uterine portion. It should be noted, however, that the "uterine" division of other oviparous urodeles contains prominent columnar gland cells that partly secrete "scleroproteins" (Fig. 5d; e.g. Vilter 1966; Wake & Dickie 1998; for a secretory columnar epithelium in this part of the oviduct see also Uribe et al. 1978).

The two kinds of tubular glands of the anterior portion of the *pars convoluta* secrete less and highly acidic sulfated mucosubstances, those of the middle part neutral and those of the posterior portion less acidic mucopolysccharides. They stain red after AB-PAS. Smaller mucous secretory cells located at the mouth of the tubular glands produce acid mucopolysaccharides. Sulphated mucopolysaccharides were demonstrated histochemically and by ^{35}S-autoradiography in the anterior segment (Boisseau & Jego 1972; Boisseau 1973a; see also Humphries 1970 for *Notophthalmus viridescens*). In certain segments sialic acid has been demonstrated histochemically (*Notophthalmus viridescens*: Humphries et al. 1968). More recently Okimura et al. (2001) identified carbohydrate moieties in the six or seven (including the uterine portion) subdivisions of the *pars convoluta* of *Cynops pyrrhogaster* using various lectins.

In the viviparous *Salamandra salamandra* the entire oviduct was subdivided into five main parts. Less differentiated small secretory cells and ciliated cells in the *pars recta*, tubular glands that stained blue after AB-PAS in the anterior part (Fig. 4a), red-blue in the middle part (Fig. 4c) and blue-red in the posterior part of the *pars convoluta* indicating altogether a smaller amount of neutral mucopolysaccharides as in *P. waltl*. In addition, small gland cells and ciliated cells were found. No type of gland cells was exclusively PAS-positive (Greven 1980a). The large uterus is lined by a simple cuboidal or flattened epithelium without gland cells. Epithelial cells, however, discharge sulfated glycoproteins possibly mediated by hormonal and mechanical stimuli (Greven & Robenek 1982) that obviously contribute to the uterine fluid (Greven 1977; Lostanlen et al. 1976). In principle the same number of subdivisons was found in the oviduct of *Salamandra atra* (Guex & Greven 1994; Greven 1998) and *Mertensiella luschani* (Polymeni & Greven 1982), although Vilter (1967b) and Niederl (1973) distinguished a fourth posterior segment in the *pars convoluta* with "plastospongiocytes" slightly different from those in the third part.

According to Boisseau (1980) the posterior oviduct of the two *Pleurodeles*-species, four *Triturus*-species, *Taricha granulosa*, and *Euproctus asper*, has two main subdivisions (OP1 and OP2-3), whereas in the viviparous species there is a tendency to reduce this part and to secrete more acid than neutral mucopolysaccharide forming more acid and fluid outer egg jelly layers (see also Greven 1980a; Vilter 1966, 1967b). Neutral, i.e. PAS- positive mucosubstances very likely contribute to the most mechanically resistant egg jelly layers. Details of the mechanical properties of the urodele egg jelly are unknown, however. After oviposition size of gland cells is markedly reduced and cells are largely free of secretions (Fig. 7; see KAMBARA 1956; ANDREOZZI et al. 1970). More detailed fine structural studies are lacking.

The vivid synthesis of secretions and the pronounced compartmentalization of gland cells can be shown already at the light microscopical level by staining the different secretory products and by demonstrating activity of key enzymes such as thiaminepyrophosphatase in the dictyosomes (Fig. 8a). In the uterine epithelium activity of several hydrolases and oxidoreductases has been demonstrated (GREVEN et al.1986) that occurs also in other portions of the oviduct (Fig. 8b). The latter indicate the strong oxidative metabolism of the tissue. Positive reactions of

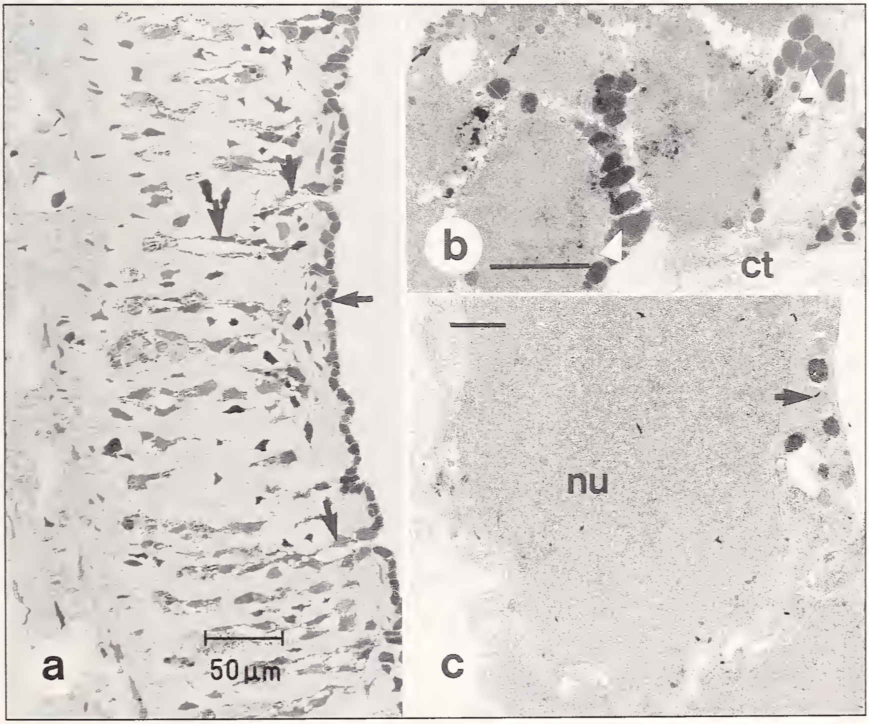

Fig. 7 a-c. The oviduct of *Pachyhynobius shangchengensis* probably a short time after spawning. **a** Epithelium of the *pars convoluta*. Note the small uniform epithelial cells extending far in the connective tissue (arrow) (1 µm semithin section, Toluidine blue-borax). **b** Low power transmission electron micrograph. Connective tissue (ct), pigment granules (arrowhead). Bar 5 µm. **c** Higher magnification of the apical border of an epithelial cell having a large euchromatic nucleus (nu). Note the few secretory granules in the apical cytoplasm (arrow). Bar 1 µm.

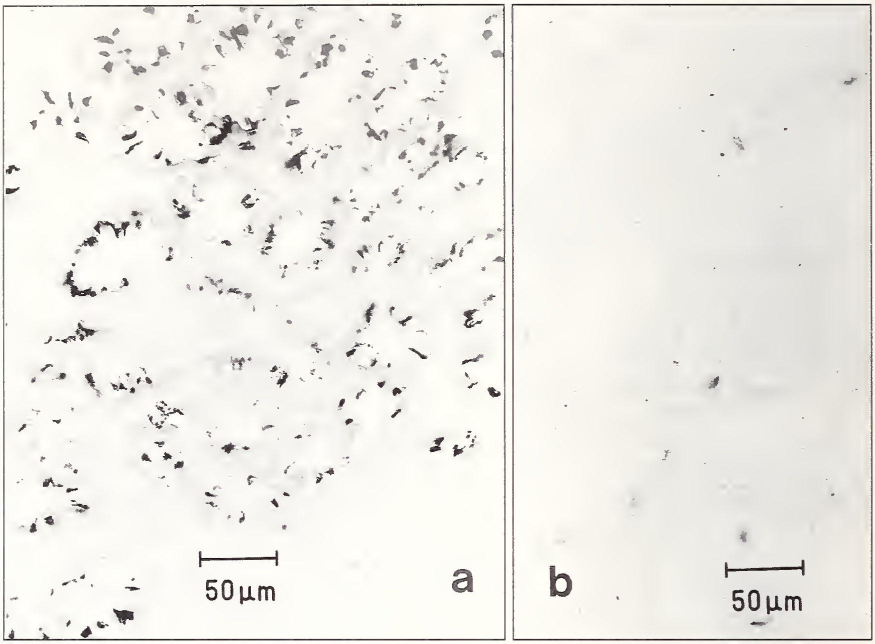

Fig. 8 a, b. Enzyme histochemistry of the oviduct of *Salamandra salamandra*. **a** Thiamin-pyrophosphatase activity in the tubular glands of the middle part of the *pars convoluta*. **b** Weak activity of succinatdehydrogenase in the *pars recta*-epithelium. Bar 50 µm.

acid and alkaline phosphatases were observed in the glandular portion of the oviduct of *Cynops pyrrhogaster* by KAMBARA (1956). Na^+-K^+-ATPase activity was demonstrated in the uterine epithelium using ^{3}H-Ouabain (GREVEN 1980b) and is discussed in section 3. This enzyme was not present at the basolateral plasmalem of the gland cells, but was demonstrable at the less differentiated cells of the *pars recta* and ciliated cells (GREVEN 1981).

Unknown as yet is the life span of the gland cells within the oviduct. VON WAHLERT (1953) cited previous authors' writings that after the spawning period the oviductal epithelium is renewed and that this process resembles a "greasy degeneration." As far as I know no investigation exists, which has seriously taken up this question. Authors, who examined the oviduct after spawning, only report on a regressive epithelium (e.g. FASOLO & FRANZEN 1970; WAKE & DICKIE 1998). Degenerating ciliated cells are said to be discharged into the oviductal lumen (FASOLO & FRANZEN 1970). Studying the oviduct of the Alpine Salamander by light microscopy NIEDERL (1981) claimed (without verifying) that a small percentage of the gland cells was replaced by new cells.

2.2.2. Electron microscopy. Only the mature oviducts of the oviparous *Pleurodeles waltl* (Boisseau 1973b, 1979, 1980), the viviparous *Salamandra salamandra* (Greven 1977, 1980a) and the ancient *Siren intermedia* (Sever et al. 1996) have been analysed more or less completely using the electron microscope. The investigation of the *P. waltl*- and *S. salamandra*-oviduct confirmed the presence of the cell types and subdivisions seen at the light microscopical level, i.e. less differentiated secretory cells in the *pars recta* with some gland cells in the transition zone, ciliated cells in the entire oviduct with the exception of the uterus in the viviparous species, tubular glands and several small secretory cells at their mouth. Gland cells have numerous dictyosomes and, depending on their seromucous (in the middle part of the *pars convoluta*) or mucous nature, different quantities of rough endoplasmic reticulum (Fig. 9a,b). The tremendous synthesising and secretory capacities of oviductal secretory units have been used to study more general phenomena of cell biology in detail, such as glandular morphogenesis from the undifferentiated epithelium of the Mullerian duct, differentiation of ciliated cells and development of secretory granules by means of the rough endoplasmic reticulum and Golgi apparatus, partly under influence of sex hormones (Boisseau 1973 c, 1975, 1980).

Some findings, however, deserve some more attention. The uterine portion of the oviparous *P. waltl* does not contain glands; interspersed among the small less differentiated cells are ciliated cells. The underlying connective tissue has a richer capillary network and a stronger muscle layer than the anterior portions of the oviduct. Homology with the uterus of viviparous salamanders was discussed (Boisseau 1980). The oviduct of *Siren intermedius* was divided in the narrow and less convoluted atrium (= *pars recta*), the convoluted ampulla and the smooth walled ovisac (= *pars convoluta*). The Sirenidae as highly derived externally fertilizing salamanders are now considered as sister group to all extant Urodela (Larson & Dimmick 1993). Sections of the oviduct at maturity showed that the epithelium of the atrium and ampulla contains ciliated cells and tubular glands. The ovisac lacks gland cells (Sever et al. 1996). Micrographs and descriptions in this study do not allow to distinguish subdivisions possible present within the ampulla.

The cells of the uterine epithelium of *Salamandra salamandra* possess numerous mitochondria (already indicated by the histochemical demonstration of isocitrate and succinate dehydrogenase). Furthermore, the epithelium is characterized by long partly distended intercellular spaces that are sealed apically by flexible *zonulae occludentes* between neighbouring cells and that open towards the connective tissues and capillaries (see Greven 1980b, c; Greven 1998; Greven & Guex 1994; Greven & Robeneck 1980). At the electron microscopical level activity of K^+-p-nitrophenlyphosphatase along the basolateral plasma membranes of the epithelial cells as well as chloride and cations in the intercellular space could be demonstrated (see section 4).

In brief, the urodele oviduct can be subdivided using histological sections, in particular stained for proteins and carbohydrates, and ultrathin sections. A consid-

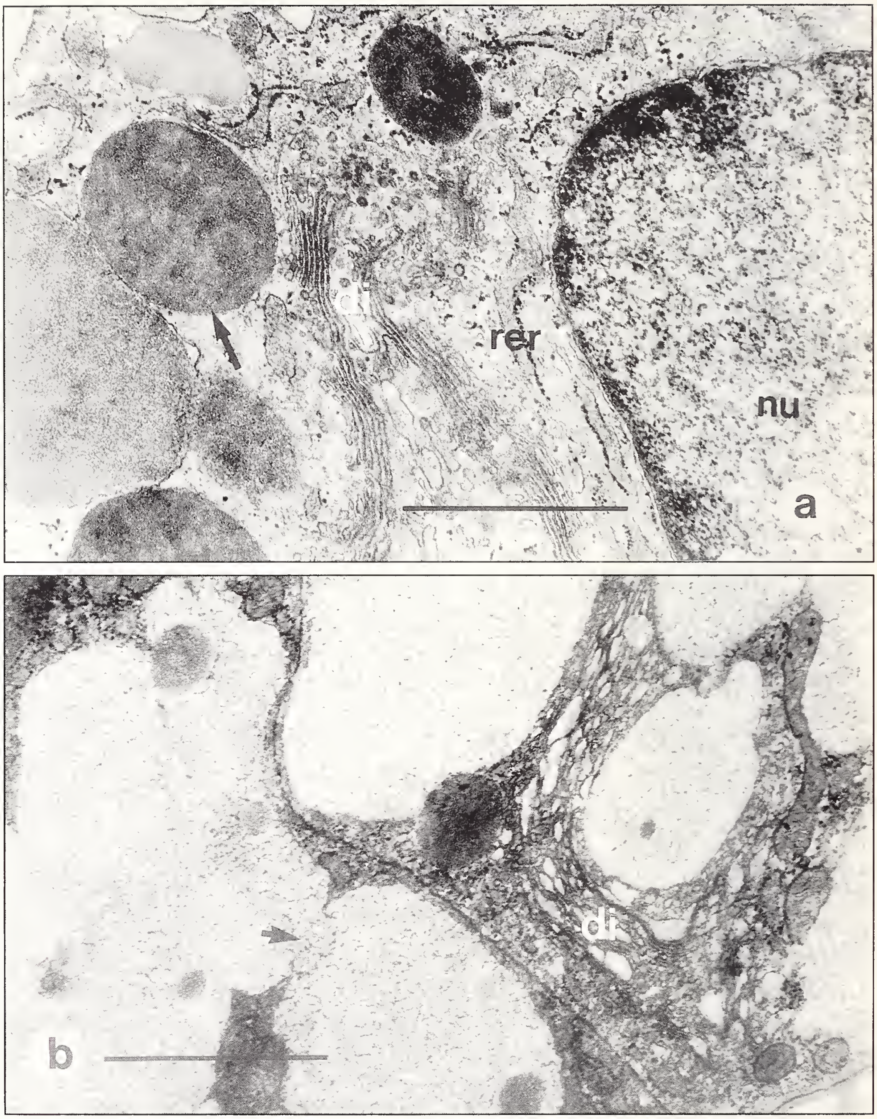

Fig. 9 a, b. Fine structure of gland cells in the *pars convoluta*. **a** Seromucous gland cell of the second subdivision (middle part) of the *pars convoluta* of *Salamandra atra*. Note the compact osmiophilic secretory granules (arrow), dictyosomes (di) and the well developed rough endoplasmic reticulum (rer). Nucleus (nu). Bar 1 µm. **b** Mucous gland cell of the first subdivision of the *pars convoluta* of *Triturus alpestris*. Note the confluent secretory granules (arrow) and the large dictyosome (di). Bar 1 µm.

erable part of the basically monolayered epithelium, above all the *pars convoluta*, is differentiated into more or less large gland cells (arranged in a monolayered columnar epithelium and/or as tubular glands). They discharge mucosubstances with different acidic groups and with different amounts of protein. The most acidic, often sulphated mucopolysaccharides were secreted by the anterior part of the *pars convoluta*. Glands of viviparous species tend to secrete rather acidic than neutral mucopolysaccharides and number of subdivisions is reduced in the posterior part of the oviduct in favor of the uterus. The number of subdivisions and the nature of secretions seem to be taxon-specific, but comparative studies using uniform criteria how to distinguish subdivisions are still to be carried out. The uterine portion of oviparous species may contain gland cells, but is never provided with tubular glands. The cuboidal or flat aglandular uterine epithelium of viviparous species secretes some mucopolysaccharides. Activity of the membrane bound Na^+-Ka^+-ATPase, numerous mitochondria, tortuos and partly widened intercellular spaces containig ions, and apicolateral *zonulae occludentes* reveal the uterine lining as transporting epithelium.

3. Some biochemical data

In contrast to the egg jelly (see section 5), there is only a comparatively small number of biochemical analyses of macromolecules in the subdivisions of the urodele oviduct. Previous studies focused on proteins, amino acids, neutral sugars, hexosamines, sialic acids and sulphate in the glandular parts, mainly of the oviduct of *Pleurodeles waltl* (for further readings and data about *Ambystoma mexicanum*, *Salamandra salamandra* and *Hynobius nebulosus*, see JEGO et al. 1986). Monosaccharides and hexosamines were analysed in the oviduct of *Salamandra salamandra* und were found to be identical with other species with the exception of galactosamine that appeared to be absent in this species (GREVEN & BALDUS 1984; see JEGO et al. 1974). HUMPHRIES et al. (1968) demonstrated sialic acid in the second and fourth of five glandular segments in the *pars convoluta* of *Notophthalmus viridescens*.

In oviductal segments of six urodele species lectins were shown to be present using a haemagglutination assay. Interestingly, haemagglutinin activity was either identified in the anterior segment of the *pars convoluta* (*Pleurodeles waltl*, *Hynobius nebulosus*, *Salamandra salamandra*) or in the posterior segment (*Ambystoma mexicanum*, *Notophthalmus viridescens*, *Triturus*-species; LERIVRAY et al. 1985; JEGO et al. 1986).

In brief, biochemical analyses show a variety of monosaccharides, hexsosamines and polypeptides present in subdivisions of the oviduct. In addition, oligosaccharide-alditols are released from oviductal secretions. Lectins can be localized in various subdivisions of the oviduct depending on the species examined (see section 5).

4. The Uterus of viviparous species and its Properties

Already early researchers paid attention to the uterus of viviparous species, since it serves as a brood chamber that even supplies the offspring with food in Salamandra atra. Certain properties of the uterine lining are predictable without any experiment, as they are typical for epithelia in general. Regarding its position between a lumen that is filled from time to time and a richly capillarised layer of connective tissue as well as the structural features mentioned above, the epithelium should be able to transport ions and solutes. This was shown for the uterus of the Fire Salamander: 1) autoradiographically by the localisation of a Na^+ K^+-ATPase at the basolateral plasmalem of uterine epithelial cells using ^3H-Ouabain, a heartglykoside, that specifically binds to the membrane-bound enzyme (see section 2); 2) electrophysiologically by the demonstration of a potential difference across the uterine wall (inside the lumen negative, -15 to -25 mV; the potential difference as well as a circuit current of 200–300 µA decreases after inhibition of the Na^+-K^+-ATPase with Ouabain); 3) by the cytochemical demonstration of a K^+-dependent p-nitrophenylphosphatase; and 4) by the precipitation of cations (among others sodium) and chloride in the intercellular space, which is considered as main route of ion and solute transportation (GREVEN 1980b, 1998; GREVEN & GUEX 1994).

Quite obviously the membrane-bound pump has to do with the adjustment of the intrauterine environment, since the ion content (measurements of sodium only) corresponded to that of the blood during pregnancy, whereas it was lower in non-pregnant animals (GREVEN 1998). Thus, the level of Na^+-K^+-activity may depend on the reproduction cycle, but nothing is known about possible changes in this respect.

Also waste products of larval metabolism (above all urea) enter the blood vessels of the uterine connective tissue. Ureotelism of intrauterine larvae of the Fire and Alpine Salamander was predictable, too, because of the water stress within the uterus (SCHINDELMEISER & GREVEN 1981; GUEX & GREVEN 1994).

Larvae of the nominate form of the Fire Salamander cover their demand of energy exclusively from the yolk and are not nourished directly by the mother during pregnancy (KAUFMAN 1913; GASCHE 1939; LOSTANLEN et al. 1976; GREVEN & GUEX 1994). They are surrounded by the egg envelope until birth. Young of the Alpine salamander, usually one per uterus, feed on the yolk when still surrounded by the egg jelly (lecithotrophic phase; 1. SCHWALBE stage). Once they had left the jelly (2. SCHWALBE stage) they feed on disintegrating eggs (embryotrophe), a fact that is known since CZERMAK (1843). Uptake of nutritive substances across the gills, that are developed strongly in this stage, as suggested by SCHWALBE (1896) and HÄFELI (1971) among others, or simply a "diffusion" as was speculated at times by VON WAHLERT appear highly improbable. Uptake of particles or macromolecules can be managed only by endocytosis which was not detected as yet (unpublished). Energy of embryotrophic eggs is not sufficient for the long gestation period that lasts up to 5 years and depends on climatic conditions (e.g. WUNDERER 1909; HÄFELI 1971; GUEX & GREVEN 1994). In the 3. SCHWALBE stage, when the offspring measures already 4–5 cm in length and shows signs of metamorphosis, another source of food is necessary. The uterine "milk" that is secreted by the epithelium starting with the 2. SCHWALBE was assumed to be an important source (VILTER & VILTER 1964; NIEDERL 1981), more essential, however, is the *zona trophica* at the anterior end of the uterus. Here epithelial cells proliferate and become detached from the underlying connective tissue, probably by necroses and/or apoptotic processes, float within the uterus and were then ingested by the offspring. Young positioned with their head to the nutritive zone scrape off cells from this area with the help of special toothed areas ("Zahnfelder") of the upper and lower jaw. Thus, often more than half the area of the *zona trophica* is free of epithelial cells and even blood vessels will be opened (Fig. 10a,b). The cells of the trophic zone did not accumulate glycogen or lipids

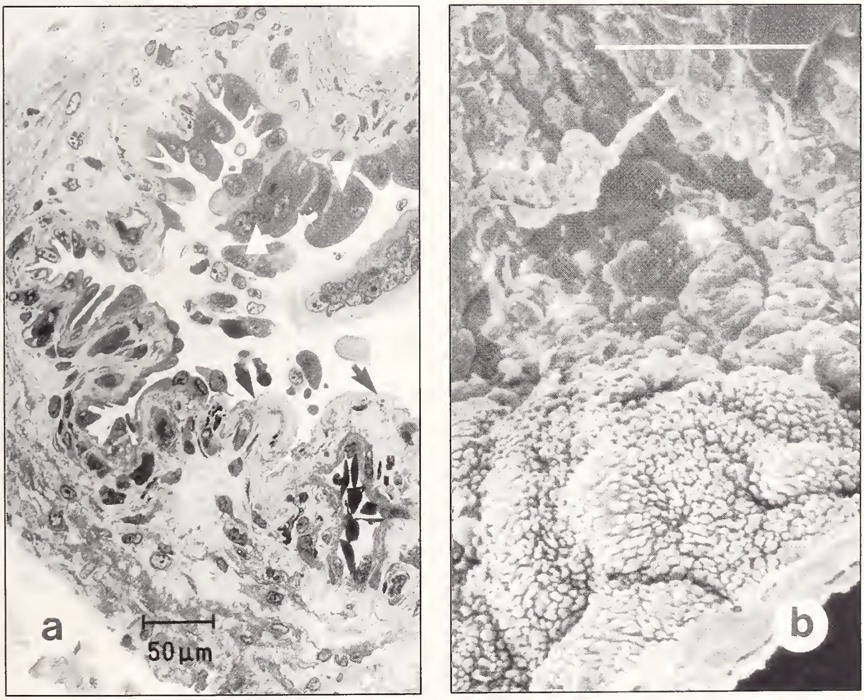

Fig. 10 a, b. The *zona trophica* in *Salamandra atra*. **a** Note large epithelial cells (arrowheads), and areas devoid of epithelial cells (arrows) (1 µm semithin section, Toluidine blue-borax). **b** Scanning electron micrograph of the trophic zone showing an intact epithelium (in the front) and areas free of epithelial cells (in the back). Bar 500 µm.

as might be expected (Greven 1984; Guex & Chen 1986; Guex & Greven 1994).

Wiedersheim probably discovered the *zona trophica* for the first time (see his figures and the description of the proximal zone of the uterus in Wiedersheim 1890). He stated that the offspring bathe in a “blood-egg-mush” and the epithelium of the entire uterus would be destroyed during pregnancy. These findings could not be confirmed by others (see among others Schwalbe 1896). Fachbach (1969) has recognised and described the nutritive zone unequivocally on the basis of histological sections and Guex (1994) showed that the trophic zone is present also in *Salamandra atra aurorae*. The *zona trophica* develops only in presence of embryos of the 3. Schwalbe stage. Thus, it appears to be formed without the influence of maternal hormones. The epithelium in this zone continuously regenerates during the period, on which the offspring feeds. After birth of the fully transformed young, the uterine epithelium is restored completely and looks like the the normal uterine epithelium (Guex & Chen 1986; Guex & Greven 1994; Greven 1998). The long gestation period and the fact that all native amphibians are protected in Europe are serious obstacles for further experimental work on this fascinating kind of parental care.

In brief, the uterus of viviparous species is lined by a monolayered transporting epithelium that secretes some mucopolysaccharides and which is involved in the adjustment of the intrauterine environment as well as in the elimination of metabolic waste products of the fetuses. Beyond that, the uterus of the Alpine Salamander possesses a cranial zone, whose epithelial cells proliferate in presence of a certain larval stage. Cells will be scraped off, if larvae are properly positioned, or will be detached by necroses and/or apoptosis. Detached cells were continuously replaced.

5. Secretion and functions of the egg jellies

During the passage down the oviduct eggs rotate and are coated by the glandular secretions that form a series of more or less discrete jelly layers (Fig. 11). This process may be facilitated by the muscles in the subepithelial connective tissue and the ciliated cells of the epithelial lining. Secretions of the smaller secretory cells, e.g. in the oviduct of *Pleurodeles waltl* may serve as a lubricant (Boisseau 1980). Contractions of the muscularis in both, the ovi- and viviparous urodele species could be induced by neurohypophysial hormones (arginin-vasotocin). Sensitivity depends on the physiological status of the animals and was modified by sex hormones (estradiol and progesterone) (Heller et al. 1970; Guilette et al. 1985). Involvement of the rich adrenergic innervation shown in the uterus of *Salamandra salamandra* on oviduct activity is questionable (Greven et al. 1985).

5.1. Number of egg jelly layers and their significance for fertilization

Despite the often confusing variety of oviductal subdivisions (Tab. 1) the statement of von Wahlert and others that each specific subdivision of the *pars convoluta* matches with the production of a particular jelly layer is in principal valid. This was confirmed repeatedly by the similarity of their histochemical reactions and/or relative positions. In view of the species-specific differences in oviductal structure and histochemistry, the number and histochemical properties of egg jelly layers should vary considerably (Tab. 1). The anterior part of the *pars convoluta* (see section 2) secretes the innermost, often very fluid jelly coat (J1), the middle part secretes the dense and light refringent J2-layer and the posterior part(s) secrete the more external jelly coat layers that vary in number and thickness depending upon the species. Therefore, at least three, often, however, more than three jelly layers that envelope the urodele egg may be distinguished (Fig. 11). According to the four segments of the *pars convoluta* in the oviduct of *Triturus vulgaris* and *T. helveticus*, von Wahlert found four different jelly layers in the eggs of these species (Tab. 1).

Using histological sections and mainly carbohydrate-specific stainings Salthe (1963) identified coverings of different consistency around the eggs of 33 urodele species ranging in number from three (*Cryptobranchus alleganiensis*) to eight (*Hynobius retardatus*). From these different layers the innermost, which often contains sulphated mucopolysaccharides (see above) liquefies after oviposition forming the capsular fluid. According to Salthe (1963) the structure of the egg jelly in some cases appeared to be dictated by the demands of the environment (Plethodontidae). In other cases, however, the systematic position of the taxon is decisive (e.g. in the Ambystomatidae). Terrestrial eggs of the

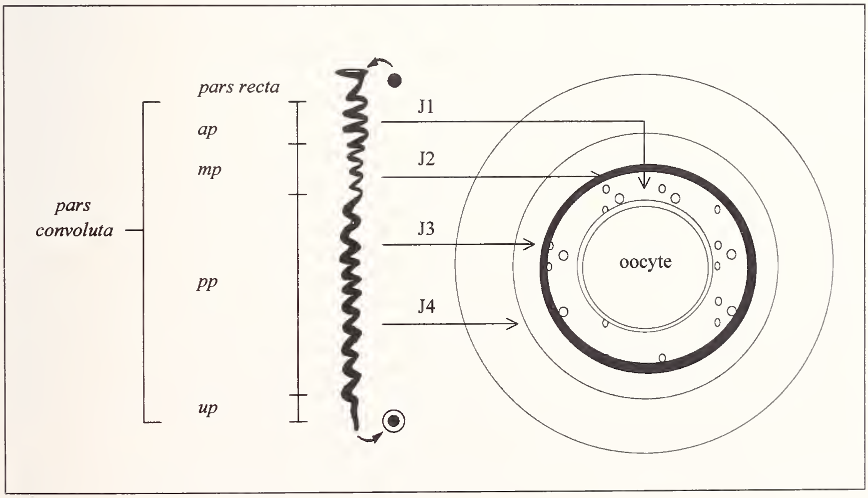

Fig. 11. Simplified diagram of a urodele oviduct with its main portions and the egg jelly layers secreted by them. *ap*, *mp*, *pp*, *up* anterior, middle, posterior and uterine portion of the *pars convoluta*. J1-J4 egg jelly layers (modified after Lerivray et al. 1985 and Jego et al. 1986).

Plethodontidae had thinner and generally somewhat stronger, but not necessarily fewer jelly layers. The egg jelly layers of some species (e.g. *Siren lacertina*, *Hynobius lichenatus*, *Ambystoma tigrinum*) include minute crystals. In some *Ambystoma maculatum*-populations, these crystals, synthesized in the tubular glands, contain a polypeptide glycoprotein with a molecular mass of 15.000 D (Hardy & Lucas 1991). Salthe (1963) tried to homologise the individual layers of the egg jellies according to their consistency, relative thickness and appearance after carbohydrate and protein stainings without knowledge of the oviductal structure. If one would infer the number of oviductal segments from the number of the egg jelly layers one should find eight (!) secretory subdivisions in the oviduct in *Hynobius lichenatus* which species is said to have eight discrete egg jelly layers (Tab. 1). In some cases the number of oviductal segments and the number of egg jelly layers correspond very well, in others such a congruence is not obvious (Tab. 1). This may be due to the different stainings and/or criteria used by researchers to visualize egg jelly layers and oviductal subdivisions. However, strict congruence may not be given in all cases. Secretions of adjacent segments similar in composition and consistency may mix, thereby reducing number of expected layers or may form precipitations suggesting additional coverings (see *Pleurodeles waltl*; Jego et al. 1986).

Histochemical and biochemical investigations of the urodele egg jelly have been available since the early fifties of the last century. In 1955, Minganti, detected mannose, fucose and hexosamines in hydrolized egg jellies of the Axolotl and expanded his studies to *Triturus cristatus* (Minganti & D'Anna 1959). Interest in carbohydrate moieties present in a considerable amount has increased in subsequent years as the egg jelly, in general, plays an important role as an effector of fertilization and polyspermy block (see section 6).

As revealed by histochemical tests the egg coverings J1, J2, J4 of *Notophthalmus viridescens* stained positively for acid and neutral mucopolysaccharidess. J2 and J5 contain perhaps sialic acids and J3 neutral mucopolysaccharides (Humphries 1966). Sialic acid in extracts of egg jelly layers as well as in the oviduct could be demonstrated also biochemically in this species (Humphries et al. 1968). Furthermore the ability to become fertilized increased the more jelly layers were acquired by the egg. Eggs taken directly from the coelom were not fertlizable (see also Good & Daniel 1943; Nadamitsu 1957). With the exception of the eggs of hynobiids (*Hynobius nebulosus*) that are monospermic, eggs of the more advanced Urodela are physiologically polyspermic, i.e. several spermatozoa enter an egg at fertilization (summarized by Iwao 2000).

Hydration, mainly of the outer (J5) and middle (J3) layer prevented further penetration of sperm, thus, limiting polyspermy (McLaughlin & Humphries 1978; see also Picheral 1977). Curiously, in oviparous species the presence of egg jelly does not seem to be necessary in each case for successful fertilization (Matsuda & Onitake 1984 a, b.).

Sialic acids are responsible for the rapid water absorption of the egg jelly after oviposition. As they are negatively charged they hold back divalent ions, which are necessary for the activation of spermatozoa. A side effect, obviously not essential for the developing embryo, is the accumulation of exogenous proteins (investigations of the egg jellies of *Ambystoma macrodactylum* by Berner & Ingermann 1990). A lectin-ligand reaction blocked sperm entry limiting polyspermy perhaps more effectively than hydration. Jego et al. (1986) investigated the composition (proteins, sugars, sialic acids) of egg jellies of various urodeles (see above). They found that sperm was stopped after a while at the limit between J1 and J2 in *Pleurodeles waltl* and at the limit of J3 and J4 in *Ambystoma mexicanum*. These results reflect the different locations of lectins in the oviduct (see section 3). According to these findings the barrier to surplus sperm cells in the viviparous *Salamandra salamandra* should be present between J1 and J2 provided that similar mechanisms work in this species.

More recently special attention was drawn to O-linked oligosaccharides and possibly species-specific carbohydrate chains in the egg jelly layers of *Pleurodeles waltl*, *Ambystoma maculatum* and *Ambystoma maculatum* probably relevant to gamete recognition (Strecker et al. 1992 a,b; Strecker et al.1994; Plancke et al. 1994; Fontaine et al. 1995). Gastrulae of *Ambystoma mexicanum* possess four proteins and glycoproteins containing (PAS-positive) egg jelly layers; in the innnermost jelly complex (layer J1, J2, J3) a polypeptid with a molecular mass of 110 kD dominates; its significance is unknown as yet (Carroll et al. 1992). Substances were now demonstrated in the egg jelly of *Cynops pyrrhogaster* that induce motility (Ukita et al. 1999) and acrosome reaction in sperm (Nakai et al. 1999; Onitake et al. 2000).

All these partly very detailed investigations consider a very small number of species. However, they give evidence for species-specific differences in composition and position of egg jelly macromolecules. Some of them may prevent excessive polyspermy, others have to do with interactions of gametes.

5.2. Some other functions of the egg jelly

I will only allude to some other functions of the egg jelly (see the review by Salthe & Mecham 1974). In some species jelly fastens the eggs to the substrate (Salthe 1963), protects them against microorganisms (perhaps by lectins outside the egg as mentioned in passing by Lerivray et al. 1985) and physically against predators (Walters 1975; Ward & Sexton 1981; Semlitsch 1988), and form an osmotic barrier. Jelly appears not to be very effective against desiccation when eggs are deposited in terrestrial sites (Heatwole 1961). Egg masses of some *Ambystoma maculatum*-populations having the above mentioned crystalline inclusions in their jelly were avoided, those lacking such inclusions were eaten by predators (Hardy & Lucas 1991). The thick egg jelly, particularly the innermost layer, of the same species houses symbiontic algae. Algae positively affect development, hatching and chance of survival of the larvae under light conditions by obtaining carbon dioxide and nitrogenous waste from the embryos (Gilbert 1940, 1944). Hutchison & Hammer (1958) assumed that oxygen production of the algae may less important as protozoans and bacteria colonize the jelly. Moreover, algae may help protect embryos against UV-B radiation by creating a green filter around embryos (for more readings see MARCO & BLAUSTEIN 2000).

Modes of reproduction in the Urodela include lentic (pond) breeders that normally lay large clutches of small eggs, lotic (stream) breeders that have relatively small clutches of large eggs and terrestrial breeders with small clutches of large eggs as well as live-bearers. Eggs are attached singly or in small or large clumps to submerged vegetation, stones etc. (see among others NUSBAUM 1985). SALTHE (1963), however, has been unable to find correlations between the reproductive mode, oviposition site, egg size and egg jelly layers (see above). This does not exclude that such correlations exist.

VON WAHLERT assumed, that those species of Urodela having tubular glands in their oviduct produce thicker jellies than those having columnar gland cells arranged in a monolayered epithelium. In fact, some measurements were presented by him to support this assumption (VON WAHLERT 1953, S. 53). He argued that eggs with a thick jelly become attached to the substrate or to other eggs forming a mass or clump, whereas eggs with a thin jelly have to be protected e.g. by wrapping them into leaves, as seen for example in *Triturus*-species. It was suggested that they do this preferentially with living plants to enhance supply of oxygen (WIMPENNY 1951). However, *Triturus*-species spawn opportunistically. Nevertheless, this behaviour effectively protects the new generation against predators (MIAUD 1994, 1995; see also SALTHE & MECHAM 1974).

VON WAHLERT considered the wrapping of eggs into leaves of aquatic plants as a form of highly developed parental care. In his view care of young can be deduced already by the structure of the oviduct and its glands not only within viviparous, but also in salamanders that lay eggs singly. He claimed „Die Betrachtung des Laichs der Salamandriden lehrt, daß die Formen mit geringer Gallertproduktion diese Materialeinsparung durch eine erhöhte Brutfürsorge kompensieren. Die wenigen bekannten Angaben über die Eizahlen verschiedener Salamandriden lassen erkennen, daß möglicherweise mehr als eine Kompensation erfolgt ist und die Formen mit höher entwickelten Brutpflege außerdem auch die Zahl der überhaupt gelegten Eier reduziert haben", (A closer look at the spawn of salamandrids shows that forms with a small production of egg jelly compensate for this saving of material by an increased care of offspring. The few known data on the number of eggs in different salamandrids show that possibly more than one compensation took place and the forms with highly developed parental care have reduced the number of eggs) VON WAHLERT 1953, p. 296). In fact, the number of eggs and newborns is reduced in viviparous species (see GREVEN 1998), as well as in embryo-guarding salamanders, that possibly evolved from lotic breeders that had already relatively small clutches of large eggs, hidden nest sites and parental care (NUSBAUM 1985).

Egg jelly surely impeds gas exchange. Its thickness may be a compromise between the necessity to facilitate the gas exchange and to support the oocyte mechanically. The relations between environment, oxygen partial pressure, oxygen permeability of the egg jellies are known for oviparous species, if at all, only basically (see SEYMOUR & BRADFORD 1995). Considering viviparous species questions arise on cause and effect resp. prerequisite and consequence of certain features. Are thinner egg jellies a consequence of viviparity or a prerequisite to minimise diffusion distances for gaseous exchange? The latter will be more probable. However, embryonic eggs of *Salamandra atra* are coated by a egg jelly nearly twice or more as thick as the diameter of the egg (WUNDERER 1909, 1910; VILTER 1962). In contrast to *Salamandra salamandra*, fetuses hatch at an earlier stage of development (SCHWALBE 1896).

Furthermore, the production of the eggs as well as the formation of egg jelly is costly. So far neither its weight, e.g. determined in relation to the egg mass, nor the energy needed for its production has been calculated as yet.

The relations of egg jelly layers with the environment are surely more complex than suggested. However, it is remarkable that no one has seriously pursued the question, whether e.g. egg jelly nature and/or thickness is correlated with the oviposition site, respiratory demands and parental care in the widest sense.

In brief, the eggs of urodeles are covered by jelly layers, whose number does not always correspond with the number of the glandular subdivisions in the oviduct. This may be partly due to the methods used and the fact that no reliable and uniform criteria are available to distinguish oviductal subdivisions and egg jelly layers. Perhaps a strict congruence between oviductal subdivisions and number of egg jelly layers cannot be expected in all cases. The surely existing taxon-specific variability in number of egg jelly layers and its possible relations with the spawning substrate as well as respiratory problems are insufficiently understood. Jelly layers have a variety of functions depending on the habitat of species and mode of reproduction. There is evidence that certain components of the egg jelly and, thus, of the secretory products of the oviduct, prevent excessive polyspermy and make possible species-specific gamete interactions.

6. Site of insemination and fertilization

About 90% of the extant urodeles practise internal insemination and fertilization (DUELLMAN & TRUEB 1986). External fertilization is practised by the Sirenidae and the Cryptobranchoidea (Hynobiidae, Cryptobranchidae), the sister group of the internally fertilizing salamanders (LARSON & DIMMICK 1993). In the internal fertilizers eggs provided with the complete set of jelly layers are fertilized when passing the spermatheca that is located in the roof of the cloaca. Thus, fertilization takes place internally, but outside the oviduct proper.

Oviductal fertilization, however, was discussed to occur in the viviparous species. In *Salamandra atra*, whose oviduct has fewer gland cells, the amount of jelly is not sufficient to encase all eggs; only the embryonic egg is provided with a complete jelly (VILTER 1962, 1967b). The follwing eggs have either an incomplete or no jelly. These eggs form later the above mentioned embryotrophe (WUNDERER

1910; VILTER 1962, 1967b; HÄFELI 1971; GUEX & GREVEN 1994). VON WAHLERT discussed the speculative meanings of older authors and suggested, that fertilization of the eggs of *Salamandra atra* takes place in the middle part of the oviduct. This was assumed obviously under the influence of the findings of WEBER (1922) who described some nuclei in the embryonic eggs and a very high number of nuclei (>200) in embryotrophic eggs. However, sperm nuclei in the embryotrophic eggs were never seen again and attempts to inseminate embryotrophic eggs were not successful (HÄFELI 1971; GUEX & GREVEN 1994). WUNDERER (1910) and in particular HÄFELI (1971) held the currently accepted opinion, that the thick egg jelly of the embryonic egg of *Salamandra atra* protrudes into the cloacal chamber and brings the uterine mouth close to the spermatheca, where fertilization takes place.

Oviductal fertilization is discussed also for *Salamandra salamandra* since 1896 (SCHWALBE 1896), and JOLY & BOISSEAU (1973) demonstrated sperm cells in the anterior part of the *pars convoluta* of this species were soon resorbed by the gland cells. One could ask, whether the chance for a successful fertilization might be lowered here as a result of the possibly still incomplete covering or whether a full set of egg jelly layers is not necessary for fertilization in this species. Internal fertilization is a prerequisite for the type of viviparity practised by live-bearing salamanders. According to VON WAHLERT the crucial step for the evolution of ovoviviparity (or viviparity, see section 7) in the genus *Salamandra* was the shift of fertilization into the oviduct. The mode of fertilization seen in *Salamandra atra* may be considered as a secondary shift of the fertilization site back to the cloaca.

There are good reasons to assume that the parent that is most closely associated with the embryo, is preadapted for future parental care. In the case of internal fertilization (not necessarily to be coupled with viviparity) normally the female is associated with the offspring most closely. GROSS & SHINE (1981) suggested that this "association hypothesis" explains most easily the correlation between internal fertilization and female care of the young. Internal fertilization and close association with the offspring offer the possibility for selection favoring retention of the embryo in the uterus, a condition that may lead to viviparity. As shown, however, internal fertilization does not mean always the same in the Urodela.

7. Oviparity, Ovoviviparity and Viviparity

An essay about the oviduct and the eggs of the Urodela should not be finished without considering the different "parities" (oviparity, ovoviviparity and viviparity) at least briefly, as the Salamandridae include the only viviparous urodele species. The long discussed facultative viviparity in *Proteus anguinus* (e.g. NUSBAUM 1907, here also older literature; for further readings see BRIEGLEB 1962) is not mentioned again in a recent review (PARZEFALL et al. 1999). Oviparity in this species was inferred from oviduct histology already by STIEVE (1918). The meaning of "viviparity" is discussed controversly and a uniform, broadly applicable and accepted definition is still lacking (e.g. SALTHE & MECHAM 1974; WOURMS 1988; WOURMS et al. 1988; PACKARD 1989).

Von Wahlert and with him a number of contemporary authors named those live-bearing species as being "ovoviviparous", that form tertiary egg envelopes derived from the oviduct. Therefore, species that lack tertiary egg envelopes were named "viviparous". He wrote „Echte Viviparie liegt nach dieser Begriffsfassung unter den Vertebraten außer bei den placentalen Säugetieren nur bei jenen lebendgebärenden Selachiern vor, die keine tertiäre Eihülle bilden sowie bei den lebendgebärenden Knochenfischen, die ihre Jungen im Ovar austragen", (according to this terminology true viviparity exists in the placental mammals as well as in those live-bearing Selachii lacking tertiary egg envelopes, and live-bearing bony fish, whose offspring develops in the ovary are viviparous vertebrates, von Wahlert 1953, p. 291). In viviparous sharks the often extremely reduced tertiary envelope is incorporated into the placenta forming a very delicate membrane between embryonic and maternal tissue. In some species the egg envelope is totally absent (for review see Hamlett & Hysell 1998). All live-bearing bony fish examined so far possess a reduced egg chorion formed by the oocyte itself (primary egg envelope) and by the follicular epithelium in some species (secondary egg envelope, e.g. Riehl & Greven 1991; Greven 1995). In all species of the Urodela including the viviparous species egg jelly layers represent a true tertiary envelope. Therefore von Wahlert's statement „Verglichen mit *Salamandra salamandra* stellt *Salamandra atra* einen gewissen Übergang zur echten Viviparie dar, da die Menge der abgeschiedenen Eihüllen bei ihr geringer ist", (compared with S*alamandra salamandra*, *S. atra* represents a certain transition to true viviparity, since the amount of egg secreted jelly is smaller, is questionable. von Wahlert 1953, p. 291). This statement may be valid for the total amount of egg jelly, since the quantity of oviductal gland cells and the length of the glandular part is reduced, but not for the embryonic egg that has a thick tertiary envelope (see above).

There are some reasonable arguments to avoid the term "ovoviviparity" (literature cited above, see however Salthe & Mecham 1974; Wake 1993). But Thiesmeier & Haker (1990) suggested that all cases, in which a salamander female gives birth to premetamorphic stages, should be called "ovoviviparity" and cases, in which the female gives birth to postmetamorphic stages should be called "viviparity." To my opinion this is an unreasonable extension of meaning.

In live bearers the offspring is born in a relatively advanced stage of development. Thus, delivery and uptake of energy is one of the most crucial problems during the gestation period (Wourms et al. 1988). To transfer nutrition from the parent to the embryo an egg covering does not act necessarily as a barrier. Egg envelopes penetrable to a variety of nutritive substances are known from many viviparous organisms including the mentioned sharks and poeciliids (see literature cited above). In viviparous salamanders the nutritive support of the young during development ranges from the initial yolk stores to oophagy, adelphophagy and epitheliophagy (see readings in Greven & Thiesmeier 1994; Greven 1998). In *Salamandra salamandra* amino acids cross the egg jelly of the intrauterine embryo (Lostanlen et al. 1976), but their uptake is not essential for the developing larvae that feed only on the yolk (Kaufman 1913; Gasche 1939; Joly 1968); therefore this species is lecithotrophic viviparous. In *Salamandra atra* sources of nutrition are: 1) the small amount of yolk (short phase of lecithotrophy); 2) the embryotrophe (oophagy); and 3) cells of the *zona trophica* (epitheliophagy). Since 2 and 3 are supplied by the pregnant female the Alpine salamander is matrotrophic viviparous. Also in some subspecies of *Salamandra salamandra* oophagy and even adelphophagy occur (for further readings see Greven & Thiesmeier 1994). In *Mertensiella luschani* oophagy has been desribed, too (Guex 1994). Both, oophagy and adelphophagy, can be regarded as a special form of matrotrophy.

Salamandra-species give birth variably to larvae as well as transformed offspring, viviparous *Mertensiella*-species only to transformed young. For practical reasons I would like to make the state of the born progeny the basis of terminology and to jettison not only the term ovoviviparity, but also the term viviparity. Thus, one might distinguish oviparity (deposition of eggs, which are fertilized outside of the female genital tract as in the externally fertilizers mentioned above or when passing through the cloaca), larviparity (deposition of larvae as in the nominate form of the *Salamandra salamandra*), and pueriparity (deposition of transformed adolescents as in *Salamandra atra*). By including other taxa, this gradual distinction can be expanded for instance to zygoparity (deposition of zygotes; to my knowledge unknown in Urodela), pupiparity (deposition of pupae as in some insects) etc. I do not want to broaden this aspect herein which is beyond the scope of this survey, but I believe that this view may have some advantages (Greven in prep). With live-bearing Urodela my intention appeared to be realized already in the last century when authors used terms such as “Kiemenlarven vivipar” (live-bearing of larvae with gills) and “Vollmolch vivipar” (live-bearing of fully metamorphosed young) (Harms 1946) to characterize newborn in viviparous salamandrids (see also Wolterstorff 1928).

In brief, there is no generally accepted definition of viviparity (and ovoviviparity). Widely used is the distinction between lecithotrophic (exclusively yolk dependent, today used synonymously to ovoviviparity) and matrotrophic (transfer of energy by the female during developmen) viviparity. Both forms are realized in viviparous salamanders. However, it is suggested neither to use the term ovoviviparity nor the term viviparity, but to make the state of development of the newborn the basis of terminology which distinguishes in the Urodela oviparity, larviparity, and pueriparity.

8. Postscript

Von Wahlert has shown in his doctoral thesis that knowledge of the structure of the entire urodele oviduct can give valuable hints on the mode of reproduction of a given species. Moreover, this knowledge is an important base for physiological, cytological, biochemical and molecular investigations as well as for the discussion about the evolution of the different modes of reproduction and life history strategies present in the Urodela. Surprisingly, some of the suggestions and ideas outlined in his thesis have never been taken up and broadened in subsequent studies This does not apply to the cloaca that was not considered in the present essay. Structure and function of this organ and its significance for the phylogeny of Urodela were investigated very carefully in recent times (see among others SEVER & BRIZZI 1998). Further studies will be promising in view of the rather limited number of investigated species confined mainly to salamandrids and the large gaps of knowledge regarding structure, development, function and control of the urodele oviduct and its secretions as well as phylogenetic implications.

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The multiple roles of the external environment in evolutionary theory

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Abstract: In tribute to the constant emphasis placed by Gerd von Wahlert on ecological aspects of evolution, I take this opportunity to examine the entire spectrum of organism-environment interactions and their multiple roles in evolutionary mechanisms. Three different interactions can be considered, those of the **environment-genotype**, the **environment-ontogeny**, and the **environment-phenotype**. The first leads to modifications (mutations) of the inheritable material. The second leads to modifications in the realized phenotype of the individual organism during its life, and hence changes in the phenotypic attributes of the organism on which selective agents act. This interaction has scarcely been considered by evolutionists although it has a most significant role in evolutionary changes of all attributes of living organisms. And the third leads to modifications in the characteristics of the population or the species over evolutionary time. A further analysis of environment-phenotype interactions leads to a clarification of many core evolutionary concepts such as natural selection, fitness, selective agents and shows the need for several new concepts such as competency of the organism, and the distinction between the three known phenotypic components of competency and fitness, namely survival features (= adaptations), direct reproductive features and indirect reproductive features.

1. Introduction

When Darwin (1859) advocated his theory how living organisms evolved (the fifth of the bundle of theories that he proposed in his *On the Origin of Species*, see Mayr, 1985), he was quite clear that two major evolutionary mechanisms exist. These are (a) the formation and transmission of new inherited variation in the population and (b) the action of the external environment as selective agents on the individuals of the population. The dual action of these two evolutionary mechanisms have been stressed over and over by leading evolutionists (see Mayr 1962, 1988; Bock 1959, 1967). Yet from the beginnings of discussions by biologists about Darwinian evolutionary ideas, the emphasis by most biologists has been on the mechanisms of genetics -- the origin of new individual genetic variation and the mode of transmission of this heritable variation from generation to generation. The reasons for this emphasis on mechanisms of genetics are clear, stemming largely from (a) the almost complete lack of knowledge on the origins and transmission of inheritable variation in 1859, and (b) the fact that most biologists have been and still are laboratory workers, and are therefore attracted much more to such studies than to analyses of the multiple set of interactions between living organisms and their external environment. Historical investigation of evolutionary work during the last four decades of the 19th century shows that there was almost no interest in the mechanisms of selective demands and of other interactions between living organisms and their external environment. This emphasis continued with the unfolding of genetics beginning in 1900. Many workers still considered genetics to be the core of evolutionary analyses (DAWKINS 1976, 1982; STERELNY & GRIFFITHS 1999), with the disciplines of genetics and evolution coupled for appointments in North American biology departments for at least four decades starting in the 1920's.

The central aspect in Gerd VON WAHLERT's evolutionary thinking is the analysis of the role played by the organism-environment interaction in the evolutionary history of diverse groups of organisms (VON WAHLERT, 1957, 1961a, 1961b, 1965). He and I discussed these problems almost immediately after we met in 1977 at Harvard University and continued these discussions while I was in Germany as a National Science Foundation postdoctoral fellow during the period 1959–61. The first result of this collaboration was our analysis of the concept of adaptation and of the form-function complex (BOCK & VON WAHLERT 1965).

In this presentation, I would like to examine the entire spectrum of organism-environment interactions and to consider their roles in the working of evolutionary mechanisms. This analysis will focus strictly on nomological-deductive explanations in evolutionary biology (BOCK 2000) which are primary and essential for any historical-narrative evolutionary explanations.

2. Organism-environmental interaction

Most evolutionists consider organism-environment interactions to be restricted to just those resulting in selective demands arising from the external environment on the individual organisms, but there is a much broader spectrum of these interactions (Fig. 1).

Before discussing organism-environment interactions, it is necessary to specify what is meant by the environment. By this term, I mean the external environment, or specifically all external factors, physical and biotic, outside of an individual organism – that is outside the boundary membranes of the individual organism. Some shadowy zones may exist such as whether the air in the lumen of vertebrate lungs or the material in the lumen of animal digestive cavities are part of the external environment. I would so include them, as I would also so consider a malarial parasite happily nestled inside of a vertebrate erythrocyte. Other more difficult examples may be whether the algae and the fungus comprising a lichen are each other's external environment, or whether they constitute a single organism. Or when bacteria destined to evolve into chloroplasts or mitochondria in eukaryotes ceased to be part of the external environment of the organisms in whose cells they exist and became part of that organism. But in virtually all cases, the boundary between the organism and its external environment is clear and definite. For an individual organism, the external environment includes other members of its species -- hence all of you listening to my lecture or later reading this paper are part of my external environment.

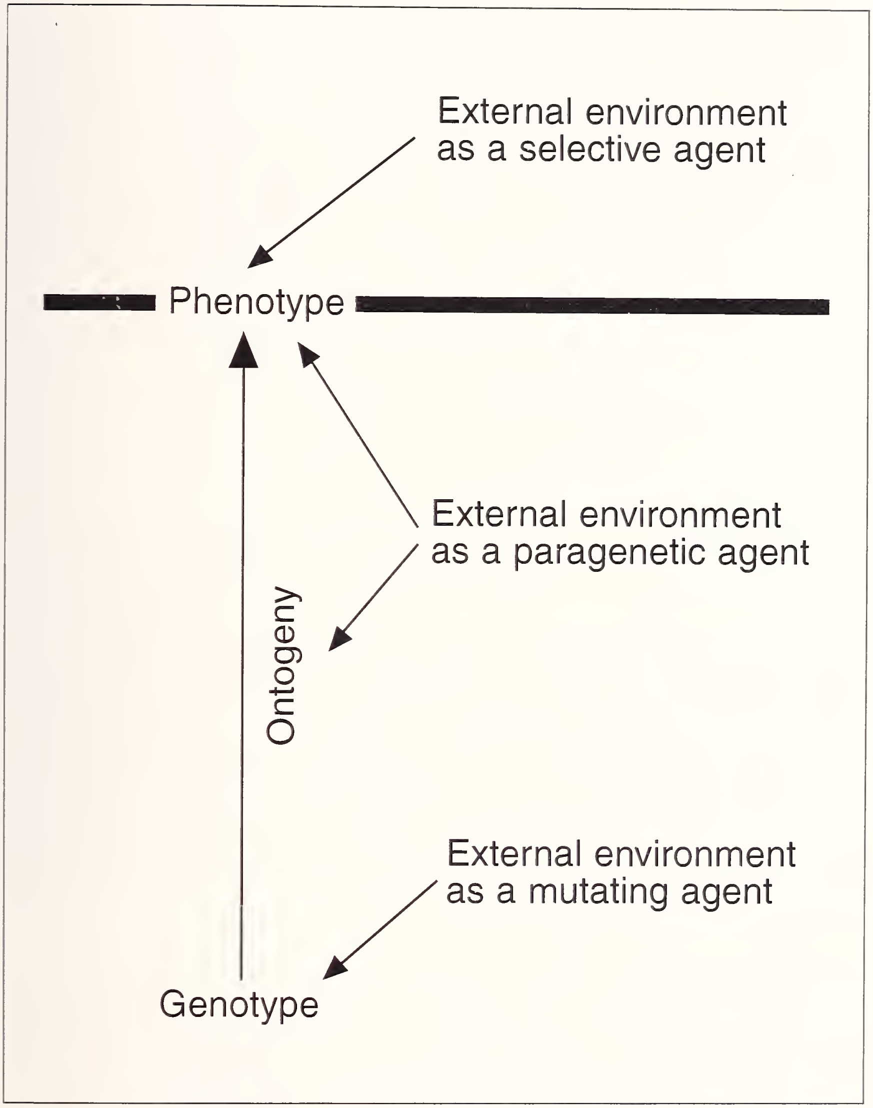

Fig. 1. Schematic diagram showing the relationships between the genotype and the phenotype with the external environment acting as a mutating agent on the genotype, as a paragenetic agent both during and after ontogeny, and as a selective agent on the phenotype. The heavy horizontal line to each side of the phenotype indicates the possible range of phenotypic expression resulting from the action of the external environment as a paragenetic agent.

A distinction has to be made between (a) the total external environment or all aspects of the environment, (b) the potential species (or individual) environment which includes the factors of the environment that could possibly be utilized or act on the species or individual (= umgebung of Bock & von Wahlert 1965), and (c) the actual species-specific (or individual-specific) environment which includes only those factors that the species or individual actually utilizes or act on it (= umwelt). The umgebung is equivalent to the potential environment and the umwelt to the species-specific environment of other authors; the species must be present to ascertain the umwelt. Empty umgebungs can exist, but not empty umwelts. The umwelt of a species is not a static, rigid system, but can change geographically and temporally, or even cyclically on a daily or seasonal basis. The ecological niche is best considered as the sum of all synergs of the individual or of the species (Bock & von Wahlert 1965) rather than the sum of the umwelt factors. Again, the species must be present to permit recognition of the niche. Niches change as species evolve. Empty niches, similar to empty umwelts, do not exist.

The environment, whether one is thinking of the umgebung or the umwelt, is always the external environment. Many physiologists and evolutionists have used a concept of the internal environment (Henderson 1913), and with it a concept of internal selection. But the "internal environment" is simply an attribute of the organism and "internal selection" is just reactive interactions between diverse features of the organism. There is no foundation on which to formulate a concept of the internal environment analogous to the external environment (Henderson 1913) and a concept of internal selective agents analogous to selective agents and demands arising from the external environment (Bock 1980, 1991). There are certainly interactions between features of the body of an individual organism which are essential for the understanding of the organization of individual organisms, but these interactions are fundamentally different from those between the organism and its external environment.

2.1. Environment-genotype interactions

The first set of interactions are those between the environment and the inheritable material. Environmental factors, such as radiation of all types, chemicals, etc., act as a mutating agent that can cause genetic mutations and therefore change the inheritable material of the individual. In spite of the claims of some workers, there is no evidence indicating that the resulting genetic changes are in any way associated with phenotypic attributes making the organism better or worst suited for dealing with selective demands arising from these environmental factors. That is, any genetic changes (mutations) resulting from the action of external environmental factors acting on the organism are stochastic (= chance-based) with respect to these environmental factors. There is no evidence of directed genetic changes with respect to any environmental factors.

2.2. Environment-ontogeny interactions

The second set of interactions are those that act on the organism during (a) ontogenetic development influencing the appearance of the phenotype resulting from the genotype, or (b) post-ontogenetic life of the individual modifying the appearance of the phenotype. The genotype and the environment serving as a paragenetic agent act together to determine the phenotype of the individual. I consider both of these processes that modify the phenotype to be the same although one acts during ontogenetic development and the other after this development has been completed. This interaction has been discussed under a series of headings such as physiological adaptation (Bock & von Wahlert 1965), phenotypic flexibility (Starck 1999a, b), norm of reaction (Levins & Lewontin 1985: 114-119; Mayr 2001: 129) and somatic modification. Although I will discuss physiological adaptation in terms of the external environment acting as a paragenetic agent, physiological adaptations also result from interactions between different features of the organism, such as muscle-bone interactions. Because of the difficulties of distinguishing between physiological adaptations resulting from the action of the external environment (which may involve a chain of feature-feature interactions) and those resulting from just interactions between diverse features of the individual organism, I will treat all under the same heading. This does not cause any theoretical problems.

The mechanism of physiological adaptation has been considered mainly by physiologists as an extension of the normal physiological activities of structures in the body, and hence has been known for decades under the heading of physiological adaptation. Prosser (1950: 2) stated that: “Physiological adaptations are those responses of an individual which occur within the genic limits of lability. The genetic limits for physiological response are much wider than is sometimes recognized. Modifying effects of the environment on morphological development are well known, as in the effects of oxygen tension on gill size in tadpoles, or of salinity on anal gills of mosquito larvae, but environmental modification is much better seen in physiological characters.” The term “physiological adaptation” is rather a misnomer – it is not simply associated with physiological attributes, but there is really no good descriptive term for this phenomenon which has been broadly accepted by evolutionists. The result of the external environment acting on the organism during or possibly after ontogenetic development is a potential phenotypic range for the genotype of that individual rather than a single phenotypic expression for this genotype. The role of physiological adaptation, as I will call this interaction, for understanding evolutionary change is much more important than appreciated by evolutionary biologists. Unfortunately this organism-environment interaction and its consequences has scarcely been discussed in the evolutionary literature.

Excluded from the concept of physiological adaptation are those changes during the life of the organism resulting from degeneration -- wear and tear. Teeth, hair and feathers wear. Cartilage tears. Cells die, leading to degeneration of tissues or organs. These degenerative changes can modify the organism significantly, but these are wearing-out modifications, not an interactive phenotypic change resulting from the environment acting on the individual organism.

Relatively few tissues and structures in organisms are not affected by environmental interactions during their ontogenetic development. I am unable to think of any in the Vertebrata. The extent of the possible modifications varies, but typically the possible modifications are rather extensive. Not all features affected by environmental interactions during ontogeny will also respond to these interactions after ontogenetic development is completed. Notable tissues in vertebrates which do not show any physiological adaptation after ontogenetic development is completed are teeth, cartilage, hair and feathers. If the phenotype of features change in response to environmental interactions after ontogeny is completed, this change is usually reversible, i.e., muscles become larger with greater use and smaller with lesser use.

The existence of physiological adaptation can be considered an evolutionary adaptation which evolved for a number of different, but reasonably closely interconnected, reasons. The evolutionary appearance and specialization of physiological adaptation in a particular feature or type of tissue could have been in response to different combinations of these possible causes such as: (a) the repair of structures in the body after they have been damaged; (b) modification of structures in the body when there are different demands on them with changes in the overall size and shape of the body during the life of the individual such as resulting from growth; (c) modification of structures in the body to maintain proper physiological activity related to demands arising from diverse evolutionary changes in the lineage, such as overall increase or decrease in the size of the organism; (d) responses to different environmental demands on the organism during its life, including seasonal changes as well as long-range changes, such as those that may occur over several generations of the species; (e) responses of organisms during development to the differing environmental demands over the geographic range of the species.

Frequently paragenetic and selective agents arise from the same environmental factor and affect the same feature of the organism. Most, but not all, phenotypic modifications resulting from paragenetic agents are generally better adaptations to selective agents arising from the same environmental factors acting on the organism. In humans, more melanin is deposited in new epidermal cells when the individual is exposed to greater solar radiation (= tanning of the skin). The increased amount of melanin serves as a better shield (= better adapted) for the skin and underlying tissues against the adverse effects of increased solar radiation. In tetrapods, the amount of haemoglobin in vertebrate erythrocyte will increase during the life of an individual if it moves to a higher altitude where the air is thinner and contains less oxygen; this change is adaptive as it permits the organism to transport sufficient oxygen to its body tissues even it the haemoglobin is maximally less saturated with oxygen. However, not all phenotypic changes resulting from physiological adaptation are adaptive. Some may be neutral, such as possibly the crossveinless condition in *Drosophila* following a proper heat shock during pupation. And some may be non-adaptive, such as the sex change (males to females) in Arctic mosquitoes following the proper heat shock during development. A most important aspect of phenotypic changes resulting from physiological adaptation is that it permits evolutionary change (measured as phenotypic modifications) from generation to generation in the absence of accompanying genetic modifications. Moreover, it may be most difficult to impossible to ascertain whether associated direct genetic changes ever appear for the evolutionary phenotypic changes resulting from physiological adaptation. Sometimes these phenotypic changes do acquire a direct genetic basis as shown over a century ago by BALDWIN (1896), and discussed ever since by evolutionists as the Baldwin Effect. But I suspect that more frequently phenotypic changes resulting from physiological adaptation never, or only very slowly acquire a direct genetic basis. For example, many groups of birds possess an articulation between the medial process of the mandible and the base of the brain case (BOCK 1960) or, between the mandibular ramus and the ectethmoid plate as in the Australian honey-eaters (Passeriformes: Meliphagidae; BOCK & MORIOKA 1970). These new articulations, which in some cases are fully elaborated diarthroses, almost certainly arose as physiological adaptations when the mandible rubbed against the braincase. This is a typical physiological adaptation of the vertebrate skeletal system in which two bones that constantly rub against one another develop a definite articulation, even a diarthrosis, with all of the attributes of these skeletal joint structures. In a like fashion, it is most likely that the new mammalian jaw articulation between the dentary bone of the mandible and the squamosal bone of the brain case arose as a physiological adaptation in the earliest mammals when the coronoid process of the dentary became sufficiently long that it rubbed against the squamosal bone of the brain case. There is no easy method, if any, to ascertain when this new mammalian jaw articulation acquired a direct genetic basis, if it ever did. That is, our jaw articulation arose as a physiological adaptation and may have never acquired a direct genetic basis.

Physiological adaptation can adjust the size of various internal organs of vertebrates to maintain proper physiological functioning as members of a lineage increase or decrease in size over evolutionary time. Consider a vertebrate, such as an elephant, rhinoceros or titanothere, becoming larger rather rapidly over evolutionary time, or reversing this trend, as in some Pleistocene island populations of elephants, and becoming quickly much smaller in overall size. As these animals became larger or smaller, all of the internal organs – lungs, heart, digestive system, liver, kidney, bladder, etc. – had to maintain the rather precise size to function properly to acquire, remove or process the needed amounts of materials required by the overall body size of the individual. If all of these evolutionary changes in this extensive set of internal organs required direct genetic changes, a large number of simultaneous genetic modifications would be required. The probability of all needed genetic changes occurring simultaneously is vanishingly small. More likely the size of these organs increased or decreased in size as a result of physiological adaptations depending on the greater or lesser functional demand on each of these organs. Hence many phenotypic evolutionary changes in these diverse internal organs would have occurred without direct genetic modifications underlying these phenotypic evolutionary changes.

This entire set of environment-ontogeny interactions have been all but ignored by evolutionary biologists which has left a major gap in our understanding of both in the mechanisms by which evolution occurs and in the explanation of the historical evolution of individual features and groups of organisms. Once this set of environmental interactions has been clarified, we will have a richer and more complete nomological evolutionary theory. Most important is that we will have a better understanding of how evolutionary changes of individual features can take place without the need of direct genetic change underlying all phenotypic evolution. And with this, a better understanding of why the oft-used definition of evolution that it is: "Genetically based change in organisms over time." is inappropriate. The better definition of evolution is simply: "Change in organisms over time, with the minimum time period being one generation." Evolution does not always occur because of selective agents favoring certain genetically-based variations, but occurs simply by selective agents favoring certain phenotypic variations which may or may not have a genetic basis. The phenotypic characteristics of individuals observed in the next generation will depend in part on the external environment and its effects as a paragenetic agent. From the time of DARWIN, evolutionists have been too easily seduced by the idea that evolutionary changes have to be based on phenotypic variations that have a heritable foundation. This idea was implied, but not absolutely so stated by DARWIN (1859: 61) in his clearest statement defining his concept of natural selection (see below).

2.3. Environment-phenotype interaction

The third set of environmental interactions is the one that evolutionists usually consider, and is the source of selective agents and their demands. Natural selection is closely linked to the evolutionary concepts of adaptation and fitness, although there is generally considerable ambiguity in the definition and application of these terms (see BOCK & VON WAHLERT 1965; BOCK 1993). These problems started with the publication of *On the Origin of Species* in which DARWIN employed several quite different concepts of natural selection, and was most vague in his definitions of adaptation and fitness. These difficulties have scarcely been clarified in the evolutionary literature, so that in their textbook, EHRLICH & HOLMES (1963) argued with considerable justification that the concepts of adaptation and fitness are redundant and that one could be dropped.

Beginning from the argument that in the environment-phenotype interaction, living organisms modify (sometimes in an extreme way) the characteristics of their external environment, some workers (e.g., LEVINS & LEWONTIN 1985; STERELNY & GRIFFITHS 1999: 257, 268–276) imply strongly that this modification of their external environment by living organisms affects, or even nullifies, currently-accepted evolutionary concepts such as selective agents arising from the environment-phenotype interaction. Nothing could be further from reality.

In many or most (but not all) environment-phenotype interactions, organisms make some, and often destructive use, of the environment and thereby alter it. If a caterpillar eats a leaf, then that leaf is gone and its environment has changed. A swarm of tent caterpillars can denude a tree, or a plague of locusts can denude an entire landscape. African elephants alter drastically the landscape of certain parts of Africa. The southern Hudson Bay population of the Snow Goose (*Chen caerulescens*) has increased so greatly over the past few decades that these birds have consumed all plants (roots included) of large stretches of their tundra breeding grounds which might not recover for decades. By building dams across streams, beavers modify significantly their immediate environment which affects not only the beavers, but a large number of other species. Nesting colonies of birds add nitrogen and other nutrients to the area around their colony which affects significantly plant growth. Additional examples of living organisms modifying their environment are endless. These modifications are the normal outcome of the environment-phenotype interaction well-known to ecologists and naturalists even if this effect by organisms on their external environment may not have been mentioned in analyses of evolutionary theory.

What significant do these modifications by living organisms on their external environment have on basic evolutionary concepts such as selective agents and their demands, adaptations and fitness. None whatsoever. All that has happened is that the external environment has been altered and with this, the resulting selective agents and demands acting on individual organisms have been changed. The selective agents acting on a group of beavers when they first settled a new stream are quite different from those that will act on these animals after they have completed their dam across the stream and flooded the area. The selective agents acting on the population of rabbits when they were first released on Laysan Island, Hawaii are quite different from those acting after the rabbits have denuded the entire island of all terrestrial vegetation. But nothing has changed in basic evolutionary theory – the external environment still serves as the source of selective agents and these selective agents still exert selective demands on individual organisms. That the selective agents and their resulting demands have changed is trivial for understanding basic evolutionary theory. Factors of the external environment are constantly changing over time, and with these modifications, the selective agents and their demands on the organisms. It does not matter one iota whether the particular organisms involved in the environment-phenotype interaction has also caused the change in environmental factors or whether this change has stemmed from other organisms or species or, whether it has resulted from a geological or climatic modification. The fact that living organisms can modify their external environment is of great interest in understanding the biology and evolutionary history of that species or group, but this has absolutely no effect on basic evolutionary theory.

2.3.1. Natural selection: A major source of the present-day confusion about the terms natural selection, adaptation and fitness are the clear definitions given to some of these terms in the beginning of the 1930's by early population geneticists (Fisher 1930; Haldane 1932) who were trying to merge Darwinian evolution with the newly acquired concepts of population genetics. These workers, accepted Darwin's (1859: 61, 81) clearest definition of natural selection, namely

> "Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection."

Hence the early population geneticists restricted the definition of natural selection to "nonrandom differential reproduction of genotypes" (Ehrlich & Holmes, 1963:326) or some similar statement, but leaving the causes unspecified. "Nonrandom differential reproduction of genotypes" is clearly a statement of an outcome resulting from unspecified evolutionary causes plus unstated initial and boundary conditions, and is quite valid both in a historical sense and in its formulation, being based on the only clear definition of natural selection offered by Darwin (1859). The problem is that evolutionists cite this outcome definition for natural selection and then use the term "natural selection" to denote either a cause or a process of evolutionary change. The result is, and continues to be, a major chaos in evolutionary thinking (Bock 1993).

The definition of natural selection (selection being a strict synonym) as "nonrandom reproduction of genotypes" is too thoroughly ingrained in the evolutionary literature to be modified, and I will not attempt to do so. It should be maintained, but only as an outcome statement describing (one type of) evolutionary change and leaving the causes and processes unstated (Bock 1993).

2.3.2. Selective agents: A term is needed for the concept of selection (both natural and sexual selection) as basically used by Darwin (regardless of his definition, 1859: 61,81) and by most evolutionists as one of the evolutionary causes. I propose that this cause be called selective agent and define it as: *A selective agent* is defined as *any factor arising from the external environment of an individual organism that interacts with phenotypic faculties (form-function complexes; see Bock & von Wahlert, 1965) of the individual and gives rise to demands with which the organism must cope successfully to (a) continue its survival as an individual or (b) produce offspring by whatever method is used by that organism.* Selective agents are evolutionary causes. Selective agents place demands on individual organisms with which the organism must cope successfully in order to continue its survival as an organism or to produce offspring. Note carefully the use of "or" rather than "and" in the phrase "to continue its survival as an organism *or* to produced offspring." Whether the organism must cope with the demands of a particular selective agent to survive as an individual or to reproduce successfully depends on the nature of the particular selective agent and the nature of the particular faculty. Selective agents are not environmental factors themselves nor are they determined unilaterally by the external environment. Rather selective agents are determined by an feedback relationship between the environmental factor and how the organism reacts to this environmental factor (BOCK & VON WAHLERT 1965; BOCK 1980) as originally argued by VON WAHLERT (1961a, 1961b). Selective agents have been referred to as selective forces (= selection forces) or selective demands, but I prefer selective agents because this term is more neutral with respect to earlier uses. Selective forces stems from the use of "force" which is very often used by scientists and philosophers alike as an incorrect synonym for cause.

Selective agents arise from the external environment and place demands on the whole organism, not parts of it, and certainly not on the heritable material, with which the organism must cope in order to continue surviving as an individual or to reproduce. Most important is that selective agents are not environmental factors themselves nor do they arise unilaterally from the external environment, but depend on how the individual organism interacts with the environmental demands (VON WAHLERT 1961a, 1961b; BOCK & VON WAHLERT 1965; BOCK 1980). This feedback interaction between the individual organism and the external environment determines the exact nature of the selective agent as has been first shown clearly by VON WAHLERT (1961a, 1961b). Moreover, features of the organism are not adaptations (survival features) or reproductive features with respect to particular factors of the external environment, but to the selective agents arising from these environmental factors; this is a point still confused by most evolutionists.

2.3.4. Fitness: Fitness, either as defined by FISHER (1930) or HALDANE (1932) or as expanded as inclusive fitness by HAMILTON (1963, 1964), is a measure of the number of offspring or the number of genes that an individual leaves in the next generation. I will use the more general concept of HAMILTON. *Inclusive fitness* is defined as *the number of offspring in the next generation possessing genes identical to those existing in an individual organism which are attributable to that individual and which may include direct and/or indirect (co-lateral) components.* Inclusive fitness is therefore a measure of the contribution of the genes of an individual to the next generation. Offspring must be counted at the same stage in the life cycle as was the parental generation. Moreover, it is best to measure fitness one generation at a time, although many workers have used measures of fitness to ascertain contributions of individuals to the population many generations into the future.

Fitness is a concept applicable to individual organisms, not to their phenotypic or genotypic attributes. Fitness is tied to selective agents in that those organisms which cope better with the selective demands acting on them would have the better fitness in a statistical sense.

Darwin used fitness in a different sense, namely for an individual that is well suited to survive in a particular environment. That is, in a varying population of individuals living in a particular environment, some individuals would be better fit than others in that they could survive better as individuals. Hence the notion "Survival of the fittest" which blissfully ignores whether "survival" is survival of the individual or of the species.

2.3.5. Competency: A term is needed to replace the Darwinian term of fitness, and I have proposed the term "competency" be used for the original Darwinian concept of "fitness" and "competent individuals" for his "fit individuals" (Bock 1993). *Competency* is defined: *as the relative ability of an individual organism in a population to survive and reproduce in a particular environment.* The most competent individuals should have the greatest fitness, and vice versa. Still needed is the development of measures of competency that are independent of measures of fitness. If this cannot be done, then competency and fitness are redundant evolutionary terms, and one can be dropped.

Competency and fitness are concepts applicable to individual organisms, and not to their component phenotypic features or to their genome. Still to be considered are the concepts that apply to the separate phenotypic features of the individual which are the components of its competency and fitness, that is the components that add up to the competency and fitness of the individual. The problem is that evolutionists, myself included (Bock & von Wahlert 1965; Bock 1980), have lumped all features of the individual organism that contribute to its competency and fitness as adaptations. A typical such statement is: "Natural selection produces adaptations – properties that cause organisms to survive and reproduce in their environments." Wilson (1992:145). Bock & von Wahlert (1965) and Bock (1979: 44), defined adaptations in terms of survival without definite reference to reproduction although we did consider success for adaptations in terms of both survival of the individual and its ability to leave progeny. Subsequently, Bock (1980: 221) gave success as survival of the individual only. These approaches are inadequate for different reasons. The problem is that attempts to group under a single heading (= adaptation) all features of an individual organism which contribute to the competency and the fitness of the organism results in a concept that is difficult to define and especially difficult to measure independently of the concepts of competency and fitness. Fitness as noted above is easy to measure empirically, although empirical measures of competency are not available at the present time.

2.3.6. Components of competency/fitness: Competency and fitness of an individual depends on two different factors. The first is survival of the individual organism as an individual - it must survive for a certain period before it can reproduce. An organism cannot reproduce without possessing the necessary organs of reproduction and a sufficient store of energy; these organs and energy store require time to develop. Survival of individuals in a population can best be summarized as a life table showing survivorship versus time. The second is the total reproductive, including both direct and indirect, effort of the individual over its entire life. Reproductive effort during each breeding season by an individual is a balance between the number of offspring which can be produced during that breeding season and the probability of the individual surviving to the next breeding season. This topic has been extensively discussed by ecologists and evolutionists, and no need exists for a separate summarization herein. What is important is that those features of individuals associated with survival and those features of the individual associated with reproduction are usually distinct and are often in direct conflict with one another. That is, many to most reproductive features are disadvantageous for the survival of the organism as an individual – are poorly adaptive – but still contribute to the competency and fitness of the individual. Hence the difficulty of attempting to group together all of the components of competency and fitness under one heading as is usually done. Three classes of elements of competency and fitness can be identified, namely (a) survival features (or adaptations), (b) direct reproductive features, and (c) indirect reproductive features. I do not claim that these three categories exhaust all classes of elements of competency and fitness, more may exist.

It should be noted that this distinction between components of competency and fitness are not the same as the ideas of K-selection and r-selection, as I stress that both survival and reproductive features are needed for the individual to possess competency and fitness. These two types of selection simply stress selection to maximize either long survival of the individual with a low but steady reproductive rate or a short life with a high reproductive rate.

It could be argued that the term "survival feature" should be used rather than the term adaptation, and that the term "adaptation" be used as the generic term for all components of competency and fitness, be it a survival or a reproductive feature. I prefer to continue the use of adaptation as a synonym for survival feature because adaptation has almost always been used in this restricted sense. A new neutral term such as "suitable features" could be used to cover the diverse features which are components of competency and fitness.

2.3.6.1. Survival features or adaptations: Adaptations or survival features have been discussed in detail by BOCK & VON WAHLERT (1965) and BOCK (1979; 1980); interested readers are referred to these papers. Adaptation as an evolutionary concept applies to individual phenotypic attributes (features) of individual organisms, not to genes, whole organisms, populations or species. An adaptation as a state of being is a quite different concept than the process of adaptation. Both are important. Basically evolutionists should be interested in first identifying adaptations as a state of being, and then ask the question of how each particular adaptation evolved. Features can be adaptations regardless of how they evolved just as H_2O is water regardless of whether it came into being by the burning of hydrogen in oxygen or by the decomposition of hydrogen peroxide (H_2O_2). The concept of "exaptation" advocated by Gould & Vrba (1982) is totally unnecessary because (a) a sharp distinction exists between clarifying the state of being of an object (e.g., whether a feature is an adaptation) and how that state of being came into existence, and (b) because it is impossible to distinguish adaptations from exaptations in well over 99.99% of all biological features. A distinction that cannot be applied to actual objects in nature is useless in science.

An adaptation, the state of being, can be defined (Bock & von Wahlert, 1965) as: *a feature of an organism having properties of form and function which permits the organism to maintain successfully the synerg between a biological role of that feature and a previously stated selective agent arising from the external environment.* Successful maintenance of the synerg means continued survival of the individual. The degree of goodness of the adaptation can be judged in several ways such as a measure of the energy required by the organism to maintain successfully the synerg, or the ratio between energy used and the energy obtained, or a balance between time required and energy spent to react to a selective agent, or some direct contest between individual organisms possessing differing phenotypes (Bock & von Wahlert 1965; Bock 1980). What is important is that adaptations can be identified and their degree of goodness judged independently of the measure of competency and/or fitness of the individual.

Adaptive evolutionary change is any evolutionary modification which results in the origin of an adaptation or in the increase of its degree of goodness (Bock & von Wahlert 1965; Bock 1980). Such changes may occur under the action of selective agents to which the feature is adapted, but they may also occur under the action of other selective agents acting on other features of the organism. Because of the complex system of genetic, developmental and structural/functional interconnections in living organisms, the details of adaptive evolutionary changes can be quite complicated and almost impossible to ascertain in the historical-narrative explanation for the evolution of individual feature of an organism.

2.3.6.2. Direct reproductive features: Direct reproductive features are all those required for successful production of direct offspring, and include the entire genital system, secondary sexual features, neurological and endocrine control of the breeding cycle, courtship and other behaviors for attracting mates and exchange of gametes, formation of the zygote, care of the developing embryo and of the young if such cares exist in the particular species, etc. Unfortunately, a shorter term analogous to that of adaptations for survival features does not exist for direct reproductive features. There has been little to no discussion of these features in the evolutionary literature aside from considerations of sexual selection and mate choice (Darwin 1871) which cover only a small portion of the spectrum of direct reproductive features. Most earlier discussions of direct reproductive features have been under the heading of adaptations which has always raised difficulties in providing definitions and measures of the degree of goodness which cover adequately both survival and direct reproductive features. As for adaptations, it is necessary to define direct reproductive features as a state of being, to outline how such features can be recognized, to provide methods to measure their degree of goodness, and finally to inquire how these direct reproductive features evolve. Such analyses have yet to be done by evolutionary biologists.

A direct reproductive feature can be defined as: *a feature of an organism having properties of form and function which permit the organism to produce offspring (= descendent kin) successfully under the demands of the selective agents arising from the external environment.* Successful production of offspring means living (= surviving) offspring that are independent of the parents at whatever stage the offspring become independent of the parents. Successful reproduction varies from releasing gametes and shedding pollen to years of parental care. The degree of goodness of the direct reproductive feature can be judged by the summation of number of offspring produced successfully in all breeding seasons, the cost of producing offspring in terms of energy utilization, increase in the probability of living until the next reproduction period, etc.

Positive evolutionary change in direct reproductive features would be any evolutionary change that increases the degree of goodness of these features. Such increase would be either an increase in the number of offspring (= descendent kin) raised successfully during all breeding seasons and/or a decrease in the cost of reproduction during a single breeding season, etc. Again the details of these positive evolutionary changes can be quite complex because of the multiple interconnections of features of the organism.

Many direct reproductive features are in definite conflict with survival features in that many to most (all ?) direct reproductive features reduce the survival of the individual as an individual. But both survival and reproductive features are essential components of competency and of fitness, and hence a balance between these components of fitness is needed to maximize the fitness of individuals.

2.3.6.3. Indirect reproductive features: Indirect reproductive features are all features required for successful production of indirect (co-lateral) offspring. They generally include behavioral features such as parental care, but may also include distinctive morphological features especially in the non-breeding castes of social insects, neurological and endocrine control of the annual cycle to fit into the breeding cycle of conspecific individuals, etc. Unfortunately, a shorter term analogous to that of adaptation (= survival features) does not exist for indirect reproductive features. Some workers have suggested "kin features" but this has serious disadvantages as discussed by Brown (1987: 302–304) because direct offspring are also kin. Most discussion of these features has been under the heading of the adaptiveness of different castes in social insects, of "helpers at the nest" in many species of birds, and certain forms of altruism which raise the same problems discussed above under direct reproductive features. As for adaptations, it is necessary to define indirect reproductive features as a state of being, to outline how such features can be recognized, to provide methods to measure their degree of goodness, and finally to inquire how these indirect reproductive features evolve. Again evolutionists have not yet inquired into these aspects of this component of competency and fitness. Indirect reproductive features correlate to the indirect component of fitness (= effects on non-descendent or co-lateral kin) of inclusive fitness as discussed by Brown (1987: 50).

An indirect reproductive feature can be defined as: *a feature of an organism having properties of form and function which permit the organism to assist successfully in the production of non-descendent (= co-lateral) offspring under the demands of selective agents arising from the external environment.* Successful production of offspring means living (= surviving) offspring which are independent of the adults which almost always means at the end of period of parental care. The degree of goodness of the indirect reproductive feature can be judged by the number of non-descendent kin produced successfully and by the cost of reproduction in terms of the loss of probability of living for another year or other appropriate period of time in the life table of the particular species.

It must be emphasized that theoretically an individual organism may have a large inclusive fitness without any direct involvement by that individual. If a particular individual has siblings which are very successful in producing direct offspring, than that individual will have a large inclusive fitness without contributing to that fitness and without having any good indirect reproductive features. Nevertheless, such an individual would have a lower inclusive fitness than its breeding siblings, and its characteristics will disappear rapidly from the population. It seems reasonable that this non-assisted contribution to co-lateral offspring should not be included in the inclusive fitness of an individual as it lacks an active cause. Moreover such individuals would possess a lower fitness than other individuals in the population and their contribution to future populations would be lost rapidly.

It must be emphasized that within a species or a population, there must be at least some individuals which maximize their inclusive fitness by having a number of direct offspring. A population cannot continue to exist if all individuals attempt to maximize their inclusive fitness by assisting in the production of co-lateral individuals.

Positive evolutionary change in indirect reproductive features would be any evolutionary change in which the degree of goodness of these features is increased. Such increase would be either an increase in the number of non-descendent kin raised successfully or a decrease in the cost of producing these co-lateral descendants.

2.4. Conclusion

Clearly organism-environment interactions have a major importance and multiple series of roles in evolutionary mechanisms. Aside from that interaction resulting in selective agents acting on organisms, these interactions have scarcely been considered by evolutionists in both the formulation of evolutionary mechanisms or in unravelling evolutionary histories of particular phenotypic features and groups of organisms. Darwin was certainly correct in stressing the importance of environmental interactions in his ideas about evolutionary theory, but even he did not realize the spectrum of possible interactions; many of these interactions were not known at DARWIN's time. Since DARWIN, however, most evolutionists continued to neglect the multiple roles of environment-organism interactions in evolutionary biology. With the rapid rise of ecology over the past 75 years, ecological studies have been more and more incorporated into evolutionary thinking until today many biology departments in North America are the so-called "triple-E" departments (ethology, ecology and evolution) with the former close association between genetics and evolution in biology appointments having largely disappeared. Unfortunately in Central Europe, training in ecology has still lags, and ecological thinking has still not achieved a core position in evolutionary thinking which has detracted from development of evolutionary thinking in this region. Without intending any criticism or denigration of the achievements of the Evolutionary Synthesis from 1937 to the late 1940's, it is clear that this synthesis was not complete. A major lack was an almost complete absence of analyses of the entire spectrum of organism-environmental interactions and the multiple roles of these interactions in our understanding of evolutionary mechanisms and in providing historical explanations for the evolution of phenotypic attributes and groups of organisms. Hopefully evolutionary biology in the future will include fully the multiple roles of environment-organism interactions.

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Use of artificial reefs with special reference to the rehabilitation of coral reefs

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Abstract. This paper is dedicated to Gerd VON WAHLERT, who first saw the possibility of studying the development of a coral reef on the basis of the settlement of organisms on harbour moles, i.e. on reef models at a scale 1:1: He had this opportunity shortly after the opening of the marine biology station in Eilat (Israel) on the Red Sea some 30 years ago. The idea of using an artificial reef as a model of a natural reef in statu nascendi has led to fundamental knowledge of the development of a coral reef. Over more than 20 years, it has been possible to observe the successive structural and ecological processes involved for the first time. In view of the scope and duration of the study, the use of this artificial reef clearly stands out from other so-called artificial reefs. Other purposes than basic reef research for which artificial reefs are used include an increase in fishery yields, the protection and development of macrophyte stands, coastal protection, attractions for diving tourism, and reef rehabilitation by prostheses. The use of the term “artificial reef” for structures incompatible with current definitions of "coral reef" is rejected. One insight in initial reef development gained from the reef models is that settlement and growth of corals on the one hand and the activity of grazers on the other hand result in the formation of a disjunct pattern of diversity with nuclei of high structural complexity and species number. They become “protoreef” communities, the empty areas between then slowly are encroached by those coral patches. This principle of nucleation is translated into practical measures in a new approach to rehabilitate and restore degraded coral reefs. Artificial mini-reefs are formed by electrochemical precipitation of calcium-carbonate from the seawater onto an aptly formed wire matrix and by transplantation of coral nubbins thereon. The community of coral tranplants and newly settled recruits may function as stepping stones to repopulate mechanically devastated reef areas. Recent experiments on the use of minireefs as reef prostheses in the Red Sea near Ras Muhamed are presented.

Key words: harbour moles, reef development, nucleation, coral transplantation, reef restoration.

1. How it all started

“Eilat – a new name in marine biology” was the far-sighted title of the first report (VON WAHLERT 1969) on the new station on the Red Sea operated jointly by the Hebrew University of Jerusalem and Tel Aviv University which had opened in August 1968. Over the past 30 years, the Marine Biological Laboratory has become one of the most successful research bases on tropical coasts. The laboratory developed at the same time as a booming leisure and watersports centre in the immediate vicinity. Step by step, hotels, harbours and a coastal road to the south made the previously remote Gulf of Aqaba (“the most desolate sea” – CROSSLAND 1939) accessible not only to Israeli watersports enthusiasts but also to sun-seekers from Europe.

Heinz STEINITZ, born in 1909 in Breslau (now Wroclaw, Poland), who emigrated to Palestine in 1933, was the driving force behind the foundation of the Marine

Biological Laboratory. He had taken up the idea from his father Walter Steinitz who had already pleaded for a marine research facility in Palestine for studies in the Mediterranean and the Red Sea in the 1930s (Clark & Aron 1972). Steinitz had also promoted his Eilat project in Germany, arguing that the new station would supplement the traditional marine biology stations in Helgoland and Naples and allow studies in the tropics – thus reviving and continuing the long tradition of research activities in the Red Sea (Mergner 1984, 2001).

I was the first scientist to use the facilities for guest researchers from Germany established at the laboratory in return for development aid. In December 1969, I arrived in Eilat with a DFG scholarship and a VW beetle full of equipment. My objective was to carry out research into the initial stages of coral reef development. Gerd von Wahlert and Heinz Steinitz had come upon this question in the autumn of 1968 when they visited the construction site of the new harbour facilities which were to equip Eilat for the future. At that time, Eilat was a small fishing village frequented by adventure-seekers and separated from the heart of Israel by several hundred kilometres of desert. Indeed it had even been used as a place of exile at one time.

It was especially Gerd von Wahlert who recognized the unique opportunity offered by these conditions for investigating the reef development process. Where conditions allow the development of reefs, we normally find fully developed reefs. A coral reef in statu nascendi is something of a rarity nowadays. Such a reef yields information on the initial stages of the reef development process, which are completely different from the processes involved in the continued existence of a reef. Such a reef also allows an analysis of the abiotic and biotic interrelationships which are gradually established. In a fully developed reef, these interrelationships are normally far too complex for analysis.

Especially interesting reef models include the moles of various harbour facilities, built up from granite and towering from the sea bed at a depth of 5 to 8 m to above the water surface (see below: reef models). These artificial reefs form a system of recesses and protrusions similar to those of a natural coral reef. Coral larvae and other reef settlers can therefore settle there in accordance with their natural preferences as regards irradiance, water current, sedimentation, the type and inclination of the substrate, etc. Artificial structures of this size are not normally available for experiments. As the construction of the harbour facilities continued for several years, it was also possible to study the initial and later stages of succession at the same time.

2. Artificial reefs – a problem of semantics

Before I turn to the general ecological results obtained over more than 20 years of development, I would like to discuss the question of "artificial reefs". What do we associate with this term, which is now so widely used? A review of the literature shows that "artificial reef" is used in a variety of different senses. Especially in the context of planning and commerce, where the term is in widespread use, the meanings attached to it appear to be almost arbitrary. A scientific discussion of reefs, especially recent reefs, can therefore not afford to ignore the anthropogenic "siblings" of the natural reef, especially in view of the considerable manipulations of the seabed near to the coast which are currently in progress.

In the following, different applications of so-called artificial reefs are reviewed, then the criteria which justify the term reef are examined.

2.1. Increased fishery yields

It has been known for centuries that fish are attracted by textured structures rising above an otherwise monotonous seabed. In Japan, attempts have been made for more than 200 years to concentrate species important for fishery at certain locations using suitable structures (Ino 1974). Following the Second World War, there was a world-wide trend to use artificial products for structural enrichment and the enhancement of fishery yields (Fig. 1). In the USA, major impetus came from the investigations of Carlisle (1962), who found that sunken ships, streetcars and special concrete "housing schemes" offered interesting retreats for fish,

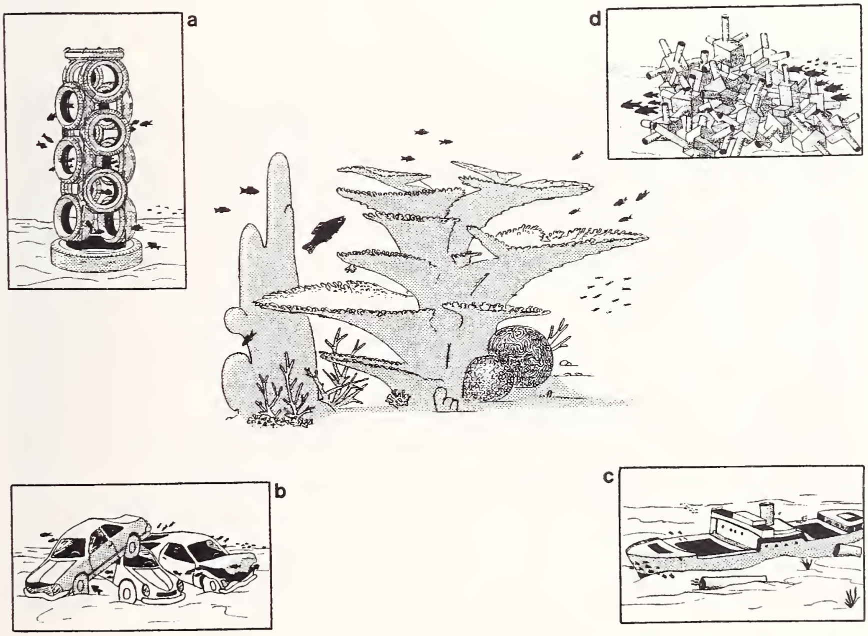


Fig. 1. Examples of artificial reefs that mimic the structural diversity of natural reefs for fishery purposes: a) tire reef with stabilizing bars, b) car wrecks, c) sunken ship, d) piled up concrete modules designed for the purpose (from Schuhmacher 1994).

attracting predatory species important for fishery. At the end of the 1960s, the often arbitrary sinking of ships and wrecked automobiles (often without the slightest attempt to remove oil and toxic paint) were superseded by the construction of tyre reefs (e.g. STONE & BUCHANAN 1970). To date, millions and millions of used tires have been disposed of in this way.

Depending on the material used and exposure to current, light and sedimentation, these artificial structures are colonized after a few years by pioneering species (e.g. serpulid polychaetes, oysters) which secrete calcium carbonate and provide a colonization substrate for corals, at least in the tropics (Fig. 2). My own observations in the lagoon of Truk (Micronesia) indicate that the remains of Japanese aircraft from the Second World War are still largely bare after some 50 years, probably as a result of the aluminium alloy used. On the other hand, the steel hulls of ships which sank at about the same time are almost entirely covered by sessile suspension feeders (although some patches of rust are still visible). In addition, a wide range of species of reef-building corals and *Halimeda*, as major suppliers of sediment, are present in abundance.

Bamboo is a versatile building material which is readily available in some areas of South-East Asia. Many thousands of bamboo reefs are probably installed each year between southern India, Indonesia and the Philippines. These are structures of bamboo rods and palm leaves interconnected by ropes and thin bamboo shoots,

Fig. 2. Section of a ship which was sunk in the lagoon of Truk (Micronesia) in February 1944; photographed in June 1992. To some extent, the succession of settling organisms can be seen: hard and soft corals have settled on the rock oysters (*Lopha cristagalli* - arrows) – the first carbonate producing organisms to take up residence.

Fig. 3. Bamboo reef as fish aggregation device. Above: decayed remains – three years after construction. Below: detail of a bamboo rod with hard and soft corals which have settled on a crust of calcareous algae and bryozoans.

between 2 and 5 m high, often in the shape of a tetrahedron. These bamboo reefs, weighted down by rocks, only survive for a few years until the plant material used for their construction has decayed (Fig. 3).

Technology has been developed specifically for the purpose of stabilizing structures permanently and ensuring that they continue to tower over the seabed in the long term. Especially in Japan, steel, plastic and concrete modules have been produced industrially for the past 20 years or so. These are assembled to form units as high as a house with a view to increasing the yield of algae, shell-fish, crabs and various species of fish.

As a result of state subsidies and pressure by industry to increase the sale of products (e.g. 1 m^3 PVC cubes originally developed for use in wastewater treatment, now used as reef modules), artificial reefs have been constructed over large areas of the Japanese shelf (e.g. MOTTET 1985).

With a view to increasing habitat diversity and the productivity of coastal regions, arguments have also been presented in favour of leaving abandoned drilling rigs in place - "rigs to reefs" (PICKEN & MCINTYRE 1989; REGGIO & KASPRZAK 1991) and of dumping ash from oil and coal-fired power stations, pressed together with gypsum to form building modules (WOODHEAD et al. 1982). All these structures and materials are mainly installed in shallow-water zones, at depths between 10 and 30 m; however, there are also some deep water reefs between 61 and 117 m (MOFFITT et al. 1989). Apart from structures on the seabed, artificial reefs are used for attracting pelagic fish. These midwater FADs (fish aggregation devices) are sail- or kite-like structures anchored to the seabed and suspended in the water. The intention is that fish should congregate in their shadows (MYATT 1985, BOMBACE 1989). Similar structures are also used as "floating reefs" (TAKEUCHI 1991) and allowed to float on the water surface.

2.2. Protection and Development of Macrophyte Stands

Off the coast of California between Los Angeles and San Diego, populations of the giant kelp *Macrocystis pyrifera* and associated algae and fish species are in decline. One reason is the growing sanding and silting up of the low-relief hard substrate as a result of wastewater discharge and sediment from continuous maintenance work on harbour facilities and coastal structures. These kelps can only settle on hard substrates, where they anchor using sturdy rhizoids ("holdfasts"). Over the course of a few years, kelps have also settled on broken rock and brick walls with a height of 1 to 2 m and lengths of up to 20 m installed at depths of 8 to 11 m (e.g. Pendleton Artificial Reef, CARTER et al. 1985). Initially, plants were transplanted to the new substrates.

Extensive meadows of *Posidonia oceanica* are characteristic of the Mediterranean. At depths from 2 to about 40 m, this endemic representative of the Potamogetonaceae has a key function both in primary production and in sediment retention. A large number of *Posidonia* stands have been ploughed up and destroyed as a result of increasingly intensive fishery using heavy bottom-trawl nets. The applicable protection regulations are largely ignored. In this situation, rocks and concrete blocks were sunk in threatened areas, firstly on the Italian coast and then on the French and Spanish coast, and piled up to form low walls (about 1 m high). These artificial anti-trawling reefs present mechanical obstacles to fishery (RAMOS-ESPLA et. al. 2000) at the same time as providing retreats for cave-dwellers such as crabs and octopuses (BOMBACE, 1989).

2.3. Coastal Protection and Effects on Local Currents

Coral reefs provide natural protection for the coastline. Where reefs are destroyed or eroded, as on various tourist islands of the Maldives, erosion of the seashore is caused by the surf and changes in currents. In some areas (e.g. Male, Maldives), artificial protection structures made up of piles of "tetrapods" have been required to replace the reefs.

Currents near to the seabed are diverted by irregularities, causing vertical turbulence. Off the west coast of the island of Schikoku (Japan), it was possible to create local upwelling areas in this way. For this purpose, concrete structures (10 m high, 20 m long) were installed at appropriate intervals at a depth of 50 m.

Plankton and fish were concentrated in these areas (OTAKE et al. 1991). As the next step, it is planned to install considerably larger hill structures to increase local productivity. Blast furnace slag (ash) has been proposed as a material.

Protective structures have also been planned for coastal sections subject to erosion where there are no natural breakwaters (e.g. the coast of California north of San Diego). In this case, soft reefs have been proposed (JENKINS & SKELLY 1994). The intention is that barriers made up of sandbags should prevent further erosion. The fact that this action is being financed by the Surfrider Foundation shows that watersports enthusiasts also wish to benefit from the surf created by these artificial barriers.

Promotion of Diving Tourism

Ships have been deliberately sunk to provide "ecological enrichment" and to make the underwater landscapes of marine leisure centres more exciting. Many diving centres now use their own wrecks or artificial reefs in their advertisements (Fig. 4). Operators of diving facilities justify the installation of artificial structures on the seabed on the grounds that these structures will reduce the pressure of tourism on sensitive natural reefs (VAN TREECK & SCHUHMACHER 1998).

Reef Prostheses and Coral Transplants

Damage to coral reefs is now widespread as a result of incidents with ships and boats, bomb fishing, and the blasting or excavation of coral for use as a building material and to clear shipping channels. Corals and other reef-dwelling species only settle the levelled reef floor, covered by rubble, with considerable delay. The mobility of the substrate, sedimentation and pressure by grazers all tend to prevent colonization by corals or the further development of established structures. HILLMER & SCHOLZ (1991) proposed that blocks of fossil reef limestone on

Fig. 4. A ship deliberately sunk near Aqaba as an attraction for divers. Three years after sinking the superstructure is populated by fast-growing soft corals (*Dendronephthya* sp.) – no frame-building organisms as yet.

land should be quarried and distributed over degraded reef areas. Blocks in fixed positions would provide a preferred settlement point and a nucleus for a newly created reef community.

Another method for providing an attractive, structured substrate for settlement is the electrochemical deposition of calcium carbonate from the seawater in situ on a wire-mesh template (Hilbertz et al. 1977, Meyer & Schuhmacher 1993, Schuhmacher & Schillak 1994, Schuhmacher 1996). The hard substrate created in this way facilitates and accelerates re-colonization by corals and other reef-building organisms (further developments of this method are described below). Where small areas are affected, the transplantation of coral fragments to destroyed sections may have a beneficial effect on the rehabilitation process (e.g. Maragos 1974; Rinkevich 1995) (see below).

3. Reef Model

Research on processes which control settling of corals, fish, and others onto reefs has a long history. However, artificial structures such as the moles of Eilat have never been investigated over such an area (Fig. 5, 9) or for such a long time from the point of view of basic research. Benthic settlement on artificial substrates has

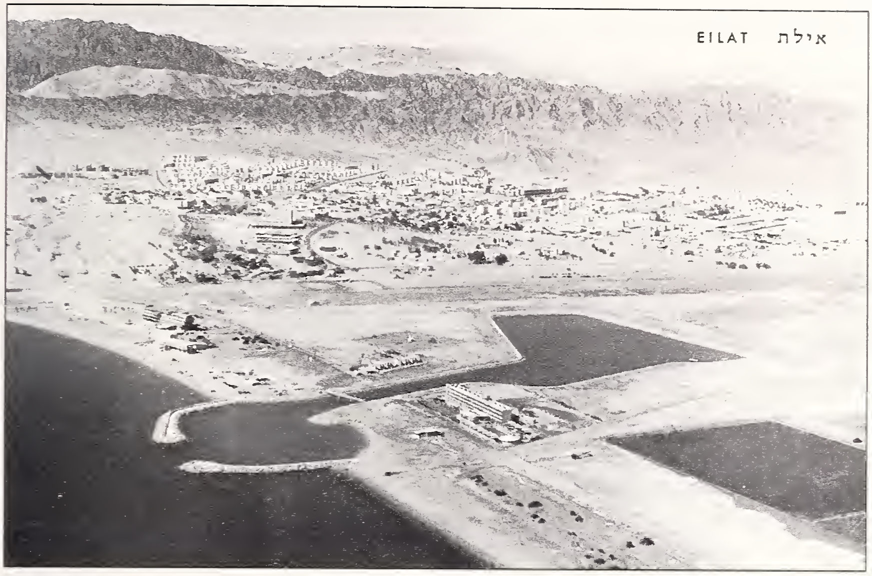


Fig. 5. Aerial photograph of the marina of Eilat on the northern shore of the Gulf of Aqaba (postcard from the year 1969). Each of the moles is more than 100 m long. Hotels have since been built on the open space in the foreground.

rarely been investigated for longer than the time required to complete a thesis and the size of the structures observed has rarely been greater than that of a pile of hollow bricks (four years observation by Ogden & Ebersole 1981) or a row of colonization slabs (nine years observation by Coe & Allen 1936).

3.1. Justification for the Use of the Term "Artificial Reef"

The examples of artificial structures on the seabed described above are all referred to as artificial reefs. In order to assess the justification for the use of this term, a comparison with a recent natural reef is useful. The definitions and views of reefs given by Cummings (1932), Ginsburg & Lowenstam (1958), Braithwaite (1973), Heckel (1974), Schuhmacher (1976), Schuhmacher & Zibrowius (1985) and Fagerstrom (1987) could be summarized as follows: "A reef living today is the physiological and physiographic expression of a hard-substrate biocoenosis which secretes its own substrate. The growth of closely meshed limestone-secreting sessile organisms results in the creation of a permanent skeleton and the accumulation of sediment. The overall structure is resistant to hydraulic loads over the long term. Temporary damage is compensated for by growth. A reef may extend from the seabed close to the water surface or even above the water surface. A typical feature is the subdivision of the structure into a variety of small habitats. The key abiotic factors, light, current, oxygen supply and turbidity are subject to steep gradients. The reef is maintained and its metabolism is controlled by a specially adapted community".

This definition presents a living reef not only as a form or structure but as a habitat with its characteristic community of organisms (reef biocoenosis). A reef must be near to the water surface because it is only here that hydraulic effects such as surf and breaking waves are to be found (RIEDL 1964, 1966). In addition, it is only here that the irradiance gradient is so steep as to allow the formation of a mosaic of habitats populated by heliophilous and sciaphilous organisms. Furthermore, the enrichment of the surface layer of the sea with dissolved and particulate organic nutrients, positively phototactic larvae and other distribution stages distinguishes it from other layers in the water column. However, the near-surface layer is not only richer in nutrients than deeper layers of the open sea; lipids which may contain toxic chemicals (such as halogenated hydrocarbons) are also relatively highly concentrated here. Without necessarily proving immediately lethal, these biocides washed in from the land, which are widely used throughout the world, impair the fitness of the organisms exposed to them to an extent which is not yet known (increased sensitivity to disease, reduced life expectancy, reduced fertility, immune suppression, developmental disorders). In this context, anthropogenic effects have given the term "reef" (structure near to the water surface) a special meaning.

Hence, "reef" is a considerably more specific term than "bank," "bioherm," or "buildup" (cf. BRAITHWAITE 1973; HECKEL 1974). These terms are not only neutral with regard to depth but also much wider and more general than "reef" with respect to the shape and size of the structure. However, it should be noted that biologists and ecologists base their views of reefs on extant (Cenozoic) examples, whereas geologists and palaeontologists compare reefs (or reef remains) from the entire history of the earth. At least the following features are characteristic of ancient reefs: "Biological control during the formation of the structures (especially by sessile organisms), rigidity of the structure and a laterally restricted topographic relief" (FLÜGEL & FLÜGEL-KAHLER 1992). This general definition corresponds to the wider term of "bioherm".

"Artificial reef" should only be used to refer to structures meeting some of the major criteria defined above for living reefs. Otherwise, the use of the term is misleading. The justification for the use of the term for some of the types of "artificial reef" mentioned above are considered below.

Re 1): It is in the case of artificial structures for use in fishery that the greatest deviation from the original meaning of "reef" is evident (e.g. deep water reef, ash reef, floating reef.). In specific cases, the size, configuration and exposure to current, light and sedimentation of shipwrecks and high artificial structures (for example of concrete modules) may be such that they constitute small artificial reefs and are colonized by hermatypic species. However, by far the larger part of structures of this type do not meet the requirements for consideration as an artificial reef. The first definition of "artificial reef" is relatively wide (Ahr 1974): "... artificial reefs are man-made structures which may be composed of a number of different kinds of materials and placed on the seabed to enhance the biological potential of the reef site. Primary benefits from artificial reefs may include in-creased sport fishing, recreational diving and research on reef ecology...". Polovina (1994) only considers the fishery aspect more precisely: "... artificial reefs may function in any of three ways: redistribute biomass which is being exploited, aggregate unexploited biomass to increase exploitable biomass, or improve survival, thereby increasing total biomass...".

More recently, specialized fishery terms have been introduced to curb the all-too-widespread use of "artificial reef" Nowadays, a distinction is drawn between "artificial habitat" and "fish aggregation device" (FAD). "Artificial habitats" include structures with hiding places where food is available, allowing species to remain there for a considerable time and to reproduce. FADs mainly include shade-producing structures (such as weighted bamboo frames, palm leaf structures, sails in open water) allowing the temporary concentration of fish so that they can be caught. The evolution in the use of the terms is evident in the title of the relevant conference, which started as "Artificial Reef Conference" (1974) and was changed to "Fourth International Conference on Artificial Habitats for Fisheries" in 1987. However, the term "artificial reef" remains very popular and Seaman & Jensen (2000) define "an artificial reef as one or more objects of natural or human origin deployed purposefully on the seafloor to influence physical, biological, or socioeconomic processes related to living marine resources. Artificial reefs are defined physically by the design and arrangement of materials used in construction and functionally according to their purpose. Items used in reef construction add vertical profile to the benthic environment. They may be either assembled expressly as a reef or acquired after being used for another, usually unrelated purpose". A wide and uncritical view is also taken by Svane & Petersen (2001): "... almost any hard substratum that has been submerged in the sea can be viewed as an artificial reef ...".

A key question in the use of artificial reefs is whether they actually increase productivity or whether the existing population is only concentrated in a smaller space where it can be harvested more efficiently. It is clear that the increased availability of niches and the larger area for settlement offer better conditions for primary producers and filter feeders and consumers dependent on these species. In the case of commercially important invertebrates such as decapod crabs and cephalopods, it may be true that populations are limited by resources such as hiding places rather than progeny numbers. However, for the majority of fish species, artificial reefs act mainly as fish aggregation devices (FADs) and only to a secondary extent as nurseries and retreats for larger populations.

Grossman et al. (1997) did not find convincing evidence that artificial reefs increased regional fish production rather than merely concentrated available biomass including previously unexploited stock segments. In the long term, the uncontrolled use of artificial reefs is therefore likely to be a factor in the overfishing of existing stocks. VON WAHLERT was also concerned with FADs. In the mid-1970s, he and his wife had set up the Appropriate Mariculture Coordination Centre (Amcoc) which worked together with fishing villagers and rural and community developers on the revival and enhancement of their extensive mariculture methods in East, South East, and South Asia. (VON WAHLERT & VON WAHLERT 1987). At that time, state development aid was mainly channelled into major projects based on European fishery technology. The local experience gained over many generations in sustainable exploitation of the sea and use of resources threatened to be lost or was in fact lost in some cases. For example, subsistence fishermen used simple methods to attract fish (such as brush parks) or to store protein reserves for bad weather periods (e.g. the storage of living *Tridacna* clams near the jetty). The objective of know-how transfer between village communities was to improve the expertise available and to introduce new, adapted techniques. At the same time, it was intended to heighten the sensitivity of the knowledge-providers to the integration of village fishing communities in a traditional complex of ecological and socio-ecological conditions (e.g. VON WAHLERT & VON WAHLERT 1977).

Viewed in retrospect, VON WAHLERT's efforts may seem to have been merely "a drop in the ocean". The population explosion and migration from the interior to the "common lands" of the coast have resulted in exploitation methods with catastrophic effects. Although officially forbidden, cyanide and blast fishing techniques (now using ammonium nitrate) are becoming increasingly widespread (BARBER & PRATT 1998; KUNZMANN 1999; HEEGER & SOTTO 2000). They represent a desperate attempt to wring the last drop out of totally overfished stocks. Even the most remote coral reefs can be reduced to rubble by blast fishing.

Nonetheless there is no alternative to VON WAHLERT`s (and others) longterm goal of protecting coral reefs and other fishing areas against overfishing and ecological degradation by appropriate management incorporating the fishing people concerned (cf. VON WAHLERT 2002).

Re 2): Artificial islands of hard substrate between and for seagrasses and macroalgae (macrophytes) cannot be considered as reefs because they are only slightly raised above the seabed and offer little potential for further growth. "Artificial bank" and "artificial buildup" would be better terms in this case.

Re 3): Reefs offer excellent protection for the coastline because of their resistance to surf. Where reefs are absent, this function must be performed by artificial breakwaters with a complex system of protrusions and recesses to absorb the energy of the waves. In shape and position, these structures can be comparable to reefs and may gradually be colonized by a community similar to that of a reef (see reef model). In such cases, the use of the term "artificial reef" is justified. On the other hand "soft reefs" are a contradiction in terms and could be referred to more precisely as "artificial sandbanks". The underwater structures used for manipulating hydrodynamic conditions, in this case for creating upwelling, are best compared with rib-shaped banks.

Re 4): "Underwater Disneylands" for divers could possibly be termed artificial reefs in areas where natural reefs also occur. The managements of facilities of this type often attempt to encourage the settlement of a wide variety of benthic organisms and fishes within a short period of time by coral transplants and similar measures.

Re 5): Artificial structures installed in degraded reef areas and possibly equipped with living coral transplants may be similar to mini-reefs. In such cases, the use of the term "artificial reef" is justified (for more details see below).

Re 6): In terms of size, structure and the resulting abiotic conditions, the harbour moles considered as a reef model are comparable to natural reefs in their vicinity. However, this does not apply to biotic interactions. While the model represents the structure of a reef, it therefore does not yet represent the reef community (cf. structural reef versus ecological reef in HECKEL 1974). The gradual process of settlement by hermatypic species and other reef dwellers and the formation of small proto-reef communities after 20 years will be dealt with in greater detail below. In this sense, these structures offer potential for self-development (self-organization and structural growth) and therefore represent artificially initiated reefs in accordance with the definition given above.

CARR & HICKSON (1997) regret that comparisons between artificial and natural reefs are typically confounded by differences in reef size, age, and isolation. For the sake of standardizing they reduce a reef to small coral outcrops in order to compare their system of hollow bricks to a respective natural counterpart. However, any problems of size, and structure are nonchalantly overlooked by OREN & BENAYAHU (1997) who call a row of PVC plates artificial reefs.

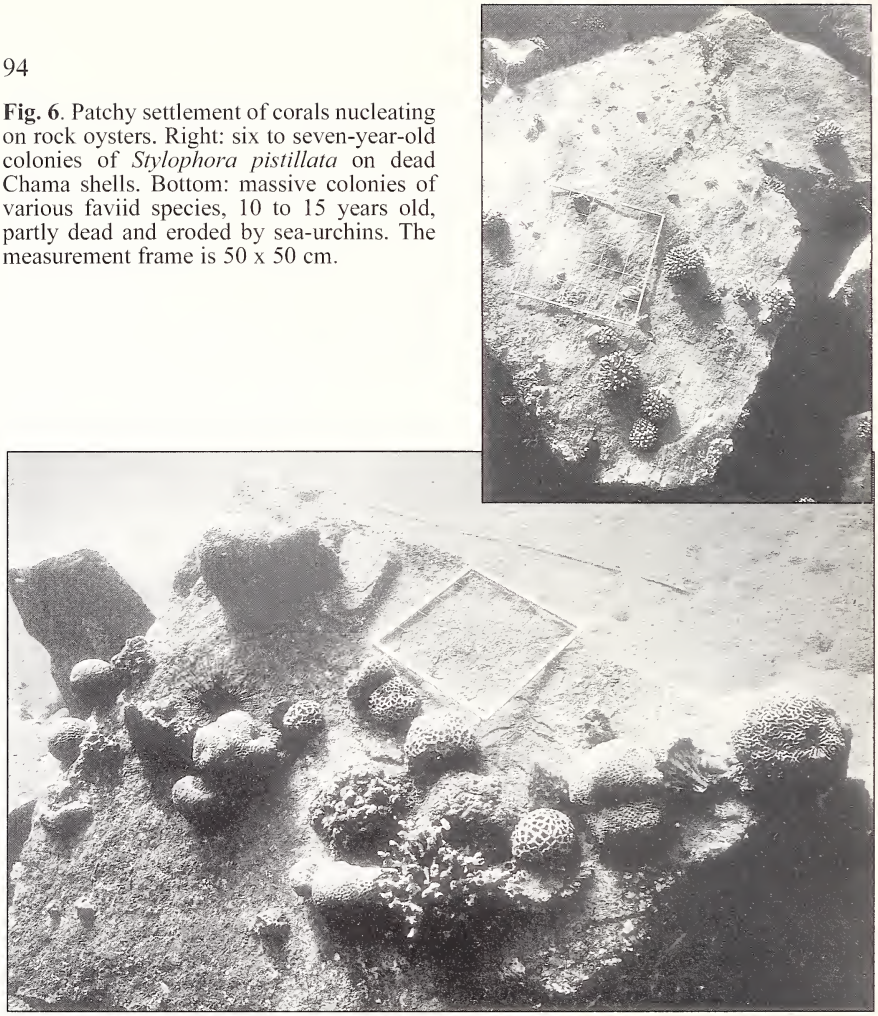
3.2. Artificial Reefs for the Benefit of Natural Reefs

This chapter focuses on artificial reefs sensu stricto, i.e. structures which mimic coral reefs to such an extent that 1) basic research on reef ecology is possible and the results are of direct benefit for e.g. the management of reefs (reef models), and 2) they serve as nucleation centres and stepping stones for the restoration and recolonisation of degraded reef areas (reef prostheses).

The reef models at Eilat mentioned above (Fig 5, 6) provided general findings over a period of 20 years (among others: SCHUHMACHER 1977, 1983, 1989, unpublished) as follows:

A) The constructive and destructive processes which operate simultaneously in a mature reef come in and proceed in sequence when a reef is in its infancy. Thus different phases can be distinguished during the onset of reef development (Fig. 7). The initial phase is direct colonization by fouling organisms, especially bacteria and short-lived algae (Fig. 8). This phase, which has no effect on the later development of the reef, has been described in detail by WAHL (1989). Among the ubiquitous, opportunistic species which colonize first are also calcareous algae, encrusting foraminifers (*Acervulina* sp.), calcareous tube worms,

Fig. 6. Patchy settlement of corals nucleating on rock oysters. Right: six to seven-year-old colonies of *Stylophora pistillata* on dead Chama shells. Bottom: massive colonies of various faviid species, 10 to 15 years old, partly dead and eroded by sea-urchins. The measurement frame is 50 x 50 cm.



and later also worm shells (Vermetidae) and oyster-like shell-fish (*Chama* sp., *Spondylus* sp.). The calcareous deposits of these organisms with their microrelief are preferred colonization sites for coral larvae (see also Wallace & Bull 1981; Sammarco 1996). The adhesion of these calcium-carbonate-secreting organisms can therefore be seen as the preparation phase. It is with the successful growth of hydrocorals and scleractinian corals that the stage of frame-building or reef-building starts. The extensive skeletons formed can be compared with the frame of a timber-framed-house (Ginsburg & Lowenstam 1958). The infill, i.e. the material between the framework, is provided by sediment and by binding organisms such as calcareous red algae, foraminifers, encrusting corals, bryozoans, etc. One prerequisite for the presence of loose sediment is the activity of boring organisms which to a certain extent loosen the structures created by the

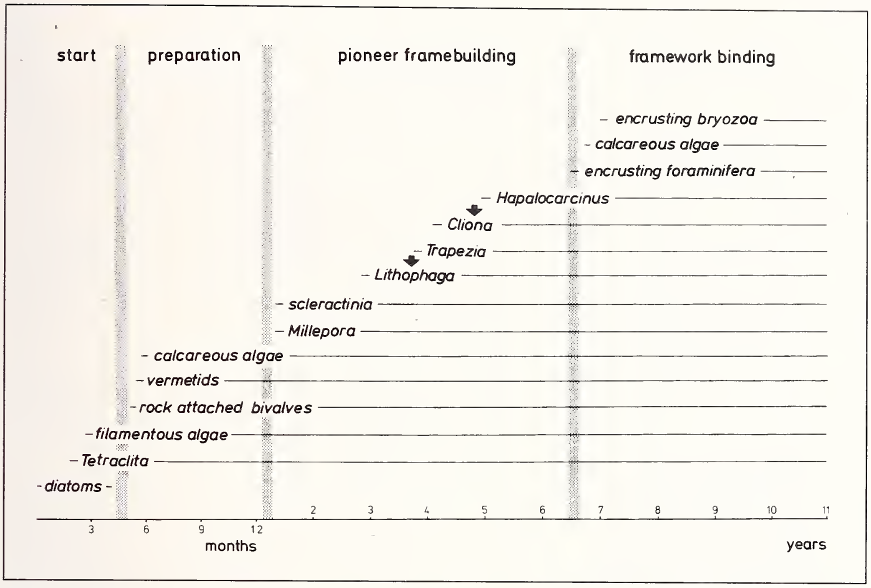


Fig. 7. Succession of reef-building mechanisms:
– "Start": immediate settlement by fouling organisms (cf. Fig. 8).
– "Preparation": sessile pioneering calcareous forms (*Fosliella* sp, *Acervulina* sp., *Serpulorbis* sp., *Chama* sp., *Spondylus* sp., *Lopha cristagalli*) secrete the substrate needed for corals and other sessile reef-dwellers.
– "Frame-building": corals with the typical characteristics of the r-strategy (mainly branching corals) and therefore short life expectancies of 5 to 12 years, starting with the construction of a three-dimensional frame.
– "Framework-binding": encrusting young coral colonies, calcareous red algae, foraminifers, and bryozoans consolidate the dead sections of frame-builders and sediment particles. The mechanism "sediment formation" does not significantly start before the death, fragmentation and bioerosion of the first generation of frame-builders although some borers (arrows) already invade and weaken living pioneer colonies (from Schuhmacher 1977).

frame-builders. Initial traces of bioerosion, sedimentation and binding were already evident on the Eilat reef models after the first generation of pioneer corals had died. The life expectancy of these opportunistic species is only between one and two decades. The final stage in reef-building, cementation, i.e. the filling of internal pores by deposits of aragonite crystals and cryptocrystalline high-magnesium calcite, only starts later. In a natural reef, the skeleton and sedimentary material with a porosity of about 50% is only converted into rock with a porosity of 10% or less below the surface of the reef, i.e. after several decades or even centuries. Within a matter of centimetres below the surface of the reef, corals acquire cement of aragonite rods and needles; the pore space is more or less occluded (Friedman et al 1974). In a fully developed reef, the processes of frame-building, frame-destruction by bioerosion and hydrodynamic forces,

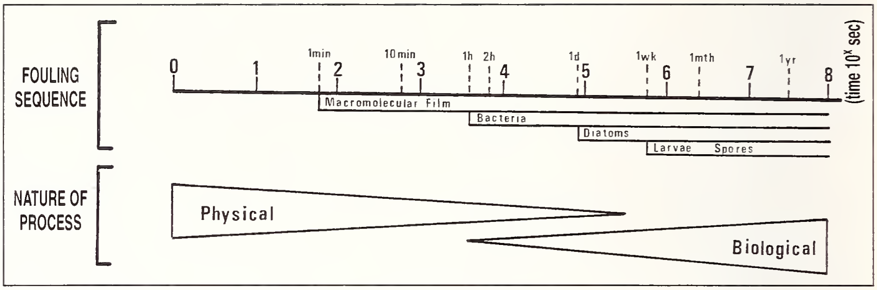


Fig. 8. Succession of first fouling stages (after Wahl 1989).

providing loose sediment, and the binding of this sedimentary material are all continuous and simultaneous. It was possible to demonstrate these processes in sequence for the first time on the reef models of Eilat.

B) Reef-building is an antagonistic process. Together with algae and sessile animals, grazers also arrive, mainly sea-urchins in the case of Eilat. However, these graze not only on algae but also on colonizing animals. Only the calcareous algae, tube worms and molluscs which were able to settle in the first few weeks (the preparation phase) and have reached a certain critical size are safe from attack. Later arrivals can only succeed in growing without being grazed in the protection of gaps and protruding limestone structures. In this way, the calcareous deposits distributed randomly during the preparation phase form nuclei for settlement by pioneer corals and later by more demanding species with the associated epifauna and endofauna. Thus insular protoreefs comprising a highly diverse community come into existence (Fig. 9). At the same time, the grazing pressure on the remaining exposed surfaces increases, keeping them free from settlement. The rather even patterning of species diversity and organism density evident in the initial phases of colonization, becomes very disjunct under the pressure of the grazers. Polarization takes place between restricted areas harbouring reef micro-communities of advanced spatial complexity and species diversity and areas still kept bare as they had been at the very beginning. They are only gradually reduced by the encroaching protoreef islets.

The long term studies on the development of the reef types of Eilat show that a reef may not form by uniform growth from the two-dimensional to the three-dimensional stage. Rather, it develops in a very disjunct pattern with insular protoreef-communities which already reach an advanced stage of complexity before fusing (Fig. 10). The term "nucleation" was coined by Yarranton & Morrison (1974) to describe an analogous process in the development of a forest from a heath stage. Artificially enhanced nucleation may also turn out as a suitable and economic tool to restore degraded coral reefs (see below).

Antagonistic processes can currently be confirmed by observation of the recolonization of reefs in the Maldives. Following the catastrophic bleaching of the reefs

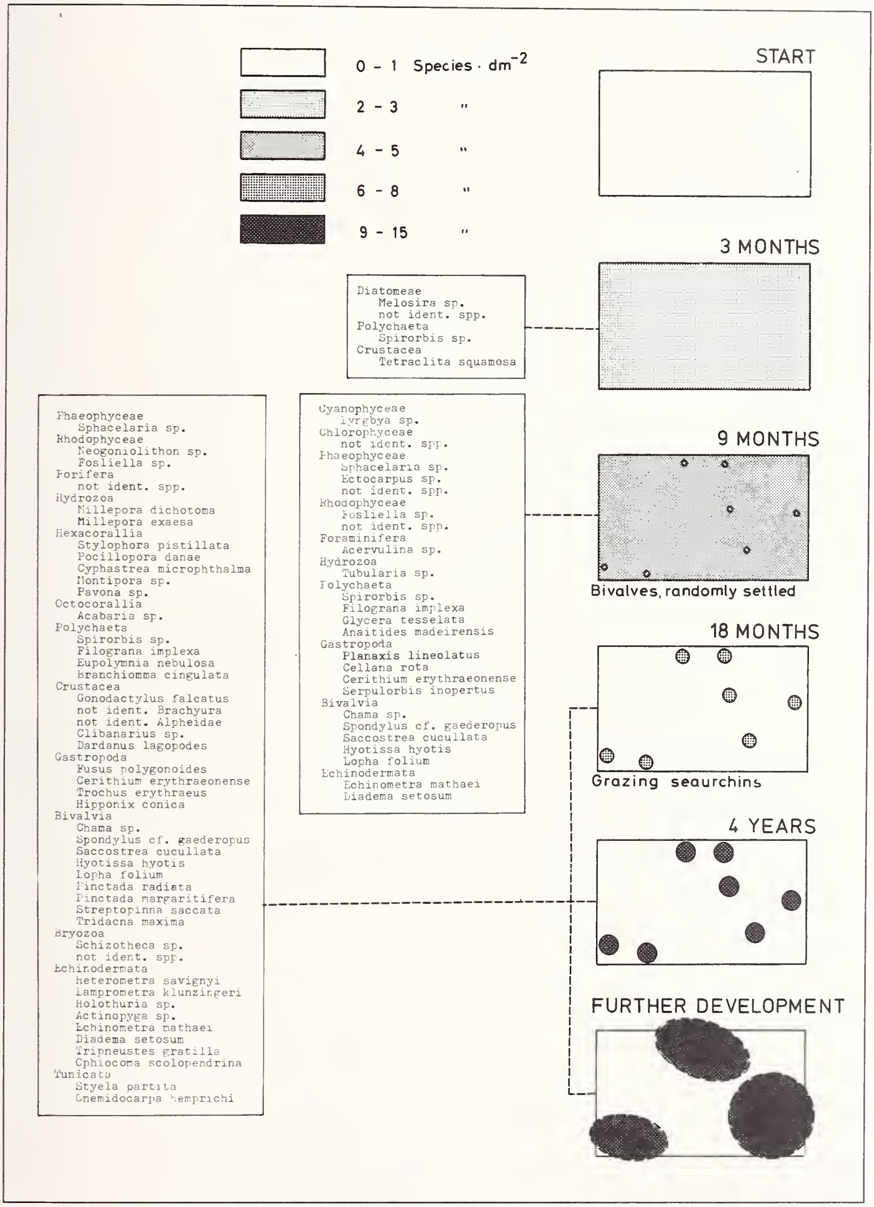


Fig. 9. Succession of settling organisms, species diversity and settlement patterns under the influence of grazing sea-urchins (*Diadema setosum*). Species representative of the various stages are shown in the boxes. Corals and other reef-dwellers can only settle successfully and gradually form protoreef communities in locations which are inaccessible to grazers (e.g. on irregular limestone crusts or the sides of rock oysters) (from SCHUHMACHER 1988).

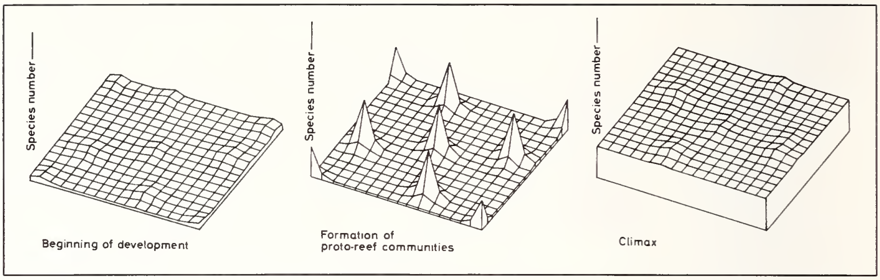


Fig. 10. Development of diversity patterns (number of species settling) during reef development. Initially the few species present are distributed homogeneously. Under the influence of grazers, highly diverse, discrete protoreef communities develop. In the (hypothetical) final stage, a uniformly high species diversity is reached (e.g. with 100 % coral cover).

in the summer of 1998, resulting in the destruction of almost all the shallow-water corals, 10 to 20 times more coral resettlements are to be found on the highly structured remains of dead plate corals (*Acropora hyacinthus*) than on the reef-flat, which is grazed continuously by fish (Loch et al. in pess).

Apart from grazing pressure, coral larvae are probably also led to their settlement sites by specific abiotic and biochemical stimuli. The larvae, which generally exhibit positive phototaxis, behave negatively phototactically immediately before settling. Sciaphilous (shade-loving) red algae act almost as a magnet on planulae searching for a settlement site. The key stimulus is a sulphated polysaccharide which induces not only the transition to a sessile existence but also metamorphosis to primary polyps in major reef-building coral species (Morse et al 1999).

As pointed out above, investigations of artificial reefs have concentrated more on settlement by fish than by benthic invertebrates. Studies of benthic settlement have tended to be limited to the time required for completing a thesis, i.e. a few years at most. The size of the substrate considered was rarely larger than a few hollow bricks or A4-sized settlement slabs. The pioneering organisms were mainly ubiquitous, opportunistic species, often with little competition, which can settle on asbestos or ceramic plates as well as on ships' hulls, harbour walls and other artificial structures. Wahl (1989) reviewed the current status of knowledge on these fouling communities and their settlement dynamics. As I have indicated above, it takes years before it becomes clear whether a fouling community is developing into a reef, i.e. before it is apparent that the structure has become self-sufficient. (A reef in the biological sense of the term is self-sufficient because it (over)compensates for erosion losses by the processes of skeleton-building, binding, sedimentation, etc.) The possibilities of accelerating the initial stages of reef-building, which proceed all too sluggishly for some people, are dealt with below.

Attempts to rehabilitate destroyed reefs using coral transplants started relatively early in the Philippines, the reefs of which were affected especially severely. AUBERSON cemented living coral branches to small concrete blocks which were placed in areas covered by rubble as recolonization centres (AUBERSON 1982). HEEGER & SOTTO (2000) were able to win over village fishers as reef gardeners in Cebu. The fisherwomen tie coral fragments to lumps of coral rock. After the fragments have grown on the rock in the coral farm (a shallow inlet), the colonies can be transferred to damaged reefs. Here, they attract fish, which are caught selectively using bamboo traps. Another source of income for the village people is the sale of living corals to hotels which use them to upgrade their underwater landscape for diving tourists (HEEGER 2000).

A rather more fundamental approach is the use of reef prostheses, artificial reefs in the narrower sense of the term, which are as near to the natural state as possible, in an attempt to rehabilitate or even restore coral reefs which have suffered mechanical damage. The distinction between rehabilitation (re-establishment of selected attributes) and restoration (return to predisturbance conditions) follows the definitons of PRATT (1994). Apart from the destructive fishing methods mentioned above, it is mainly vessels and anchors that wreak havoc in the "sea's china shop". While bomb fishing is especially widespread on the overpopulated coasts of South-East Asia, damage caused by ships is mainly a problem on coasts frequented by tourists and in shipping bottlenecks such as the

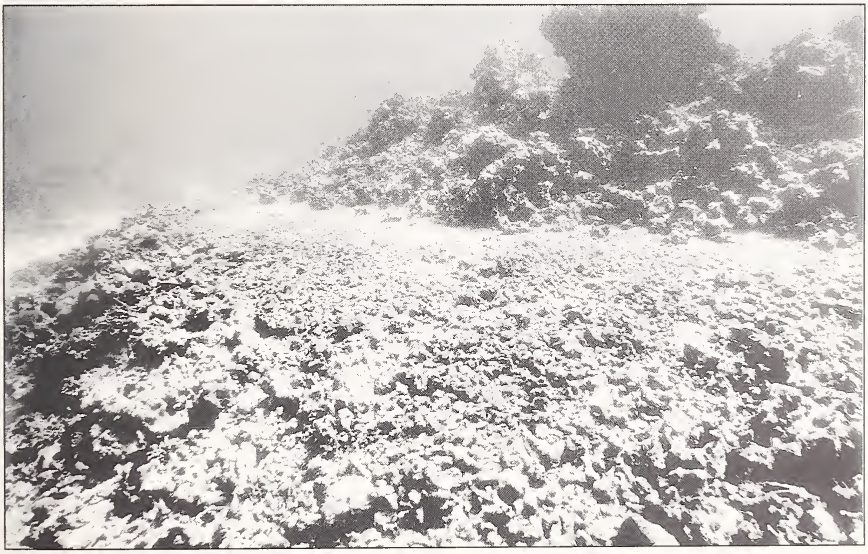


Fig. 11. Position of a grounded ship near Aqaba, four years after the ship flattened the reef frame.

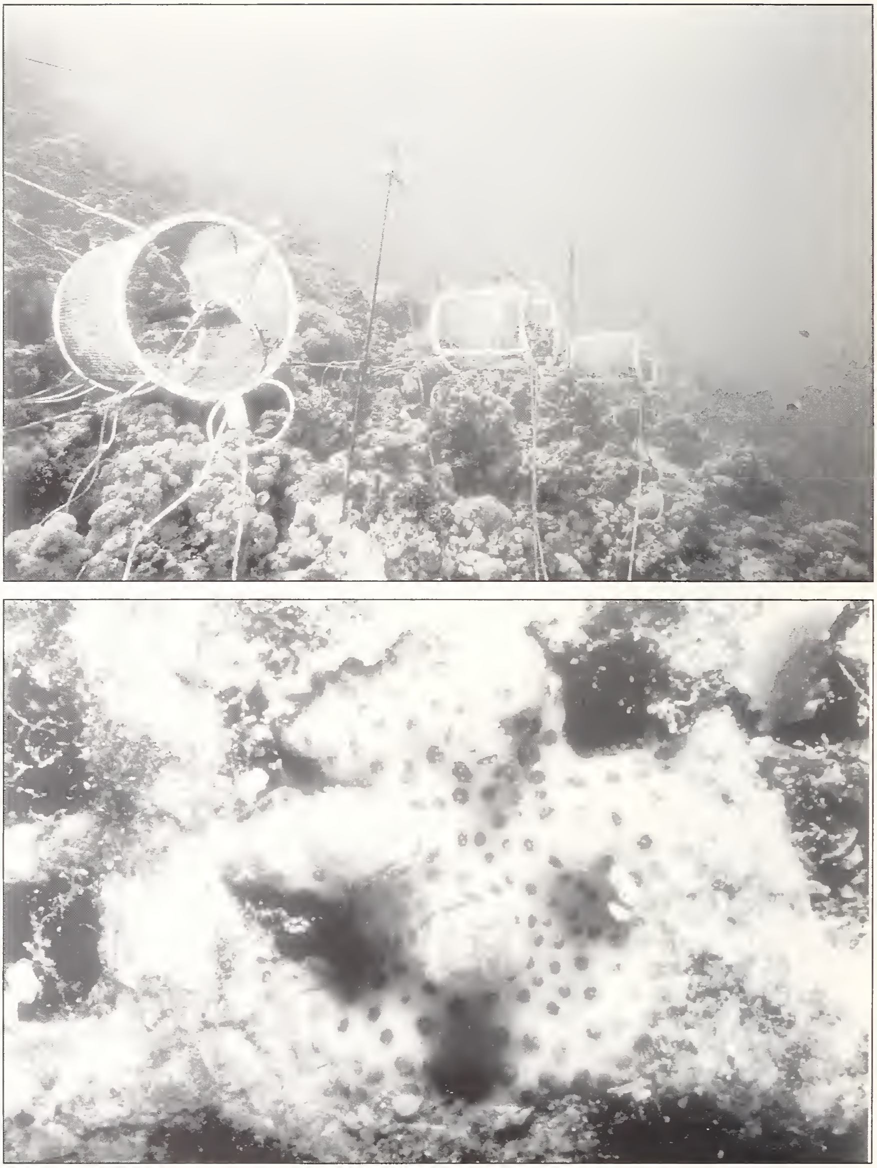


Fig. 12. Hard substrate deposited electrochemically on the reef near Aqaba and settlement. Top: The cathodes, which take the form of a wire mesh cylinder, are covered by a crust of calcium carbonate. Bottom: 11 months after the current has been switched off, the substrate has been settled by a *Pocillopora damicornis* colony (diameter 2 cm).

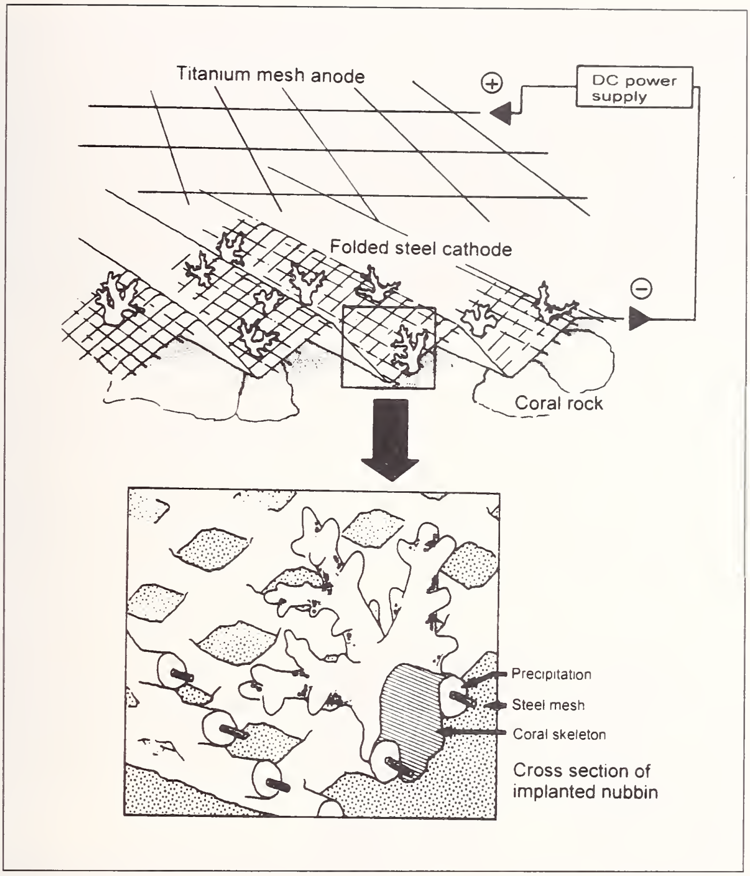


Fig. 13. Principles of coral transplantation onto the hard substrate matrix produced by electrochemical deposition (from VAN TREECK & SCHUHMACHER 1997).

Straits of Tiran (Red Sea). In the Florida Keys, more than 1000 vessels are reported as running aground each year; it is estimated that there are more than twice as many unreported incidents where boats which have run aground can free themselves by their own efforts. On the Egyptian Red Sea coast, especially around Hurghada and at the southern end of the Sinai Peninsula, the numbers of boating and anchoring incidents are steadily increasing despite all the complaints which have been made. The number of diving boats is continually increased in response to growing demand without taking into account the capacity of diving areas. After being squashed and flattened by a ship (Fig.11) or ploughed up by anchors, reefs and coral populations which were once richly structured present the

Fig. 14. Coral nursery in the Mersa Bareika, Ras Muhamed National Park (Egypt). The living coral fragments in the tent-like cathode matrix were collected from the reef following incidents with ships. They are used for transplantation or as a source of other coral fragments. Height of the "tent": 90 cm.

Fig. 15. Section of the settlement point for an *Acropora granulosa* nubbin 8 weeks after transplantation; note the widened base of the colony, which has grown beyond the electrochemically deposited material. The cathode is still live. Mesh spacing 10 mm.

appearance of a levelled heap of rubble. These areas are not recolonized by corals for at least eight years. The steady grazing pressure of fish and sea-urchins may be the reason.

In the experiment conducted near Aqaba, where grazing sea-urchins were excluded, steady grazing by acanthurids (doctor-fishes) and chaetodontids (butterfly-fishes), previously not suspected of bioerosion, not only resulted in bare surfaces but in a loss of 2 to 3 mm per year from the limestone substrate (Van Treeck et al 1996). Calcareous algae and other encrusting organisms may consolidate areas of rubble over the years, but only very rarely does this lead to the formation of three-dimensional limestone structure with the small-scale irradiance, current and sedimentation gradients required for colonization by corals. The damaged surfaces largely remain inhospitable and empty.

In this situation the process of nucleation (see above) is initiated artificially. The installation of artificial reef modules represents a possibility of accelerating coral recruitment and facilitating the restoration of an extensive, irregular reef surface. Since 1998, Peter van Treeck, Markus Paster and Michael Eisinger, members of my department, have constructed mini-reefs in the Ras Mohammed National Park (Sinai peninsula, Egypt) on the basis of experience gained from experiments in the Mediterranean off the coast of Corsica (Meyer & Schuhmacher 1993, Schuhmacher & Schillak 1994, Schuhmacher 1996) and on the reef near Aqaba (Jordan) (Van Treeck & Schuhmacher 1997, Eisinger et al. 1998). On the basis of pioneering experiments made by Hilbertz (e.g. Hilbertz et al. 1977), calcium carbonate can be deposited on a cathode of any shape by electrolysis. We use steel wire mesh which can be bent and folded to a shape offering corners and niches suitable for settlement by benthic organisms following encrustation with

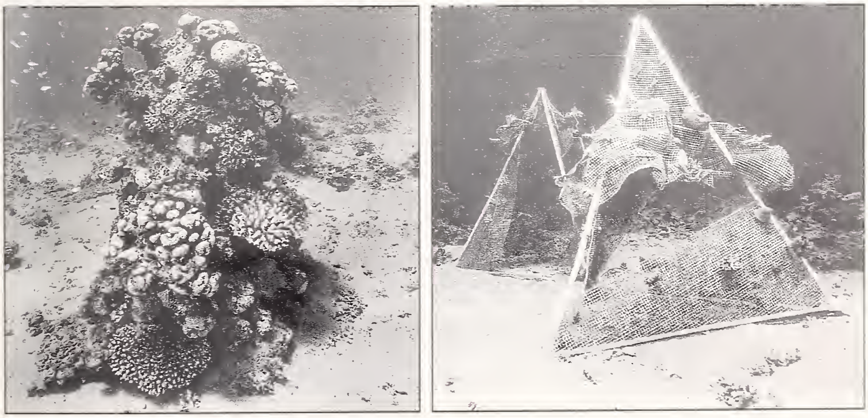


Fig. 16. Natural (left) and artificial coral pinnacles (120 cm high). Ras Muhamed National Park – stepping stones in the reef. (photo Eisinger)

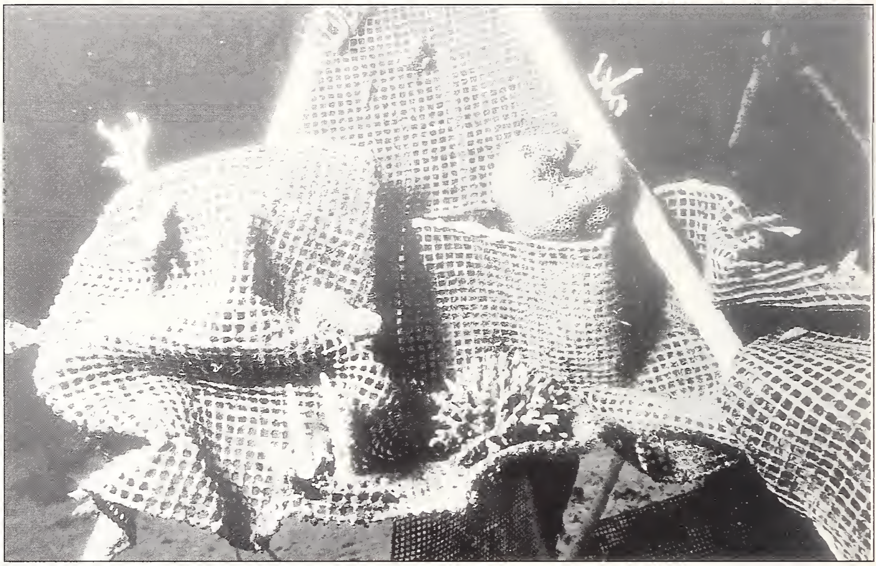


Fig. 17. Section of an artificial mini-reef module from Fig. 16 with transplanted coral colonies three months after transplantation. The cathode is still live (photo Eisinger).

calcium carbonate. In Aqaba, these hard substrates were settled by corals (together with Foraminifera, sponges, Bryozoa, bivalves, etc.) within six to nine months (Fig.12). The project CONTRAST (Coral nubbins transplantation study) was inaugurated in cooperation with the Ras Muhamed National park authorities in order to skip the early stages of coral development, in which the polyps or mini-colonies are especially sensitive. For that purpose fragments of living coral colonies were transplanted to the wire matrix (Fig. 13, 14, 17). The method is simple: coral pieces are positioned in the gaps in the wire and continue to grow. At their base, they are cemented into the structure by the calcium carbonate that continues to be precipitated. In addition, the coral fragments show a rapid growth especially at the base hereby enlarging and even more securing their foothold on the matrix (Fig. 15). It has still to be investigated whether the calcification is accelerated by the live cathode.

The method is highly environmentally compatible as the reef modules can be adapted to the topography at the individual location (Fig. 16) and no extraneous material is transferred to the seabed with the exception of the wire mesh. Only coral fragments produced by boat incidents are used as transplants and the energy needed for electrolysis is generated by a photovoltaic system. The reef modules are between one and several metres higher than their surroundings and are therefore especially attractive for both motile (e.g. featherstars) and sessile organisms (stone, soft and horn corals). Within the damaged reef, they function as prostheses: they are inserted into wounds in the reef and initially perform the functions of colonization substrate exposed to the current and retreats and meeting-points for fish and other mobile organisms. Over the course of time, they become increasingly complex and extensive in a similar way to the small protoreef communities on the moles in Eilat. Gradually, they grow to form a single unit with the natural reef.

4. Conclusion

Artificial reefs are used for a variety of purposes and the term itself is used for a variety of structures. Only a few of these uses are in accordance with the true meaning of the term, meeting major criteria for reefs or some parts of them. A general objective in the rapid development of shallow shelf areas with extraneous structures and materials – independantly from their purpose – is to ensure that they are durable and long lasting. However, structures now installed with little thought may stand in the way of better solutions in the future. Non-biodegradable materials resist natural metabolic processes in a reef in a perfectly unecological way. These processes also include destruction by bio-erosion. Carbonate crusts produced by electrochemical processes are settled by boring algae and abraded by grazers – thus fitting into the natural processes of growth and decay. If necessary they even may be removed much more rapidly by reversing the polarity, simply dissolving the entire structure.

In view of the increasing encumbrance of the coastal shelf with underwater structures, irrespective of purpose and material, ecologically oriented planning is required. What we need is an independent discipline of seascape ecology, similar to the discipline of landscape ecology established some 60 years ago. Landscape ecology analyses and assesses the physiographic characteristics of a landscape affected by climatic and geological factors, vegetation and cultural history. Before embarking on a specific underwater construction project, it is also necessary to identify and take into account the parameters which are typical of the site and characteristic of the region. Among other things, these include small-scale and large-scale current patterns, which determine the drifting distances of organisms and the potential for resettlement.

One area of the as yet hypothetical discipline of seascape ecology would describe and explain the communities of corals and other structure-determining organisms typical of sites in specific regions. More detailed analysis would investigate the age structure and the predominant life strategies of these communities (e.g. the proportions of short and long-lived species). On this basis, models („Leitbilder“) of reef communities which could be used as a basis for specific rehabilitation projects could be developed. Regional models would also be used for the long-term monitoring of reefs. To date, our views of what constitutes a “healthy reef” are still rather subjective. Are a wide variety of fish, a multi-coloured appearance or high skeleton production essential features? For fishery, the first of these aspects (which could be ensured, at least in the short term, by FADs) is certainly most important. For diving tourism, appearance is also important (opportunistic soft coral species such as *Dendronephthya* sp., see Fig. 4, quickly create a picturesque background). However, at a time when the sea level is rising, the last of these three aspects is very important. A combination of controlled hard substrate construction and the transplantation of corals, from special nurseries (similar to tree nurseries) is an environmentally compatible tool for sustainable reef management. This could be used for the maintenance of the most important tropical coastal ecosystem and, last but not least, for the benefit of the people who depend on it, entirely in accordance with the intentions of Gerd VON WAHLERT.

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The evolution of flowering plants, flower visitors and interactions between them – al look at flower biology with G. VON WAHLERT

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Abstract. Gerd VON WAHLERT was not a flower biologist; however, he often used study cases related to floral biology to teach his thoughts and insights about higher development, self-layering processes, and co-evolution. His synecological approach is still helpful to improve our knowledge of flower biology. Using publications of Gerd VON WAHLERT as a starting point and continuing his line of argumentation, the following study cases are treated in this paper.

The higher development of land plants is influenced by the water dependence of sporophytic growth and of sexual reproduction. It is shown that the water dependence for sexual reproduction of land plants was reduced step by step. Free water as a substrate for swimming spermatozoa, pollination droplets secreted as pollen receiving organs, and dry pollen collection tissues were stepping stones during this process. It is discussed that the pollination droplet enriched with sugars could have been the original floral reward for flower-visitors.

Self-layering processes led to a co-existence of taxa dependent on the same basal requirements. VON WAHLERT demonstrated that newly developed taxa of angiosperm feeding insects evolved different feeding habits, and that that newly developed taxa of insectivorous vertebrates use insects as food at different times and in different habitats.

Co-evolution between flowering plants and flower-visitors has often been postutated. To be discussed is whether long-spurred orchids and long-tongued hawkmoths, colourful flowers and colour vision or colour-released behavioural reactions in bees co-evolved.

A synecological approach is taken to study examples of association between species of the original angiosperm families and members of the original families of insect orders as pollinators. To be discussed is whether this relationship indicates long-time co-evolution or recent opportunist switches of food plants.

Key words. higher development, coevolution, self-layering process, synecology, pollination biology.

1. Introduction

Gerd VON WAHLERT characterizes evolution as a multidimensional net of interrelationships in which each new taxon and each new interaction between taxa, develops improved abilities leading to an increased productivity of the ecosystem. Gerd VON WAHLERT has indicated how to detect and analyse synecological processes and interrelationships, how to optimize our knowledge on that points, and how to constantly improve our understanding of evolution.

Flower biology was not the focal point of Gerd VON WAHLERT's work. His studies on subjects related to floral biology are in all cases tied to more general, synecological aspects of evolution. None of his publications were solely devoted to floral biology. However, the titles in which Gerd VON WAHLERT touches problems of floral biology, are informative as they characterize the general synecological processes of interest to him.These are:

Phylogeny as an ecological process* (VON WAHLERT 1973)
Evolution is growth – A look at the contribution by insects* (VON WAHLERT 1975a)
Evolution as history of the ecosystem 'biosphere'* (VON WAHLERT 1978b)
Co-evolution is everywhere* (VON WAHLERT 1978a)
Self-layering in the sea and on the land; in: What DARWIN could not know. The natural history of the biosphere* (VON WAHLERT & VON WAHLERT 1981)
Survival by adaptation* (VON WAHLERT 1975b)

Gerd VON WAHLERT studied the phylogeny of flower-visitors and of flowering plants, and he related them to each other. The evolutionary processes determining the interactions between flowers and pollinators since the Cretaceous period were clearly characterized by him as higher development (anagenesis; Höherentwicklung), self-layering (Überschichtung), and co-evolution (Koevolution). The contributions of Gerd VON WAHLERT`s synecological approach to understanding animal-plant-interrelationships focus on the impact of taxa above species-level. This is exceedingliy valuable for today flower-biology which emphasizes contributions of single species and even individuals.

Anagenesis

In his chapter entitled "Evolution as history of the ecosystem 'bio-sphere'*", which appeared in the book "Evolutionary biology", co-edited by KATTMANN and WENINGER, Gerd VON WAHLERT (1978b) analysed the origin and development of land plants. One of the points he stressed is the size of the photosynthetic-active layer in ocean and land habitats. The average depth of water in oceans amounts to 4000 m; the photosynthetic-active layer of oceans is limited to the top 100 m (Fig. 1).

In coastal regions, the size of the photosynthetic-active layer may be smaller in accordance with lower water depth. The development of the photosynthetic-active layer on the land is a striking parallelism. Green algae were the earliest land plants and formed a thin cover over wet land, amounting only a few millimeters at maximum. "Higher plants" have increased photosynthetic-active layer size: cushions of mosses measured a few centimeters. Herbaceous ferns, clubmosses and shave grasses reached some decimeters. Tree-like ferns, shave grasses, gymno- and angiosperms built an upto 100 m thick photosynthetic-active layer on land comparable to that in water habitats.

The evolution of phylogenetically higher plants from phylogenetically lower ancestors is thus paralleled by the development of physically higher plants from physically lower ancestors. However, tall representatives with a tree-like habit have evolved in different lines: lycopod trees of the genus *Lepidodendron*

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* Translated from German by the author.

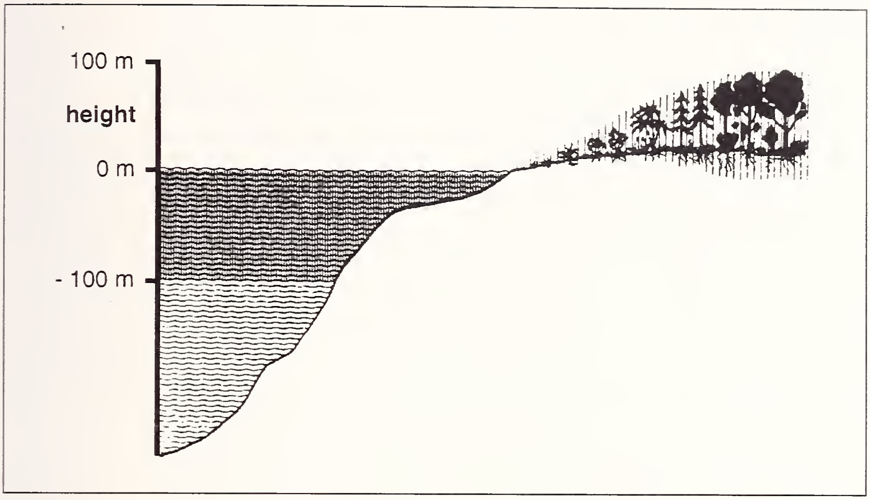


Fig. 1: Dimensions of photosynthetically active layers in ocean and land habitats. Modified from von Wahlert (1978b).

(Lycopodiatae) grew up to 40 m; horsetails of the genus *Calamites* (Equisetatae) had a tree-like habit and reached up to 30 m; both dominated the Carboniferous forests. Extant tree ferns, e.g. *Alsophila*, grow up to 15 m. Both gymnosperms and angiosperms surpass the 100 m-level, e.g. the giant sequoias (*Sequoiadendron giganteum*), and some Eucalytus trees. As other taxa with tree-like representatives, the angiosperms had also primitive forms with herbaceous habits (Gottsberger 1999).

In contrast to oceans, where the photosyntetically active layer is limited by the lack of light reaching deeper ocean layers, access to light in terrestrial biotops is completely different. In dense terrestrial vegetation, access to sunlight is positively correlated to the height of plants. During the evolution of land plants the competition for access to light presumably became more and more important in terrestrial biotops.

Several key adaptations involving water regime determine the anagenesis of land plants. Due to recent progress in the phylogenetic reconstruction of land plants (Chase et al. 1993; Donoghue 1994; Schmitt 1994b; Endress 1997) the key adaptations related to the water regime can be superimposed to a cladogram (Fig. 2). It shows that most key adaptations in the above mentioned context are positioned on the line of ancestors: a cutin cuticle with low permeability for gases and water enveloping the cellulose wall was already present in liverworts. Adjustable stomata enabled mosses to control water loss via evaporation. Development of specific water-conducting tracheides and lignin as a supporting substance characterize cormophytes which are able to take up water from the soil by their roots, to

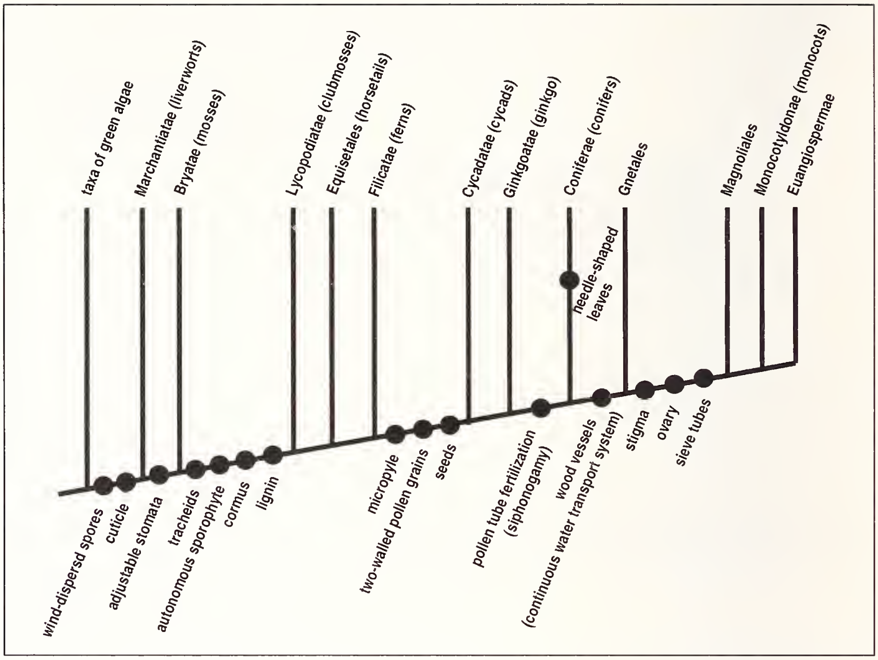


Fig. 2: Cladogram of land plant with key adaptations related to the water regime. Combined after Chase et al. (1993), Donoghue (1994) and Schmitt (1994b).

conduct it through a solid stem towards the green leaves in which water is used for photosynthesis. Conifers developed needle-shaped green leaves which substantially reduce water loss by evaporation because of their small surface area and special coating. Gnetales and angiosperms evolved wood vessels, a continuous water transport system, which again improved water transport from roots to green leaves.

Gerd von Wahlert (1973) considers the history of land plants as a giant global succession. Competition and selection at various locations lead to improvement of economy, finally resulting in an increase of biomass and productivity. Primarily vegetation-less areas were gradually colonized by plants of respective productivity. The increase in productivity during anagenesis can be appreciated by increasing investments in woody tissue, which was made possible by more effective transport of water and other substances as a precondition for a more intense metabolism. Nitrogen fixation of land plants surpasses five-fold that of submersed plants in the oceans (von Wahlert 1978b).

Adaptations of land plants to a more and more xeric environment do not only comprise those in the context of water balance of the sporophyte, but also those in the context of water dependency of sexual reproduction (Fig. 2). When land plants conquered drier land, their sexual reproduction remained dependent upon water.

The spermatozoids of mosses need dew or rainwater to actively swim from an antheridium to an archegonium which in heteroecious species develop on different individual gametophytes. In both, synoecious and heteroecious forms the gametophytes grow on the top of the sporophytes. Therefore, a continuous water film between antheridia and archegonia of conspecifics is a necessary prerequisite for successful sexual reproduction. Such a continuous water film occurs only up to a very limited heigth, on rare rainy days, or in wet climate. Spraying droplets caused by rain drops represent rare and insecure opportunities to bridge a small distance between two neighboring mosscushions.

Pterydophytes have a dominating sporophyte generation. The gametophytes are very small and grow close to the moist soil surface. However, the sexual reproduction of clubmosses, horsetails and ferns relies on water. The wind-dispersed meiospores only germinate on a wet soil surface, and the small and soft prothallia grow only under moist conditions. The flagellate spermatozoids released by the antheridia have to swim to the egg-cell of the archegonia in water. Homosporous species have prothallia with antheridia and archegonia on the same individual. Heterosporous species develop micro- and macroprothallia, the former produce antheridia, the latter archegonia. Again, a continuous water film is needed for sexual reproduction to bridge the distance between the antheridia and archegonia of conspecifics.

Cycads and ginkgos have developed seeds and seed-containing fruits for dispersal. The meiospores are no longer necessary for dispersal. Instead of being dispersed, the meiospores or pollen grains are transferred from the stamens, their site of production, directly to the micropyle, their target. Although depending on strictly homologous processes, sexual reproduction in seed plants (Spermatophyta) undergoes dramatic changes as compared to their relatives. Pollen grains are homologous to microspores; germinated pollen grains are homologous to the microprothallia. The embryosac on the sporophyte is homologous to a germinated macrospore, that is, a macroprothallium.

Siphonogamy, the fertilization of the ovules via non-flagellate nuclei transported by the growing pollen tube, is a key innovation of higher seed plants. However, pollination still requires water. The original pollen collecting area of gymnosperm flowers were pollination droplets (Stützel & Röwekamp 1999). The pollen grains germinate in the liquid of the pollination droplets.

The process of pollen capture via pollination droplet is exemplified with *Pinus mugo* (Fig. 3). Pollination in this wind-pollinated species with a hanging pollination droplet was studied by Stützel & Röwekamp (1997). The morphology of the twigs with needles and that of the cones generate air motions which guide the pollen grains to the appendages of a micropyle as exemplified in other *Pinus* species (Niklas 1984). In *Pinus mugo*, the pollen grains adhere to one of the two sticky appendages hanging downwards from the micropyle. For only a short period, a few hours, a pollination droplet is exposed during night time and kept between the two appendages. The liquid of the pollination droplet dissolves the sticky secretions and the pollen grains ascend in the pollination droplet to the nucellus of the ovule. The so-called airsacs of the pollen grains work as buoys in the pollination droplet as was already proposed by Doyle & O'Leary (1935). The air sacs apparently reduce the specific weight of pollen grains. The small specific weight of pollen grains may help to increase transport intervals in the air, or may make possible upward-transport in a hanging pollination droplet and thus reduce the time span up to fertilization. Support for the buoy-hypothesis is the observation that so-called air sacs are almost exclusively found in gymnosperm species with hanging pollination droplets in which the pollen grains have to ascend to their target. Additional evidence for the buoy-hypothesis are measurements of the sinking velocity of pollen grains in the air which, according to data summarized by Kugler (1970), seemingly is not strikingly reduced in species, in which the pollen grains have air-sacs.

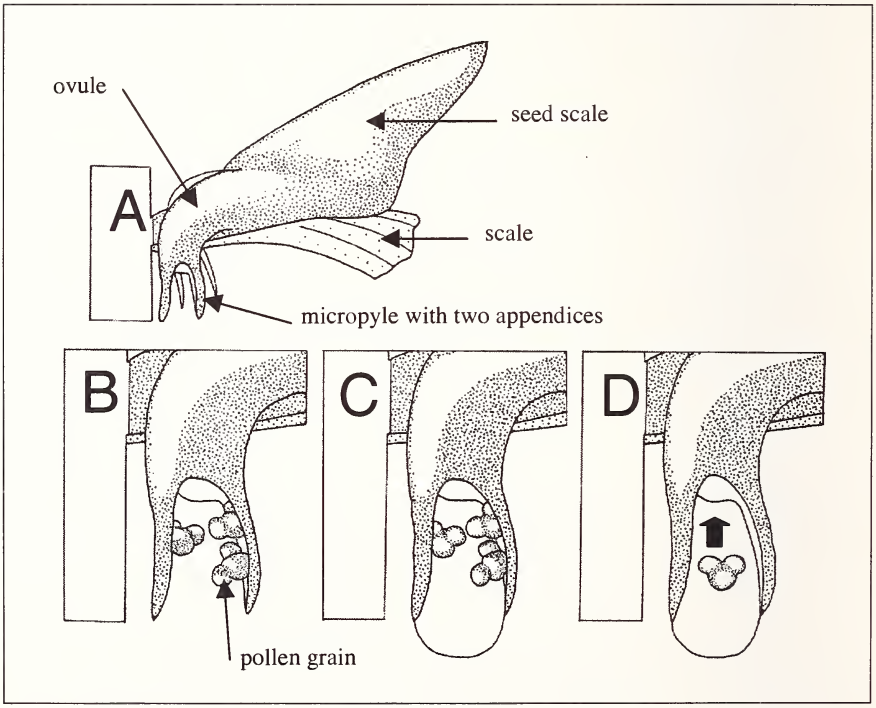


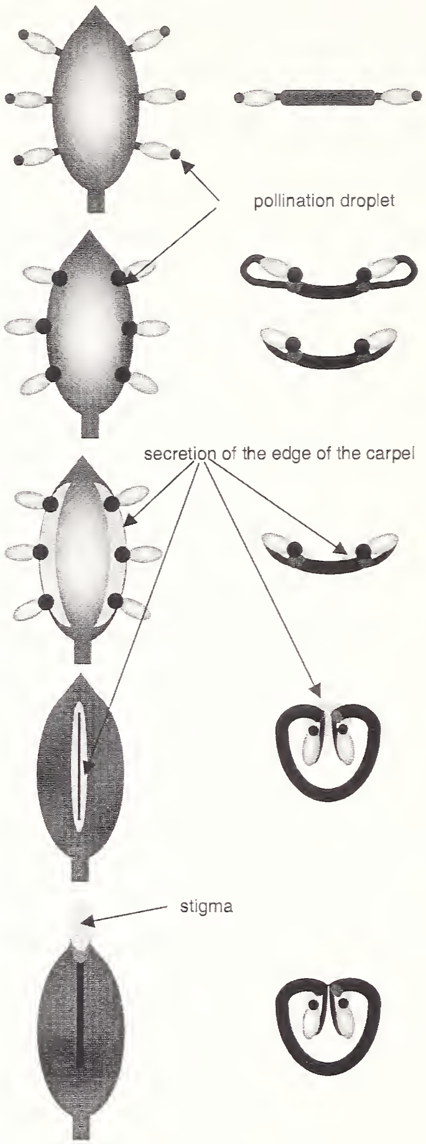
Fig. 3: Pollination system of *Pinus mugo* (Pinaceae, Gymnospermae). Pollen collection by the pollination droplet and pollen grain transport towards the ovule are shown. Modified after Stützel & Röwekamp (1997).

The pollination systems based on pollination droplets suffer from the small pollen collecting area of the pollination droplet, from evaporation especially in dry and hot climates, and from total losses following rain or shaking of the plant. Shaking caused by wind may have been a quite normal aspect. Because gymnosperms are wind-pollinated, pollen dispersal is optimal in windy periods. The hanging exposure of pollination droplets obviously reduces evaporation as does exposure during night time due to the lack of direct insolation. Short exposure intervals of pollination droplets, as was demonstrated for *Pinus mugo*, reduce the probability of total losses and of evaporation as well. The pollination system via pollination droplet is improved by the secretion of sugars into the liquid of the pollination droplet in several aspects. Dissolved sugars increase the viscosity of pollination droplets leading to an improved resistance against total losses caused by vibrations. Pollination droplets of high viscosity are more resistant against vibrations; an increase of the pollination drop volume is possible taking the same risk of total losses caused by vibrations. Sugar-rich pollination droplets show a reduced evaporation.

However, a sugar-containing pollination droplet may have attracted insects to feed on this nutritious solution. This represents one hypothetical starting point of entomophily via insects with sucking mouth parts.

The exposition of liquids such as pollination droplets, irrespective, whether they are large or small, is critical for the plants ability to colonize dry habitats. There are several evolutionary lines, in which the pollination droplet has been replaced by stigma-analogous pollen collecting structures. In some species of the Podocarpaceae, the nucellus grows and overtops the micropyle to directly collect pollen grains with its papillate surface. The larch (*Larix decidua*) has a papillate outer surface of the micropyle serving as a receiving organ for pollen grains. True stigmata and ovaries are innovative key characters of angiosperms.

STÜTZEL & RÖWEKAMP (1997) developed a model for the evolution of closed sporophylls (carpels) and of stigmata in angiosperms (Fig. 4). The main steps are as follows: Primarily, the ovaries adhered laterally to a leaf-shaped carpel. The pollination droplets were exposed outwards. They were of limited size for physical reasons. If the ovaries remained in the inverse position of the bud, the pollination droplets could rest on the edge of the carpel. Inverted ovaries could increase the pollen collecting area by enlarged pollination droplets and additional secretions of adjacent areas at the edge of the carpel. By remaining in the inverted bud stage, an almost closed carpel developed. The whole central suture acted as a stigmatic tissue. The most distal areas of the stigmatic tissue collected more pollen than the proximal parts. Plants benefitted by further enlargement of the superior pollen collecting parts in terms of pollination success. The distal areas developed into an enlarged pollen collecting area, the stigma. The proximal part of the carpellate suture was tightly occluded. Its function changed from pollen receptive area into tissue for pollen tube growth inside the closed carpel.



pollination droplets exposed outwards are of limited size for physical reasons.

If the ovary remains in the inverse position of the bud, the pollination droplet can rest on the edge of the carpel, and can be enlarged considerably.

Inverted ovaries additionally increase the pollen collecting area by secretions of the edge of the carpel.

By remaining in the inverted bud stage an almost closed carpel develops with secretory stigmatic tissue along the whole ventral suture.

Distally enlarged stigmatic area serves improvement of pollen catch. The proximate part of the carpel is tightly occluded. The originally receptive areas develop into tissue for pollen tube growth inside the closed carpel.

Fig. 4: Model of the evolution of stigmata and closed carpels in the Angiospermae. Modified after Stützel & Röwekamp (1997).

Not all angiosperms have evolved closed carpels in which only the distalmost parts serve as a stigmatic tissue. In the primitive angiosperm families, Winteraceae and Annonaceae, the flowers have kept an intermediate state; the whole suture line serves as stigmatic tissue.

As has been shown, the angiosperm stigma is a dry pollen receiving tissue. The replacement of the pollination droplet by the stigma makes the sexual reproduction completely independent of free water. The water-independent sexual reproduction may have been a decisive precondition for the colonization of dry and/or hot habitats.

As a by-product of the evolution of the stigma, the association between received pollen grains and ovaries changed dramatically. The pollination droplet is a pollen collecting mechanism for one single ovary, whereas the stigma is a pollen receiving organ for all ovaries of one carpel, and even for all ovaries of some fused carpels. In some orchids, many thousands of ovaries can be fertilized by pollen collected on a single stigma. In this way, the fertilization success can be considerably increased in the case of a constant pollination success. The waste of conspecific pollen is considerably reduced.

The classical view of the evolution of the ovary is that of an adaptation in the context of zoogamy. This hypothesis assumes that ovaries could have protected the ovules against flower visitors and pollinators. It argues that the original flower-visitors had chewing mouthparts such as beetles. Those flower-visitors might not only have fed on pollen, but also on floral tissue, ovules and developing seeds (see GOTTSBERGER 1974, 1988). An alternative hypothesis of STÜTZEL & RÖWEKAMP (1997), which is presented here, implies that the increasing independence of pollination from the exposure of pollination droplets might have been the strongest selective pressure for the evolution of closed carpels.

Though pollination became largely independent of water, fertilization did not. Pollen grains, which land on a stigma, need water for hydration and for pollen tube growth. Especially the swelling processes associated with pollen tube growth are based on the uptake of water which is provided by the stigmatic tissue. Pollen is rich of the free amino acid proline, which may account for up to 2 % of the dry weight of pollen. Proline plays a decisive role in pollen hydration and the swelling processes associated with pollen tube growth (BRITIKOV & MUSATOVA 1964; BRITIKOV et al. 1966).

Interestingly, a pollen-eating insect, the syrphid fly *Eristalis tenax* L. (Syrphidae, Diptera) can taste proline by its tarsal and labellar taste sensilla (WACHT et al. 2000). No other substances of pollen are known which, in natural concentrations, stimulated the taste sensillas of flies. Moreover, GILBERT (1985) discussed, whether syrphid flies use proline as a substrate for the production of ATP via the respiratory chain as is known for other flies. This would represent a direct parallel between nectar and pollen in the context of the metabolism of energy.

In the light of new ideas on the evolution of pollination via pollination droplets and stigmata presented above, we can discuss the concepts of the original flower

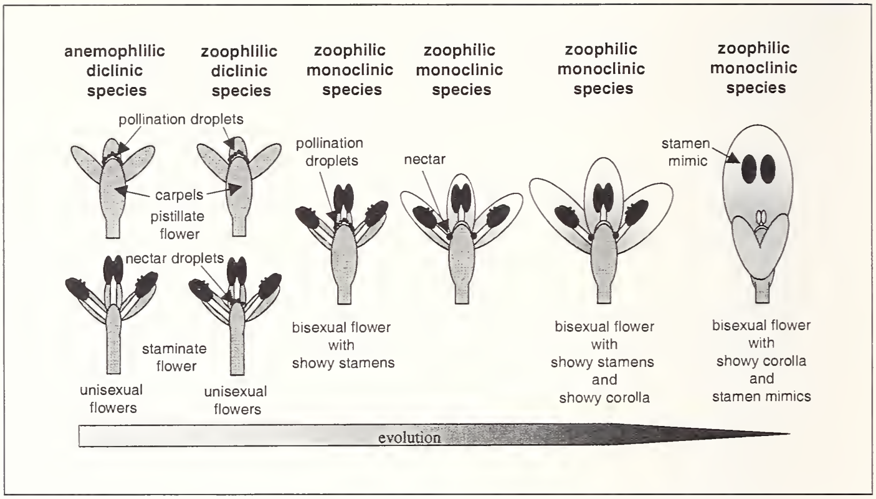


Fig. 5: Model of the evolution of flowering plants with the pollination droplet mechanism as a starting point.

visitors and original angiosperm flowers. Was the original flower a large *Magnolia*-type flower, flowering on a tree, and offering pollen to flower-visiting beetles with gnawing mouth parts? Or, is it alternatively possible that at the base of angiosperm evolution was a small and soft-bodied flower on an herbaceous plant attracting insects with sucking mouthparts such as moths and flies to feed on sugar-rich pollination droplets (SUN et al. 1998; GOTTSBERGER 1999)? In both cases, the benefits of a target pollination by insects compared to the non-target pollination by wind must have been great, because the angiosperms gave up unisexual in favour of hermaphrodite flowers. By this, they accepted additional costs for the preservation of cross-fertilization.

Certainly, the original visiting insects used flowers as a source of food, whether it was sugar-containing pollination droplets or pollen (LUNAU 2000). It is plausible, that the insect flower-visitors concentrated and restricted their visits to rewarding flowers, offering the resource in demand. Those insects fed on pollination droplets or on pollen without acting as pollen vectors. In the original diclinous seed plants, sugar-containing pollination droplets were offered only on pistillate flowers, whereas pollen was offered only on staminate flowers. Flower-visiting insects might have easily discriminated between staminate and pistillate flowers by means of reward, such as nectar and pollen, or reward-producing organs such as carpels and stamens. Selective feeding on pollen or pollination droplets would have decreased the reproductive success of seed plants. Only when plants evolved bisexual flowers were they able to effectively use foraging insects as pollinators and only then every flower-visit of an insect equaled a chance for pollination, and every flower-visit but for the first equaled a chance for cross-pollination. Moreover, the evolution of androgyny suspended the sex-specific differences between carpellate and staminate flowers which insects might use to discriminate between them. The "nectar" of pollination droplets could have been easily replaced by nectar secreted by special nectar glands and concealed in the floral tubes (Fig. 5). From studies of Osche (1979, 1983) it is evident that pollen and anthers became important signals of the visual display of entomophilous flowers in contrast to nectar and nectar glands (Vogel 1993).

Extant species of the Gnetales, the sister group of the angiosperms, and extant species of the original families of the Angiospermae have pollination systems, which may hold the key to the problem of the origin of insect pollination. Among the Gnetales, entomophily is known for all three genera, *Ephedra*, *Welwitschia* and *Gnetum*. Kato & Inoue (1994) described the derived pollination system of *Gnetum gnemon*: Pollination droplets with a sugar concentration up to 13 % are secreted by ovules on female strobili and mimicked by nectar droplets on sterile ovules of male strobili (Fig. 6). The attraction of pyralid and geometrid moths is

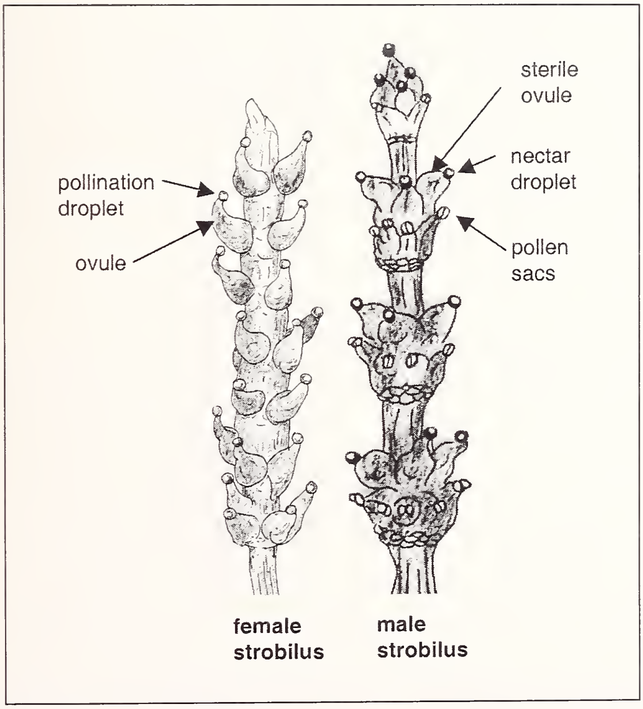


Fig. 6: Female and male strobilus of the moth-pollinated *Gnetum gnemon* (Gnetaceae, Gymnospermae). The female strobilus possesses a pollination droplet on each ovule. The male strobilus has pollen bearing pollen sacs and nectar droplets on sterile ovules.

based on fragrant strobili. Flower visits of *Gnetum gnemon* by the nocturnal moths were observed between 18:00 and 21:00. A similar pollination system with staminate and carpellate flowers, which both offer nectar, is also adopted in *Nepenthes gracilis* (Nepenthaceae); in this species the sepals of the inconspicuous staminate and carpellate flowers secrete nectar (KATO 1993). The authors believe that the moth attraction in *Gnetum gnemon* derived from unspecialized entomophily as observed in *Ephedra* and *Welwitschia*. Even the pollination of hermaphroditic flowers may be based on stigmatic exudates. The primitive angiosperm *Pseudowintera colorata* (Winteraceae) is pollinated by pollen eating halodid beetles and by stigmatic exudate-eating chironomid flies (*Smittia*) (LLOYD & WELLS 1992).

Among the early angiosperm families, some extant species of the Winteraceae are pollinated by dipters, which feed on sugar-containing stigmatic secretions (LLOYD & WELLS 1992). Extant species of the Magnoliaceae are pollinated by pollen-eating beetles, flies or bees (VAN DER PIJL 1960; PELLMYR & THIEN 1986). Some extant species of the Ranunculaceae offer both, pollen and nectar. Nectar is secreted by different organs; *Trollius europaeus* and *Ranunculus acer* secrete nectar at the base of the petals. The nectaries of *Pulsatilla vulgaris* are located on the connectives of the stamens, those of *Caltha palustris* on the ovary, and those of the species of *Helleborus*, *Aconitum*, *Aquilegia* and *Nigella* on specific nectar leaves. GOTTSBERGER (1999) derived from our knowledge of pollination systems in extant species of primary angiosperm families that early angiosperm pollination was not strictly related to beetles but was more generalistic. It was thus related to different taxa of insects such as Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Thysanoptera, which all existed at the origin of the Angiospermae 120 million years ago.

Self-layering process

Different phases of higher development in land plants can be roughly sketched by fossil evidence: Lower vascular plants were dominant in the Carboniferous period. Gymnosperms dominated the fossil record in the Triassic period. In the Cretaceous period an enormous radiation of angiosperms began, including grasses, trees and herbs (Fig. 7). An indicator of the increasing metabolic capacities, accompanying the higher development, is the increasing investment in structural tissue (xylem), which was made possible by more effective transport of water and substances. Higher land plants with better metabolic capabilities did not replace lower land plants. Nowadays, both forms co-exist. At the same time higher land plants re-colonized moist habitats such as mosses peatland, horsetails carboniferous forests and water lilies freshwater habitats (LÖSCH 2001).

Habitats, which primarily had no vegetation, were colonized step by step by plants which had suitable capabilities. This colonization changed the microclimate and opened these habitats for the colonization by plants with lesser capabilities. The great and ecologically important stands of plants in terrestrial habitats are determined by a combination of physiological capabilities, which were developed in different evolutionary lines: Lichens use co-evolutionary synorganisation between lichen algae and lichen fungi. Forest trees need mycorrhiza fungi for ion and water supply and/or nodular root bacteria for nitrogen fixation. These symbiotic partnerships are based on the exchange of substances. In mutualistic relationships with animals, land plants make use of the animals' mobility for pollen transfer (zoophily) and seed dispersal (zoochory).

In order to characterize these evolutionary processes, the co-existence of taxa with different capabilities which all rely on the same basic vital needs, VON WAHLERT coined the term “Überschichtung” (self-layering process).

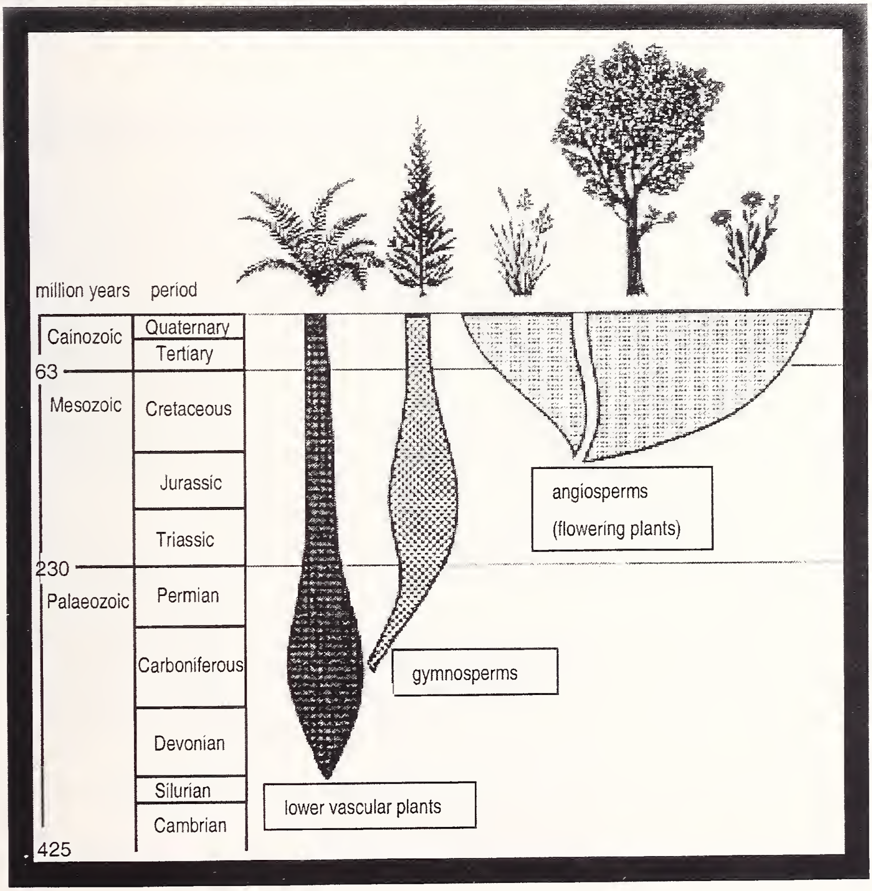


Fig. 7: Development and species richness of land plants. Modified after VON WAHLERT & VON WAHLERT (1981).

Gerd von Wahlert (1973) pointed out that the evolution of land animals cannot be understood as a mere parallel development. Land animals have different origins, i.e. the evolution of terrestrial arthropods and of terrestrial vertebrates is related to two separate processes. According to von Wahlert every group of animals had two options at the time and place of its origin. One option was to use a pre-used food source in a new way. The other option was to make a totally new food source accessible. The processes related to the use of old food sources in a new way lead to a remarkable co-existence of animal groups which had evolved consecutively. Von Wahlert (1978b) gives an impressive example of vertebrate groups, which all feed on insects. The evolutionary success of angiosperms is linked to that of (phytophagous, nectarivorous and pollen feeding) insects and the latter is linked to the striking co-existence of insectivorous vertebrates such as salamanders, frogs, lizards, birds, shrews and bats. Nocturnal and slow salaman-

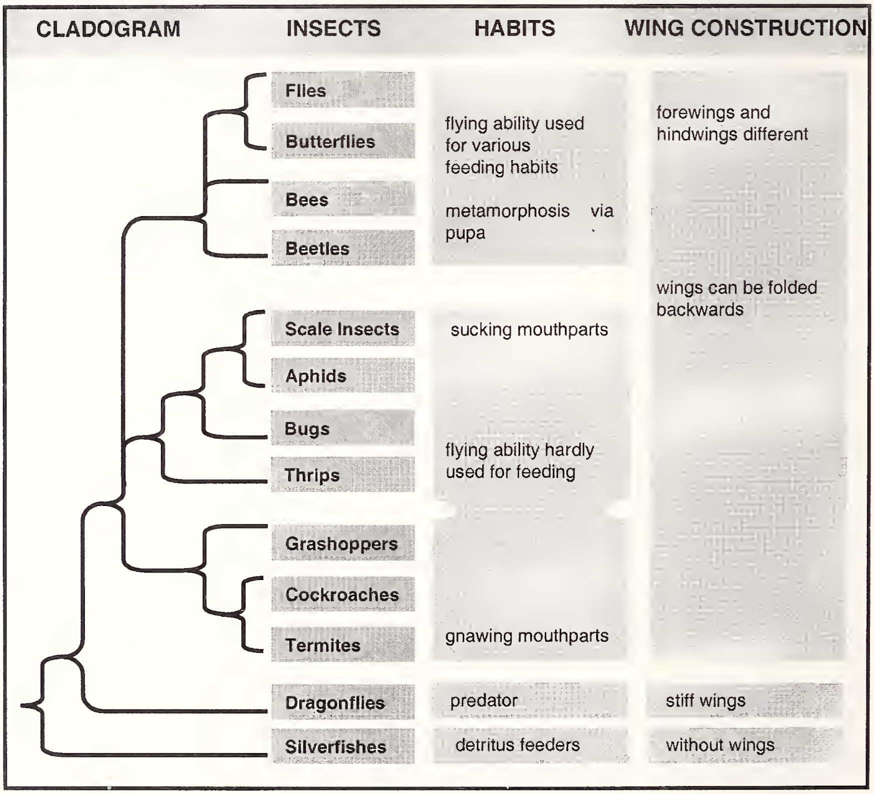


Fig. 8: Cladogram of insects (Insecta) with information about feeding habits and wing construction. Modified after von Wahlert (1978b).

ders have very limited access to insect food. Frogs and lizards hunt insects in habitats rich in sun energy; however, they are inactive in cold regions and in cold seasons. Birds predate on insects under unfavourable climatic conditions, and even do so in the tree tops and air space. The earliest vertebrates were nocturnal insect predators. Finally, bats developed an echo location system enabling them to hunt insect in air space at night time. As described by the circumstances of predation on insects, each of the insectivorous vertebrate groups did not develop in direct competition with the pre-existing ones, but adapted to use insects as a food source under new conditions (locations, day-times, seasons, climates). Self-layering defines the processes that contributed to the evolution of co-existence between insectivorous vertebrate groups based on the evolutionary success of insects.

Gerd von Wahlert (1978b) also indicates us to the fact that the evolutionary success of winged insects (Pterygota) is grounded on the utilisation of anthophytes as food source. With the aid of a cladogram of the Insecta (Fig. 8) he demonstrates how new evolved insect taxa used angiosperm plant-food in a new way. This self-layering process among insect taxa began with apterous insects feeding on plant detritus. Phytophagous winged insects with sucking mouthparts used xylem- and phloem-sap, those with gnawing or chewing mouthparts used green leaves and other parts of the plants as a food source. Holometabolous insects were the first that used their flying ability for various feeding habits. Flower visitors such as beetles, bees, butterflies and flies feed on nectar and pollen. Pollen, however, had already previously been used by apterous springtails, feeding on pollen detritus from the soil surface (Scott & Stojanovich 1963).

Co-evolution

The term "co-evolution" is used by many authors to characterize the interaction between animals and flowering plants in the context of pollination (Paulus 1978, 1988; von Wahlert & von Wahlert 1981; Pellmyr 1992).

In its strict sense, "co-evolution" means evolutionary interaction between two species in a manner that each species represents a selective pressure for the other. As a result, each species develops (co-)adaptations. Gerd von Wahlert (1978b) accepted a definition of "co-evolution" in a broad sense to characterize evolutionary interactions between species and between taxa above species-level. In this way, Gerd von Wahlert challenged the consideration of synecological aspects of evolution. In his contribution to the 20th Phylogenetic Symposion entitled "Co-evolution is everywhere", Gerd von Wahlert (1978b) explains in detail his idea, that interaction between two species is not restricted to symbiosis and parasitism. Species also interact via competition, mutualism and predator-prey-interdependences. "No species is alone" and "No group is alone" are his concise statements about co-evolution between species and higher taxa.

An anecdote with a floral biological center part, which in its main parts was already written down by Charles Darwin (1859), is placed at the beginning of Gerd von Wahlert´s work about co-evolution (1978b). It explains how the stability of the British Empire is dependent on its old maids and is as follows: Old maids keep cats. Cats eat mice. Empty nests of mice are favourable places for bumble bee queens to found their colonies. Bumble bees pollinate red clover. Red clover is eaten by cattle. The meat of the cattle serves the nutrition of the sailors of the Royal Navy, upon which the strength of the British Empire is founded. The pattern of interrelationships represented by this anecdote, represents a chain of interrelationships, including predator-prey-systems, competition for nesting sites, flower-visitation and herbivory. This chain of interactions can easily be tied into a net of interactions by linking with other chains of interactions among species. Considering co-evolution between neighbouring members of the chains, the missing of co-evolution is hard to see for Gerd von Wahlert. However, he gives an example: Though lions, grass eating ungulates, and grass species are linked in a short food chain, Gerd von Wahlert believed that "lions and grasses did not influence their evolution reciprocally*."

Is the interrelationship between bumble bees and red clover co-evolutionary interaction? The answer probably would not have been difficult for Gerd von Wahlert. Co-evolution in the strict sense requires the naming of two species which adapt at each other. Red clover (*Trifolium pratense*) is pollinated by long-tongued bumble bees such as *Bombus hortorum*, which can reach the nectar hidden in the 10 mm deep spur. Short-tongued nectar-robbing species such as *B. terrestris* may also visit the flowers as nectar robbers without pollinating them. In this case the answer to the former question depends on the species of bumble bees. Moreover, co-adaptations as a result of co-evolution are hard to prove. Since both species, *B. hortorum* and *T. pratense*, have also other partners, it is uncertain, that the spur depth of *T. pratense* and the tongue length of *B. hortorum* are reciprocal co-adaptations. One-sided adaptation of one partner to a pre-existing system is of equal probability. Even Darwin (1859) knew that honey bees are not able to take nectar from spurs of red clover. It is clear that only long-tongued bumble bees can take nectar from deep spurs. Hovever, short-tongued bumble bees need shorter handling times on flowers with short spurs than do long-tongued bumble bees (Ranta & Vepsäläinen 1981). To sum up, co-evolutionary interaction between bumble bees and spurred flowers is not evident from the fact that the species in question are adapted to each other.

One of the most intriguing study cases is that of the star orchid of Madagascar. Charles Darwin predicted the pollinator of the star orchid *Angraecum sesquipedale* (1862). Darwin studied several flowers and found nectar spurs up to 29 cm long which were filled with nectar only up to 3.75 cm height. Darwin predicted the existence of a long-tongued sphingid moth in Madagascar capable of sucking nectar from *A. sesquipedale*. Darwin's prediction was ridiculed by many entomologists, because no insect with a matching long tongue was known at his time. The pollinator candidate was recovered by Rothschild & Jordan (1903) and described under *Xanthopan morganii praedicta*. Darwin's famous predicted interaction between *Angraecum sesquipedale* and its pollinator hawkmoth, although continuously revolving in the scientific literature, eluded empirical documentation (NILSSON 1998). According to DARWIN's classical model of a co-evolutionary race, the sphingid moth is compelled to insert its tongue into the very base, and thus to selectively pollinate deeper flowers than its tongue reach (NILSSON 1988). Thus, long-tongued sphingid moth gain fitness advantages over those with short tongues, and deep-spurred orchids surpass the reproductive success of individuals with less deep spurs (Fig. 9).

Remarkably, the model of a co-evolutionary race has been doubted by WASSERTHAL (1997). WASSERTHAL assumed that *X. morganii praedicta*'s tongue elongation has primarily evolved to increase distance against predators ambushing on flowers. One-sided adaptive evolution of the plant partner for pollination by long-tongued hawkmoth is the consequence of WASSERTHAL's model. WASSERTHAL

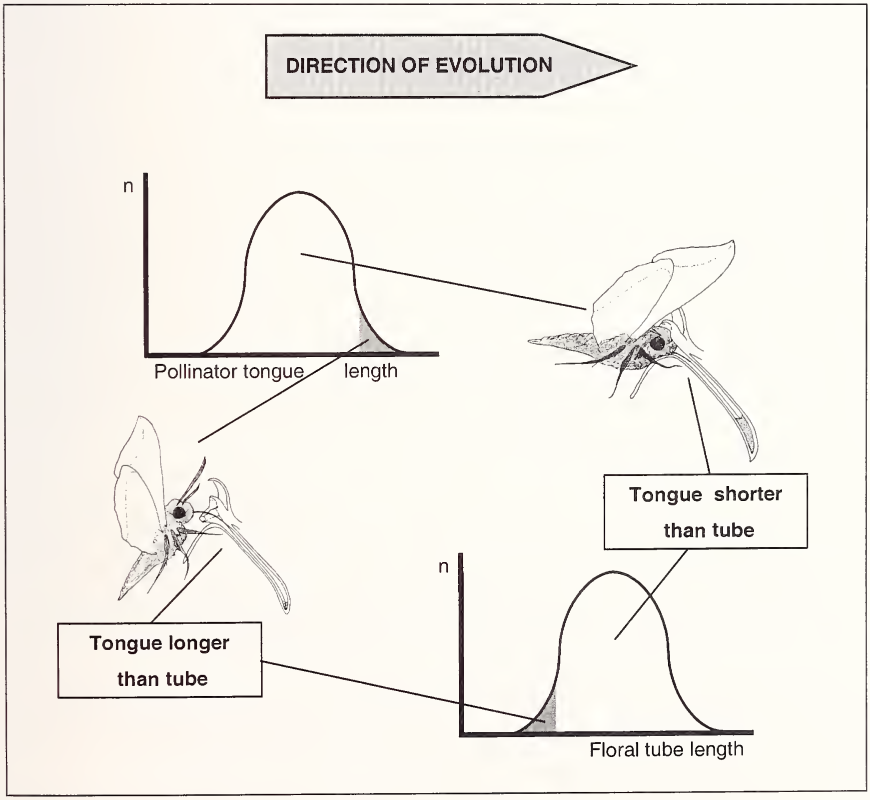


Fig. 9: Co-evolutionary race between long-tongued sphingid moths and flowers with deep spurs. Modified after NILSSON (1988).

postulated two independent one-sided adaptation processes without co-evolutionary interaction (in the strict sense) between food plants and sphingid moths; Sphingid moths evolved longer tongues in the context of distance-keeping to the flowers when sucking nectar. Those individuals which had a longer tongue had a better chance to escape ambush predators on the flowers. When the sphingid moths had switched from original food plants with short spurs to new ones with medium long spurs, those individual new food plants with longer spurs had a better chance for pollination. Food plants with long-spurred flowers evolved flowers with extremely long spurs to increase pollination success.

Observations of pollination of *Angraecum sesquipedale* by *Xanthopan morganii praedicta* in natural populations are still lacking. The star orchid grows epiphytically in the coastal rainforest of Eastern Madagascar. Because this habitat is disappearing the exploration of DARWIN's prediction is a race against time (NILSSON 1998).

A textbook example for coevolution is that of visual flower detection by bees. Did trichromatic colour vision of apoid hymenopteral bees evolve in the context of flower visitation, visual flower detection and floral colour preference? CHITTKA (1996) plotted the maximal sensitivity values of the photoreceptor types of arthropod species superimposed on the cladogram of these species (Fig. 10). His study shows that most likely the ancestor of all taxa of the Apoidea had trivariant colour vision, based upon a UV, a blue, and a green type of photoreceptor. Even the ancestor of all taxa of the Insecta had trivariant colour vision. Sets of UV, blue, and green types of photoreceptors are most likely a plesiomorphic condition in the Insecta. Hence, insects had trivariant colour vision about 400 Ma before the extensive radiation of the angiosperms which started in the Cretaceous (120 million years ago). Bees were thus preadapted for colour vision of flowers. Even the wavelength position of maximal sensitivity of each type of photoreceptors is similar in species of Apoidea and of non-flower-visiting species of Hymenoptera and other Insecta. No shift of the peak sensitivity wavelength position can be detected which could be related to flower-visitation.

This set of three photoreceptors is a necessary precondition for trichromatic colour vision. Whether or not ancient arthropods integrated the information from the set of three types of photoreceptors for trichromatic colour vision, is a matter of speculation (CHITTKA 1996). However, the capacity of colour vision was demonstrated not only in flower-visiting species of the Apoidea, but also in non-flower-visiting species of the Hymenoptera (CHITTKA et al. 1992) and in Crustaceae (MARSHALL et. al 1995). It is thus most likely that a trivariant photoreceptor system in insects predated the onset of coloured angiosperm flowers. Hence, bees were preadapted for flower preference and flower discrimination on the basis of flower colour signals.

A noteworthy exception is the solitary bee *Callonychium petuniae* (Andrenidae) which has an additional red photoreceptor type, and thus a tetravariant colour vision system. This neotropical bee is an oligolectic specialist forager of *Petunia* flowers. The additional red type of photoreceptor in *C. petuniae* may have evolved in the context of flower recognition. The violet *Petunia* flowers reflect blue and considerable amounts of red light. These reflection properties represent a strong selective force for the evolution of sensitivity in the red range of wavelengths. In *Callonychium petuniae* a shift of the peak sensitivity of the green type of photoreceptor towards the red range of wavelengths did not evolve but the evolution of an additional 4th type of photoreceptor occurred.

The hypothesis that true bees' photoreceptors are tuned to code for particular classes of coloured objects, such as flowers, can be rejected on the ground of CHITTKA's (1996) study. The alternative hypothesis that the spectral reflection properties of angiosperm flowers developed via one-sided adaptation towards a preexisting colour-vision system is supported by CHITTKA's data.

However, from these findings we may not infer that there was and is no co-evolution between flower-visiting bees and flowering angiosperms in the context of flower detection by colour signals. Bumble bees (*Bombus terrestris*) are spontaneously attracted towards colour signals of artifical flowers (LUNAU 1991; LUNAU et al. 1996; GUMBERT 2000). Experienced foragers exhibit different lear-

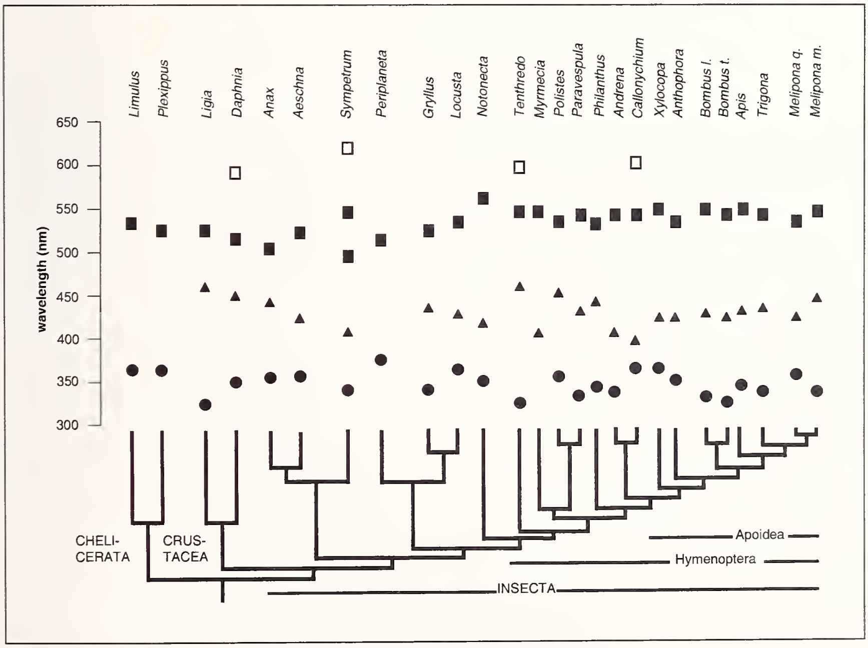


Fig. 10: Sensitivity maxima of photoreceptor types superimposed on a cladogram of the Arthropoda. Modified after CHITTKA (1996).

Fig. 11: Naive bumble bee approaching an artificial flower. The approach is precisely directed towards the dummy anthers in a manner that each antennal tip makes contact with a dummy theca.

ning speed and learning capacity in relation to different colours, as has been demonstrated for the honeybee, *Apis mellifera* (MENZEL 1979). Naive bumble bees, for example, possess a neurosensory filtering mechanism (sensu WEHNER 1981) tuned to a common colour pattern of bee-visited angiosperm flowers. In behavioural experiments individuals, which are inexperienced with flowers and not pretrained, are attracted by a distinct set of colour signals emitted by model flowers. They make contact with their antennal tips at visual stamen signals of dummy flowers preceding landing (Fig. 11). Beside the shape of anther dummies, the colour purity of the anther dummies and their colour contrasts with the surrounding corolla efficiently released the antennal reaction (LUNAU 1991; LUNAU et al. 1996). In natural flowers, the signal components releasing the antennal response of naive bumble bees, are displayed by conspicuous and UV-absorbing yellow stamens of pollen flowers and colourful stamen mimics of flowers in which the stamens are concealed in the flower (Fig. 5) (LUNAU 2000).

Synecological approach

For Gerd VON WAHLERT, the key to understanding evolution is a synecological approach integrating anagenesis, self-layering processes, co-evolution, and other phenomena. In his article about evolution as history of the ecosystem "biosphere"

Gerd von Wahlert (1978b) up-dates a study case from Leppik (1960, 1972) about floral differentiation of angiosperms as demonstrated by the fossil record of some families of the Angiospermae and some taxa of flower-visiting Insecta. The fossil record of angiosperm families and taxa of flower-visiting insects have been assessed by some authors to demonstrate anagenesis (Höherentwicklung) of angiosperms, self-layering (Überschichtung) of flower-visiting groups and co-evolution between zoophilous angiosperms and their insect pollinators (Leppik 1960, 1972; Paulus 1978; Crepet & Friis 1987; Schmitt 1994a; von Wahlert 1978a). That the fossil record is a suitable measure of phylogenetic age is demonstrated in Fig. 12, in which the fossil record of several families of the Angiospermae is compared with a cladogram of these taxa according to Chase et al. (1993).

The compilation of information about floral evolution of angiosperms and its correlation with the appearance and progression of insect taxa as shown by von Wahlert (1978b) helps to co-ordinate floral evolution into a continuous historical sequence, as follows: apomorphic, haplomorphic, actinomorphic, pleomorphic, stereomorphic, and zygomorphic flowers. It suggests that the parallel diversification of taxa of the holometabolous insects has a causal connection with the diversification of angiosperms (Fig. 13). Fossils represent direct evidence for the

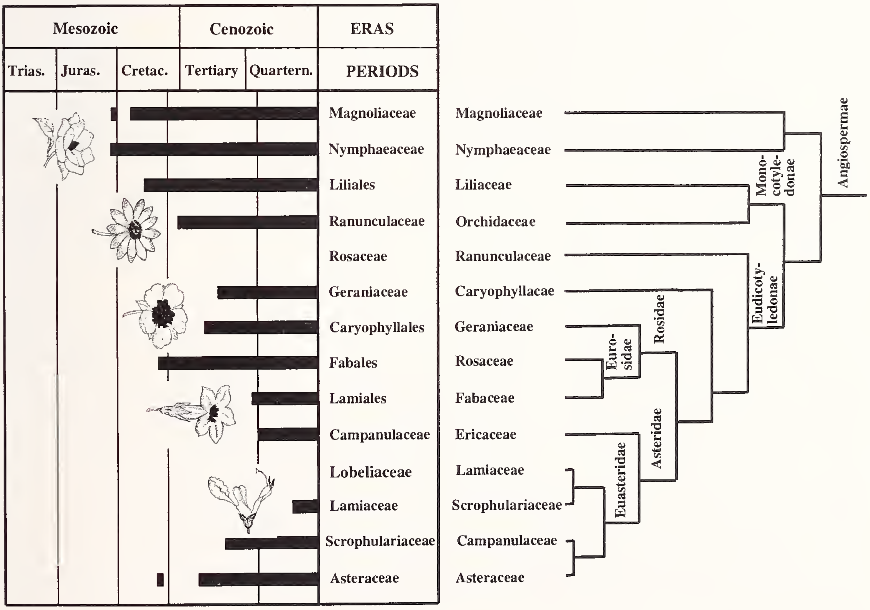


Fig. 12: Fossil record and cladogram of the Angiospermae. Modified after Leppik (1960, 1972) and Chase et al. (1993).

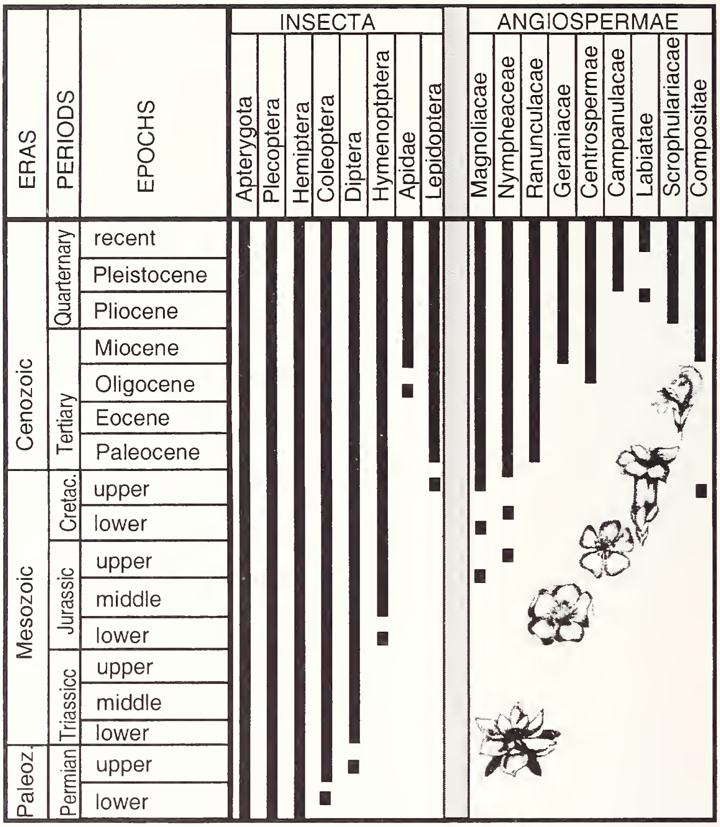


Fig. 13: Fossil record of land plants and flower visitors. Modified after von Wahlert (1978b).

first appearance of taxa and their changes in character. Though the fossil record of insects and particularly angiosperms is very incomplete, recent additional findings of fossil angiosperms (Sun et al. 1998) and insects (Grimaldi 1999) did not fundamentally change the view given above (Fig. 14). Labandeira & Sepkoski (1993) showed that the diversities of fossil families within insect orders began 245 million years ago and was not accelerated by the expansion of angiosperm during the Cretaceous period. In contrast to these results, Grimaldi (1999) shows that the radiation of bees (Apoidea, Hymenoptera) (Fig. 15), bee flies (Bombyliidae), Diptera and butterflies (Ditrysia, Lepidoptera) did not begin until the radiation of angiosperms 115 - 90 million years ago. Grimaldi superimposed the known fossil record onto a cladogram of the insect taxa. According to the data of Labandeira & Sepkoski (1993) it seems true that many insect

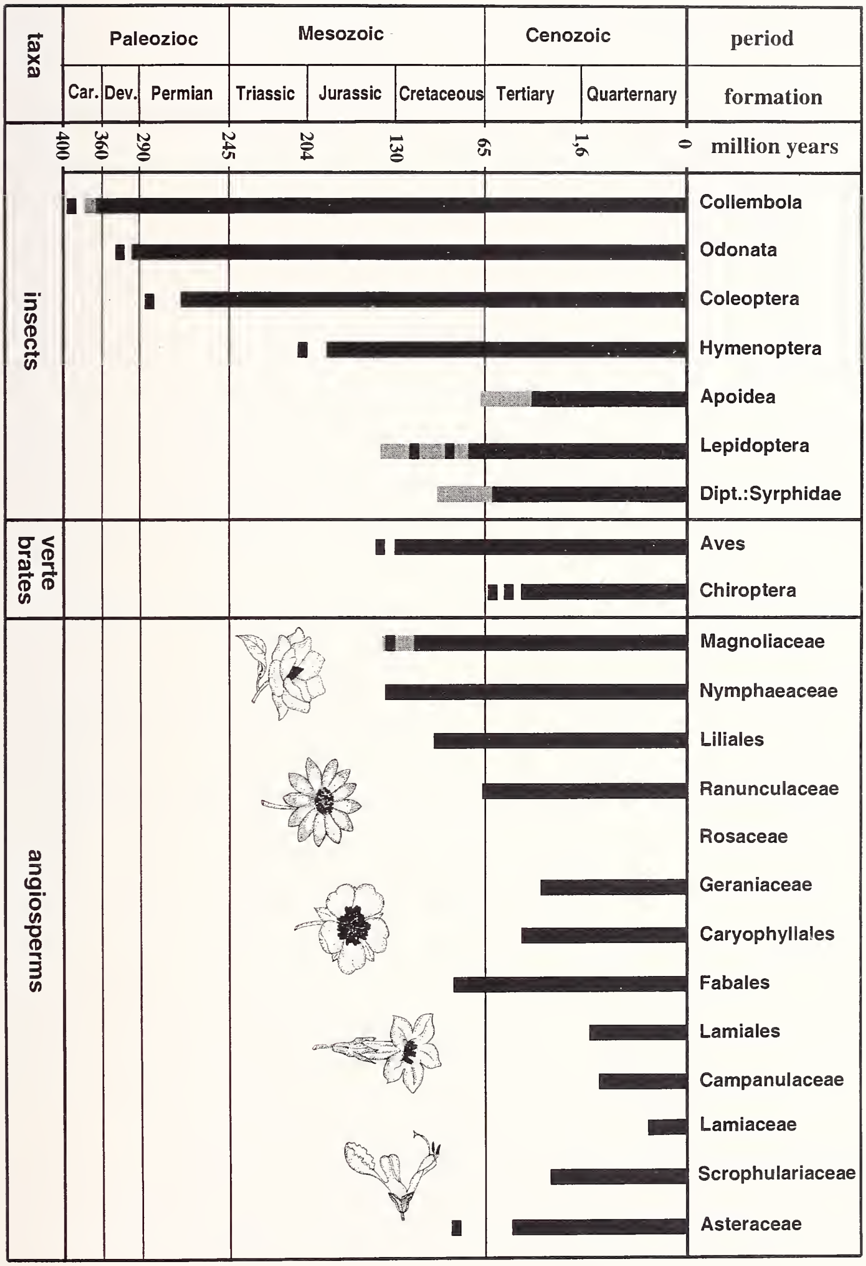


Fig. 14: Fossil record of land plants and flower visitors. Modified after Leppik (1960, 1972). Recent data of Grimaldi (1999) are indicated in the grey columns.

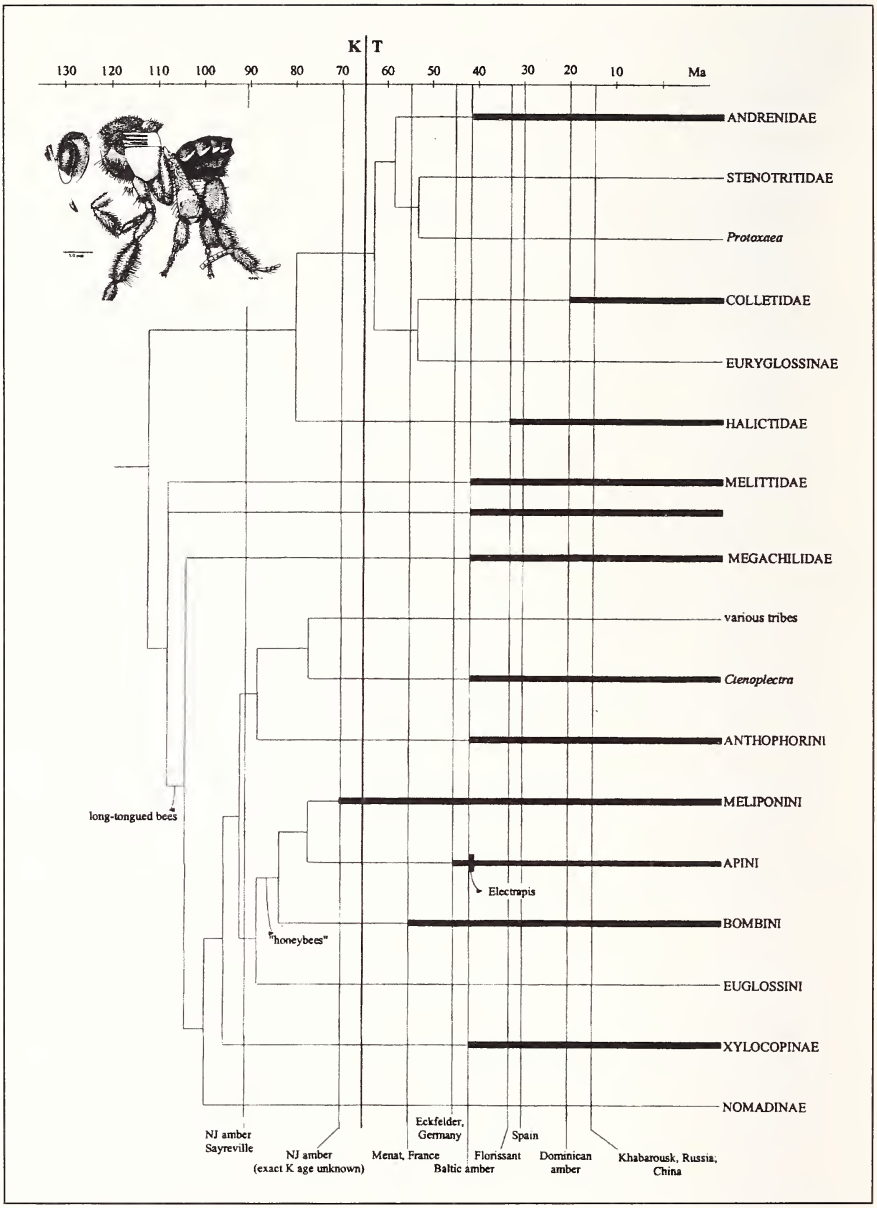


Fig. 15: Fossil record and radiation of bees (Apoidea). Inset: The oldest known bee Cretotrigona prisca (Meliponini, Apidae), in amber from the Cretaceous of New Jersey. From of Grimaldi (1999).

families appeared well before the angiosperm radiation. However, GRIMALDI's data show clearly that diversification of insect species, genera and subfamilial taxa occurred parallel to angiosperm diversification.

Further evidence for co-evolution among insects and angiosperms are the pollination syndromes of ancient angiosperm families. However, as will be shown, it would be very misleading to extrapolate from relationships between extant species, that these relationships continuously co-evolved since ancient times.

GOTTSBERGER (1988, 1989, 1999) studied the pollination biology of different *Annona*-species of the ancient angiosperm family Annonaceae. He discovered a highly derived pollination syndrome with heat production of the flowers, odour emission and specific pollination chambers formed by the fleshy petals. The species *Annona crassiflora, A. cornifolia, A. coriacea, A. dioica, A. tomentosa*, and *A. monticola* were pollinated by two species of beetles, *Cyclocephala atricapilla*, and *C. quatuordecimpunctata*, both members of the Dynastinae, a subfamily of the Scarabaeidae. The fossil record shows that the Dynastinae did not evolve before the Tertiary period (CROWSON 1981, *fide* GOTTSBERGER 1999). The-

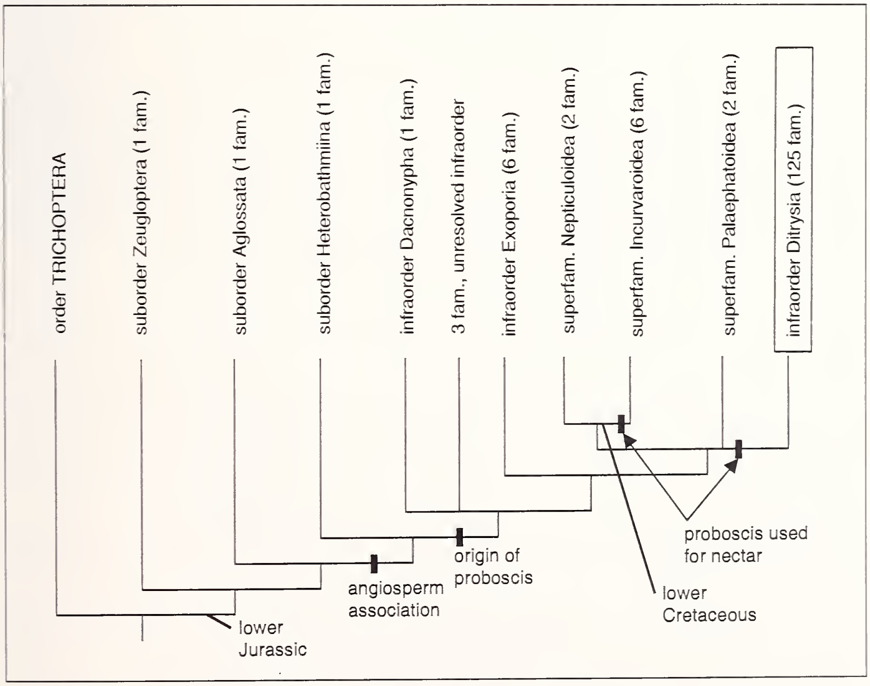


Fig. 16: Cladogram of butterflies (Lepidoptera). Modified after PELLMYR (1992).

refore, the evolutionary interaction between Dynastinae and Annonaceae probably represents a derived rather than a relictual lineage association.

When Thien et al. (1985) and Pellmyr et al. (1990) studied the pollination biology of the ancient angiosperm family Winteraceae in New Caledonia, they were impressed by the finding that species of the genus *Zygogynum* were visited and pollinated by micropterigid moths of the genus *Sabatinca*. The organisms involved represent lineages with suitably old fossil records that they may have coexisted for more than 100 million years. The Micropterygidae, a family of the Lepidoptera, are placed as the sole family in the suborder Zeugloptera. They have strikingly primitive characters such as mandibles, and maxillae that do not form a proboscis. The micropterigid moths of the genus *Sabatinca* fed on pollen and mated on the flowers. However, the authors found no evidence for a parallel radiation of the New Caledonian Winteraceae with their pollinating micropterigid moths. Other species of *Sabatinca*, present in the same habitat and simultaneously with the species pollinating *Zygogynum*, were typical spore feeders on ferns like other micropterigid moths. One isolated opportunistic switch of one *Sabatinca*-species leading to the colonization of *Zygogynum*-hosts, seems to account for the interrelations between the members of the two ancient families. A cladogram of the order Lepidoptera shows that the suborder Zeugloptera evolved before association with angiosperms. Even the proboscis evolved before it was employed for nectar drinking (Fig. 16) (Pellmyr 1992).

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G. von Wahlert: Stimulations to Evolutionary Ecology

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In the last 30 years, the method of phylogenetic reconstruction which was developed by Willi Hennig between 1950 and 1966 has been applied very successfully to many groups of animals and plants. The results which one attains when using this method are graphically presented as cladograms, which are based on apomorphic features of the organisms being investigated. Cladograms are indispensable when discussing character transformations, biogeography, evolutionary ecology and other topics. Each cladogram represents hypotheses for relationships between groups and reveals the arguments used for coming to these conclusions. Using this method, suggested transformations of characters become clearly visible. However, a cladogram does not seek to explain why and how new groups arise. An analysis of evolutionary ecology, which as advocated by Gerd von Wahlert at around the same time that Hennig was improving his theory of phylogenetic analysis, helped to fill this gap. In his analysis, transformations in morphology, physiology or behavior are investigated on the basis of an argumentatively founded phylogeny and are discussed as consequences of evolutionary adaptations in etho-ecology. Meanwhile, all indications suggest that the evolutionary-ecological approach is gaining more and more acceptance, both influenced by him or independently of von Wahlert's approach.

Combining four conceptual components

Gerd von Wahlert enriched the field of evolutionary biology with several specialized terms like "key innovation" (adopted from A. H. Miller: Schlüsselcharakter; 1957c, 1961a; later Schlüsselmerkmal), "ecological change of function" (ökologischer Funktionswechsel; 1961a) and "self-layering process" (Überschichtung; 1978a, b). However, we are particularly indebted to him for his causal analysis in seeking to understand both phylogenetic events and the evolution of groups and body plans (Baupläne). A well-read man with many interests, he picked up different conceptual threads in the fifties and tied them together into an evolutionary ecological approach for explaining what he later called "phylogenetic sequences" (1965, 1971). The following four concepts formed the basis of his ideas:

1. The principle of sister taxa from Willi Hennig

Von Wahlert himself did not actually attempt to reconstruct phylogenies to get cladograms. However, he had integrated Hennig's method in his approach, and he used it competently in his arguments. It was clear to him that cladistic analysis and evolutionary biology analysis reciprocally complement and support one another („wechselseitige Erhellung"). Feedback on cladograms reconstructed by out-group comparison and discussion on parsimony arises from a functional and ecological analysis. When the transformations claimed in a hypothesis on phylogeny have been shown to be improvements in efficiency, then the statements on transformations in the cladogram become more substantive.

2. The concepts of ecological niche and ecological zone from Klaus GÜNTHER

GÜNTHER (1950) defined the "ecological niche" as the multidimensional interrelationships of a species with the totality of its environment, and VON WAHLERT (1961a, 1965) was one of the few who used the term in this sense. He also believed that the species-specific ecological niche (econiche) was the main component in determining the species concept (e.g. 1973), and he thought the evolution of econiches was the central process in evolutionary change (1961a, 1965). However, in my opinion, he unfortunately did not pay enough attention to this singularly important, elementary process. The problems of speciation (splitting of species) and alterations within species towards a separation of niches were not his central focus. Much more important to him was the "ecological zone" (ecozone) which, like the econiche, is not a spatial concept (SIMPSON 1944; GÜNTHER 1950). Instead, it reflects all of the ecological interrelationships of all the species in a larger taxon. VON WAHLERT even went so far as to define specific econiches as the smallest ecozones (1978a: 118, 1978b: 26). He sought to explain the origin of larger taxa and new body plans, or what is usually called "macroevolution".

3. The concept of preadaptation according to Walter BOCK and Günther OSCHE

The concept of preadaptation as defined in the framework of evolutionary biology by BOCK (1959) and OSCHE (1956, 1962) became very important to VON WAHLERT as an aid for shedding light on the evolution of new groups of organisms with new body plans.

4. The idea of "behavior as a pacesetter" for evolutionary change

VON WAHLERT also fully realized the significance of behavior in promoting ecological adaptations in animals, an idea that has been pursued by I. I. SCHMALHAUSEN, WICKLER (1961) and others. He said that behavior determines the selective direction of morphological change.

Aspects of evolution

Three evolutionary processes must be distinguished: anagenesis, cladogenesis, and extinction (Fig. 1).

1. Anagenesis is every single transformation of features in a species lineage. It is not only evolution to a "higher" or "more advanced" stage, but also the reorganization, new acquisition, and the – occasionally complete – evolutionary retrogression of structures.

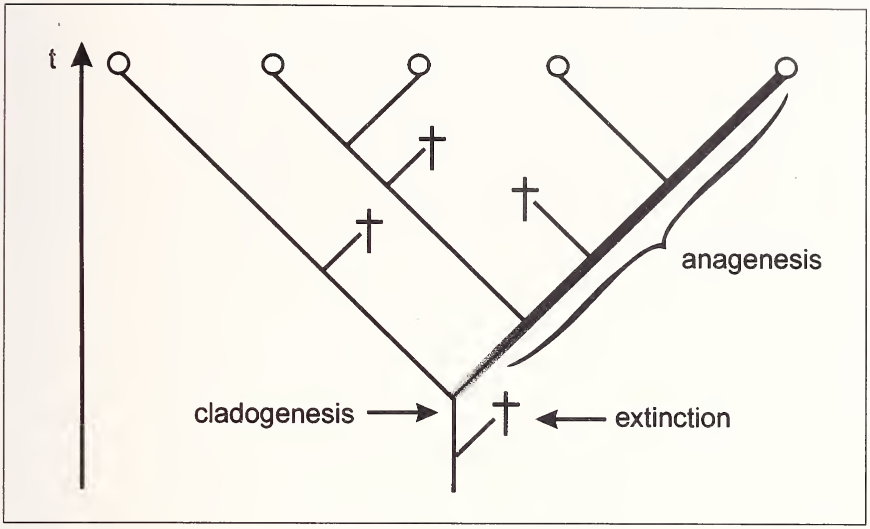

Fig. 1: Phylogenetic tree showing the three evolutionary processes anagenesis (change in a lineage), cladogenesis (speciation), and extinction (end of a species over geological time = t).

2. Cladogenesis describes the splitting of species (speciation) as the elementary process of branching of lineages. Starting from a stem species, an "adaptive radiation" (or radiation) occurs when many individual speciation events follow each other within a relatively short period of time, resulting in an absolute minimum of three different species.

3. Extinction is the irreversible loss of a species. The former existence of a species that can't be detected today is either substantiated by fossils or, in more recent history, by actual specimens in museums or through human documentation.

When working with a group, it is a very ambitious goal to attempt to reconstruct all speciation events, all transformations of features and the sequence of such changes in a lineage, including all extinct lineages. On the other hand, an important goal is to try to be able to give why and how explanations for a particular event.

Establishment of ecological zones within the group of vertebrates

Von Wahlert (1965) presented a shortened diagram of the realization of ecological zones for three of the most important vertebrate monophyletic groups: the Chondrichthyes, the Teleostei, and the Tetrapoda. The group encompassing these three taxa is the Gnathostomata, shown to be monophyletic based on the apomorphic character of the archipterygium (with internal skeleton) in both paired and unpaired fins (VON WAHLERT 1962). According to him, their epibenthic stem species had an organ which functioned both as lungs to breathe atmospheric air and hydrostatically as a swim bladder ("lung/swim bladder organ") and had a close relationship to the bottom, which was used as a resting place and as a spawning site. Both these features probably still existed in the † "Rhipidistia". During the adaptive radiation and evolution of the three groups mentioned above, each group lost its respective relationship to one of the three primary environmental factors – either water, bottom, or air. The following sums up the major changes which occurred (Fig. 2).

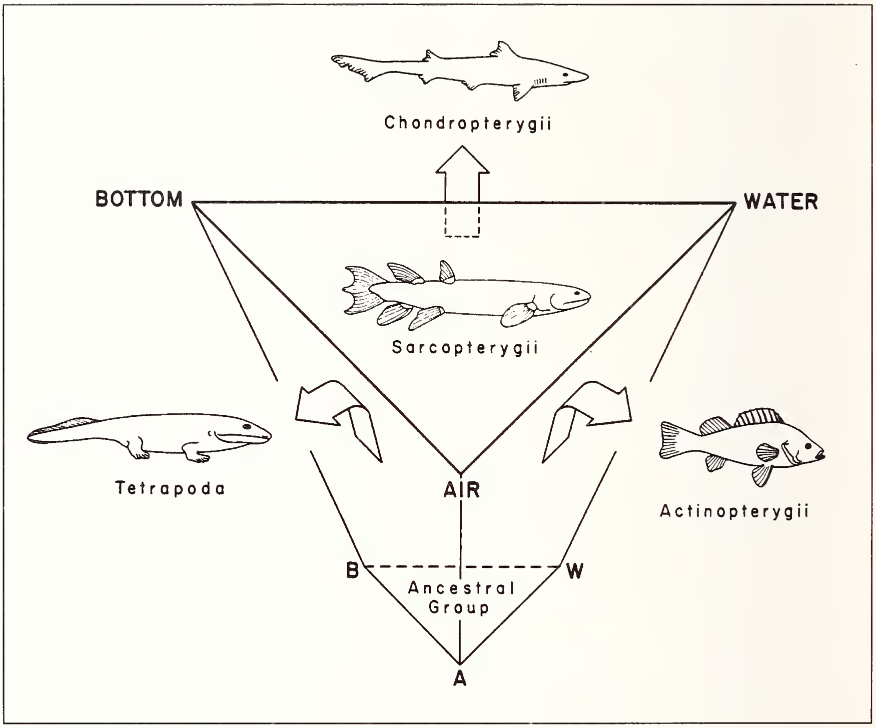

Fig. 2: A simplified scheme illustrating the radiation and establishment of ecological zones of major Gnathostomata groups. Ancestral fishes in the lower ABW-triangle combined obligatory relationships with the air (A), the bottom (B), and the water (W). †*Eusthenopteron* ("Sarcopterygii"), illustrated in the upper triangle, has maintained this ancestral relationship to a large extent. The evolution of the Chondropterygii (represented by a dogfish-shark) is marked by the cessation of connection with the air but a continued relationship with the bottom and the water (BW). The Tetrapoda (AB), represented by †*Ichthyostega*, have reduced their ties with the water. The Actinopterygii (represented by a perch) eliminated benthic traits (AW) and eventually the bond with the air (only W) (from VON WAHLERT 1965).

– VON WAHLERT believed that cartilaginous fishes (Chondrichthyes) gave up breathing air and completely reduced the lung/swim bladder organ. However, these fishes maintained their relationship to the epibenthic zone. Only a few lineages have secondarily invaded the pelagial zone (see below).

– The Teleostei retained the lung/swim bladder organ, but likewise gave up breathing air. This gave them the licence to transform that organ into a swim bladder whose sole function was hydrostatic, allowing them to live as free swimmers in the pelagial zone. Some Teleostei fill the swim bladder just once in their life, inhaling the necessary air at the surface when they are young. Others are capable of freeing themselves from the atmosphere entirely by filling the swim bladder by gas secretion from the circulatory system alone (euphysoclists). Some lineages within the Teleostei have grown more and more independent from the bottom. They have evolved schooling behavior, and even finally separated from the bottom with respect to reproduction. They spawn in the free water, lay huge numbers of eggs and develop as pelagic larvae without parental care. The larvae then were able to make use of food resources that could not have been utilized by adult Teleostei. With all of these prerequisites in place, the open sea could be colonized.

– Terrestrial vertebrates (Tetrapoda) in the stem lineage of the Amniota finally separated from the water and have become adapted during evolution to live on land. Similar to the teleost fishes, the terrestrial vertebrates' detachment from the ancestral mode of life occurred very late in the functional sphere of reproduction and development.

Fig. 2 introduces the problem. However, it is too rough to help in understanding the origins of the different high level groups and their distinct body plans. The evolution toward such groups first takes place in individual populations within a species. That means that in trying to grasp the intricacies of what has occurred, the logical starting point is at the species level.

The species as an ecological program

Contrary to characterizations of species which emphasize reproduction, a topic which is predominant in literature on the subject, VON WAHLERT (e.g. 1973: 249, 1978a: 118, 1978b: 26) supported and developed an ecological species concept. "Species are groups of organisms which develop or maintain an ecological niche over generations." If we ask why organisms are so similar to each other in their features that we can put them together in a group and call them a species (the aspect of "morphospecies", Fig. 3), then we are provided with answers from the usual views which one must take into account in biology: proximate, ultimate and historical (SUDHAUS & REHFELD 1992: 7):

– The “ecospecies” is the **ultimate** answer. The establishment of a specific econiche guarantees the continued existence of the species, as it avoids or restricts competition with other species. An econiche can be maintained most effectively by interbreeding.

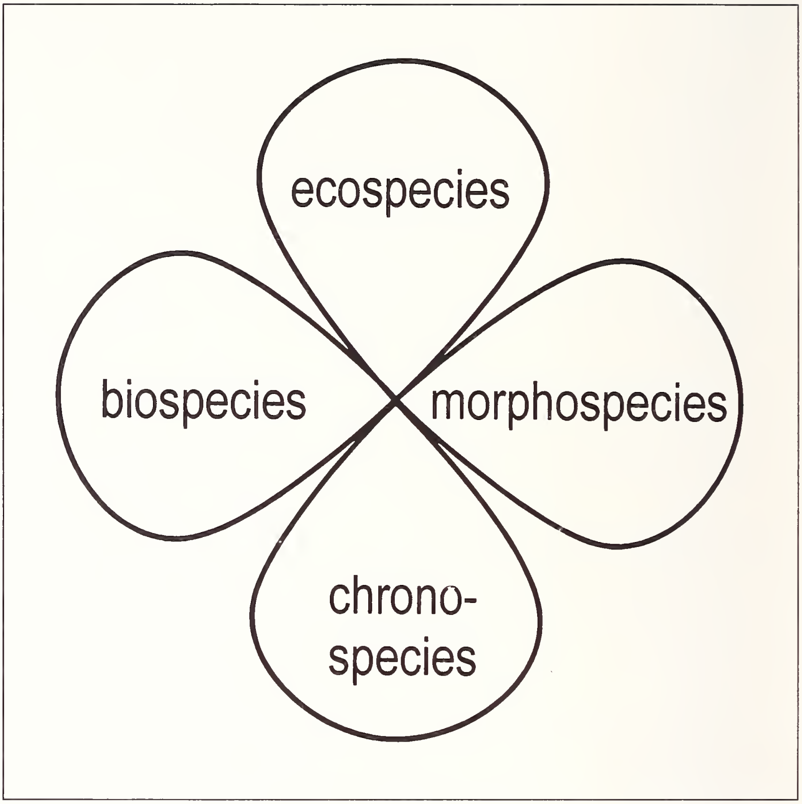

Fig. 3: Four different aspects of the species concept.

– The **proximate** reason for the uniformity of individuals in the species is the mechanism/s which members of a bisexual reproductive community use to recognize each other (the "biospecies" aspect). Reproductive mechanisms are usually the most easily-recognized indicators of species identity.
– Finally, the **historical** component of a species is the common history in a lineage of descent between two subsequent speciation events. When discussing either species which are still alive or those which became extinct before they could split, it includes all members of the lineage starting from the last speciation event (This is a modified definition of "chronospecies").

With respect to the species concept, which is thus based primarily on ecological relationships, it is important to keep in mind how evolutionary biologists have viewed the "ecological niche" since Klaus GÜNTHER (1950). He focuses on the entirety of the interchanging relationships of individuals within a species along with their biotic and abiotic environments. According to him, the econiche is therefore multidimensional (Fig. 4). It consists of connections between the necessities of life which are demanded by organisms and what the environment can supply, called "ecological licences" (GÜNTHER 1949). The interaction between the organismic and environmental dimensions mesh were called "synergs" by BOCK & VON WAHLERT (1965). The econiche is equivalent to the accumulated sum of the synergs. The realization of the species specific econiche is possible only where the environment satisfies all of the ecological demands of the individuals of a species during their entire life cycles. Because it is very difficult to investigate all ecological demands, comparisons of the econiches of different species usually actually only compare one or a few synergs (e.g. the "feeding niche").

To refer umambiguously to the concept of the ecological niche in the sense discussed above, and also in honour of Klaus GÜNTHER, I have called this concept of a niche the "GÜNTHER-niche" (SUDHAUS 1996), a term which has been adopted in JAHN's "Geschichte der Biologie" (1998). The dynamic aspect of the GÜNTHER-niche concept for evolutionary theory is that it leaves room both for gradual changes in the niche and for the organisms in a population. Hitherto unexploited resources offer an ecological licence and can be used by certain individuals. On the other hand, individuals can also give up special demands they make on the environment. This allows new synergs to form and others to lapse. And if such

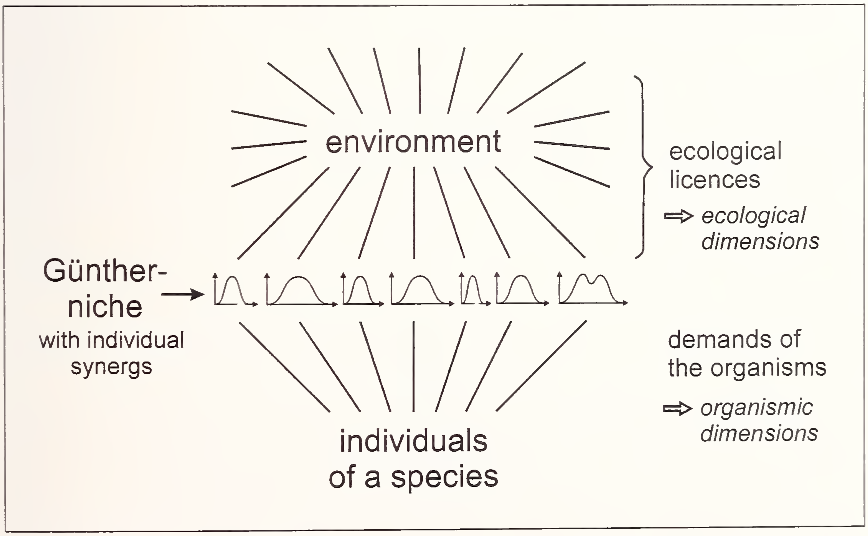

Fig. 4: Visualization of the ecological niche called the GÜNTHER-niche. Statistical curves describe interaction of Available Resources (x-axis) and Species Utilization (y-axis) in different synergs.

individual changes spread through a population and at last prevail, their accumulation reflects the step-by-step alteration or transformation of the species-specific niche. Econiches are therefore "actively" formed or transformed during evolution by the interactions of organisms with their environment, and are then realized by the organisms. An ecological niche is by no means an alcove that can be "occupied". It does not exist without the species. It disappears when a species becomes extinct.

Even early in his career, VON WAHLERT (1957a, b, 1961a, 1965) pointed out that heterobathmy exists in the econiche just as it does in morphological organization. In the terms of G. DE BEER he described it as "mosaic evolution". The "mosaic" of plesiomorphic and apomorphic dimensions in the econiche indicates that its evolution is gradual, just like the evolution of morphological features. This is very clear for instance in vertebrates that invaded terrestrial environments and apomorphically began acquiring their food in terrestrial habitats, but continued (plesiomorphically) to fertilize eggs externally and to develop in water for a very long evolutionary period. In general, not all of the challenges presented by "functional spheres" (Funktionskreise) in a new ecological zone were solved simultaneously. Some ecological hurdles were only overcome at later times in a taxon's evolution, and for some taxa, problems remain in some functional spheres which have yet to be effectively resolved. For example no bird – no matter how well it flies and uses the air in different activities – can reproduce independently of a firm substrate (VON WAHLERT 1957a, 1961a: 38, 1965: 298).

Organisms as "protagonists"

VON WAHLERT (1957b: 280) probably first demonstrated that organisms are active participants or "actors" on the "stage of life" in a publication on salamanders (Urodela), where he discussed changes in their modes of life which were subsequently followed by transformations of features. Every organism has to "passively" keep pace with changes in environmental conditions, e.g. climatic changes and its effects, to which they have to be adapted. It is necessary to be able to react to some extent to changes in order to survive. In a metaphorical sense, however, they also "actively" change their way of life within a given habitat, although each case is of course determined by the Darwinian mechanisms of genetic variation and selection. Adaptations to this new way of life then follow.

I am not sure how the idea of "active" contributions by organisms was received by those few scientists that still supported orthogenetic ideas or by all of the others that argued against that particular misconception. That organisms do contribute actively to their own evolution, however, was shown by VON WAHLERT (e.g. 1965, 1973: 253) in a didactically impressive fashion. He compared early land-inhabiting vertebrates (Tetrapoda) and lungfish (Dipnoi), modelling his initial efforts on ROMER's ideas of the importance of seasonal droughts. These two groups exhibit two different behavioral strategies for coping with intermittent dry seasons:

– Lungfish like *Lepidosiren* and *Protopterus* have a passive adaptive strategy for surviving dry seasons. They burrow in the mud of dried-up bodies of water and wait therein for the water. They are dormant, curled-up within a "cocoon" formed by a mucus which they secrete from their skin. Deposits with fossil burrows containing remnants of lungfish prove that this method of survival has existed since the Devonian.

– When faced with the same factors, the ancestors of tetrapods left the drying habitat, using their extremities to actively crawl in search of a new body of water in which to live. Only a lineage of organisms possessing such a behavior could eventually invade land. Selection favored mechanisms which aided survival out of the aqueous environment. This then became an evolutionarily "successful" lineage with the great diversity for which the tetrapods are well-known.

It is important to realize that a change in environmental conditions is not at all necessary to change the behavior of a fish leaving the water. The existence of dry seasons is not a precondition. One can point at various fish which leave the water temporarily for different reasons. Some, like the eel (*Anguilla*) or *Anabas*, are in search of a new body of water. Others leave it to feed, like *Periophthalmus*, species of Blenniidae or *Hoplosternum littorale*. Some fish sleep out of the water (species of Blenniidae) and males of this group can stay with the nest of eggs during low tide, while *Copeina arnoldi* or *Leurethes tenuis* even leave the water in order to spawn. For the tetrapod lineage, von Wahlert (1973, 1978b) assumed that temporary visits to land initially helped them avoid the problems posed by frozen bodies of water in winter, which allowed them to colonize bodies of water in such regions. This pattern can still be observed in some Urodela today.

What the evolution of the tetrapod lineage teaches us is that evolutionary change does not just mean that changes in abiotic and biotic environments force appropriate evolutionary responses in organisms. Evolutionary change also depends a great deal on the behavior of the organisms involved, and through that behavior they have an influence on the further course of selection. Von Wahlert (1965: 299) viewed both the evolution of ecological behavior caused by genetic variation and selection and the evolution of econiches and ecozones as the fundamental processes in the evolution of animals! The rules are somewhat different for micro-organisms and plants; instead of "behavior", each single physiological change which allows a different exploitation of resources has to be taken into consideration.

Tetrapod ancestors: transforming an ecological niche and opening a new ecological zone

Transformation of an econiche means creating new synergs and giving up older ones. In order for that to occur, ecological and organismic prerequisites are necessary. Little-used or unused ecological licences must already exist; for example, food in sufficient quantities. The organisms' design must also allow them to use what the environment is supplying. This requires so-called "organismic licences" (Osche 1983), for example, the ability of a water-dwelling vertebrate to survive on land, at least for short periods of time. An important factor in this scenario is both the absence of potential competitors for special resources and of potential predators, although this might also be included indirectly in the term "ecological licence". At the time of the origin of the Tetrapoda, for instance, there would not have been a licence for fish-like vertebrates to colonize land if other competitors already existed in these habitats. The fact that other lineages of fishes throughout geological history never truly managed to invade terrestrial habitats again can be understood to be at least partially due to stiff competition by representatives of the amphibians and amniotes since Permian times.

The circumstances which enable "key events" in the phylogeny of a group such as land-living vertebrates have been described by von Wahlert (1965) as an "evolutionary situation." In that situation, some potentially competent species have the opportunity to realize an ecological breakthrough, thereby becoming the starting point for a new radiation which will in turn establish a new ecological zone. Special geographical and historical conditions characterize such an evolutionary situation. Both the ecological licences for a new mode of life have to be offered and the organisms have to be endowed with specific functional structures and ecological capabilities. These organismic prerequisites, or "preadaptations," were adaptations to an older mode of life. However, they were also suitable for coping with problems in the new ecozone, and were therefore helpful for the transition. Adopting this perspective, von Wahlert (1971, 1978a) spoke of "hidden reserves" as potentialities when confronted with new evolutionary situations. One example is fleshy or lobed fins, which were used by the †"Rhipidistia", both for maneuvering when swimming and for propping itself up on the bottom, but which could also be used as extremities to support a sinuous, crawling movement on land. When concurrent with special ecological licences, such preadaptive features can become "key innovations" in establishing a new ecozone.

Fundamental in animals are "ethological key innovations" (ethologische Schlüsselmerkmale, von Wahlert 1961b), which allow them to exploit existing resources in new ways. Evolutionary change in behavior or physiology in order to exploit a new resource can put organisms and their preadaptive structures into a new ecological situation. The changed behavior thus at first brings an extension of function, but then might also lead to an ecological change of function (von Wahlert 1961a). In retrospect, such changes of behavior therefore end up being the "pacesetters of evolution" (Wickler 1961). They precede morphological changes and effect various alterations in structure as they influence the further direction of selection and evolution of characters. Organisms and all their properties, preadaptive and otherwise, are governed by new selective forces caused by a new relationship to their environment. Over many generations this leads to evolutionary change which improves the adaptations to the new mode of life; that means that they become more economical in terms of the energy output necessary to maintain them. "Ethological key innovations" are thus followed by adaptations in morphology to a new mode of life ("morphological key innovations", morphologische Schlüsselmerkmale, von Wahlert 1961c). These structural changes improve the corresponding exploitation of resources, but the organism must pay a price in evolutionary flexibility.

Changes in behavior can cause phylogenetically old (plesiomorphic) features to assume new functions. These characters can thereby obtain a new quality as "key innovations". Examples are lungs and fleshy fins in the ancestral lineage of tetrapods. When interpreting such examples, it would be wrong to say that structure precedes behavior.

In an "evolutionary situation" like that characterized above, with certain environmental conditions and certain organism features combining to allow a special mode of life, the possibility that a new ecozone can be established exists. This requires, however, a radical change in the species' mode of life and the establishment of a huge number of new connections with the environment. It pushes the reorganization of the species, and in the end establishes an ecozone through adaptive radiation through subsequent speciation events. The features that are important in maintaining the ecozone become characteristics of the body plan and henceforth are subject to stabilizing selection. In retrospect, the ecozone can be characterized as all of the corresponding dimensions of the econiches of species that exhibit the new body plan which fuelled the radiation.

Not only monophyletic taxa but also paraphyletic groups can establish an ecozone. If a new ecozone which is based on an old one has been opened and filled by a monophyletic group, then the paraphyletic "leftovers" have remained in the old ecozone (Fig. 5).

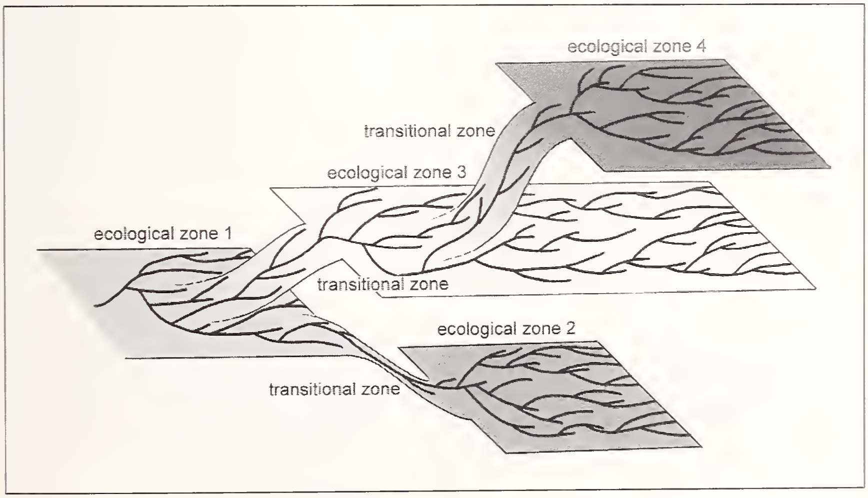

Fig. 5: Scheme illustrating the self-layering process which occurs due to a sequence of radiations into different ecological zones. Such radiations began when a lineage had passed through a transitional zone and reached the new adaptive level of a new ecological zone (after Schmitt 1992: 67).

Flatfishes as models

The concept of the establishment of ecological zones was developed by VON WAHLERT (1961) in a case study of the peculiarly asymmetric Pleuronectiformes, or flatfishes. The "ethological key innovation" in the ancestral lineage of flatfishes involves the sleeping posture, where the fish lies on one side on the bottom. This trait, which is also known in the closely-related symmetrical carnivorous Serranidae, began to be retained by Pleuronectiformes when awake. These fish therefore extended the functional context of "lying on the side". This opened the way to a new mode of life for those fishes when hunting, allowing them to lie in wait for prey in ambush, buried in the sand. Structural adaptations to this behavior followed in the course of evolution and represent "morphological key innovations" which acted to channelize this mode of life: the body is laterally compressed, the two sides have diverged into a functional underside and a functional upperside, the eye from the functional underside has migrated to the margin of the head and then to the functional upperside to enable binocular vision, and in the flounders (Pleuronectoidei) the fish is camouflaged and adapted to a benthic life by its physiological ability to alter its color. By this new mode of life the sandy ocean bottom now could be exploited. The stem species with this new body plan radiated to more than 500 recent species. These species have in no way replaced the representatives of the original (plesiomorphic) mode of life. Instead, they've just added a new ecological layer or stratum (see below).

The evolution of the Teleostei zone

The evolution of different groups of fish is mainly characterized by transformations of the feeding apparatus (Fig. 6). Fishes with relationships to the epibenthos such as sharks have mouths which are located beneath the rostrum. The morphological key innovation of the bony fishes (Osteognathostomata), an anterior shift of the mouth caused by an extension of the lower jaw, was selectively directed by suction-feeding. This position of the mouth favored a more precise food intake

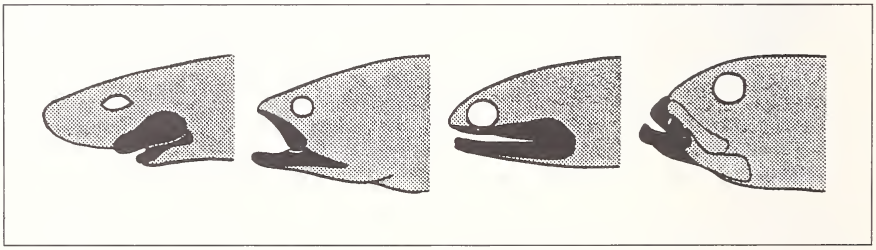

Fig. 6: Comparison of mouth position and position of jaw joint in sharks, *Latimeria*, † "Palaeonisciformes", and Acanthopterygii (from left to right). Bones which form the functional jaw are in black (based on VON WAHLERT 1968).

(VON WAHLERT 1968: 25). In *Latimeria* and others, the mouth is made larger by means of a new joint in the skull, which helps in overpowering larger prey.

In another evolutionary sequence (Actinopterygii), the morphological key innovation was that the mouth slit was enlarged posteriorly. The evolutionary sequence itself displays a complex interplay of many different morphological factors. The enlargement of the mouth implies that the gills had already transferred their primary respiratory function to the lung organ and had only maintained their excretory function, because the mouth would have otherwise caused a conflict between feeding apparatus and breathing apparatus. The reactivation of the gills as a breathing apparatus which later occurred within the Actinopterygii had an important effect on the structure of the skull. Compact skulls like those found in the †"Palaeonisciformes" became thereby less constrictive; different elements became "movable". Within the Teleostei, the maxilla no longer formed the margin of the mouth. It became bowed and was integrated into the cheek region. Teleostei are named for their terminal mouths which they can protrude because the mobile premaxilla is only loosely attached. This innovation opened new avenues in the search for food.

The Teleostei are an an evolutionary example of animals whose mode of life has changed without a corresponding change in habitat. Starting with the ancestral Actinopterygii, which were behaviorally rooted to the bottom in nearly every functional sphere, fish have evolved that are at home in the three-dimensional world of the open water. Their new ecological zone represents not only a new stage of behavior, but also a new mode of life and a new utilization of resources. Feeding on smaller planktonic prey in the open water opened up the use of a vast new food resource which other larger vertebrates were not able to utilize because they lacked the appropriate feeding structures. These small plankton offered the ecological licence for the new ecozone which became established with the evolution of the Teleostei and resulted in the tremendous diversity and functional variety of this group.

During this evolutionary process, transformations of different organs and structural complexes were of course always interdependent, although they can usually be described in a linear series in a historical narrative. Different alterations in the evolution of feeding habits, movement and utilization of the open water were dependent on each other. The minute particles of food necessitated long feeding periods, which meant permanent swimming. This in its turn required an enhancement of the kinetics of the gill apparatus to provide more oxygen. Selection therefore favored a restructuring of the gill apparatus, which in turn had repercussions on the feeding apparatus. As mentioned above, this resulted both in a terminal mouth which can be protruded and a cheek which was supported by the maxilla. The maxilla thereby assumed a new function and no longer lay within the boundaries of the mouth. This kinetic pharyngeal jaw region improved the new mode of utilizing and ingesting food. Simultaneously, the breathing improvements to the gills released the organ which had been functioning as a lung/swim bladder from its repiratory function, allowing it to become a pure hydrostatic organ. This generated more buoyancy and enabled the Teleostei to swim more economically in terms of energy requirements, making them more independent of the bottom. As part of this process, fleshy fins were also transformed to lightweight fins with a strong but flexible ray structure (ray-finned fishes). All of these key innovations now licensed the establishment of this Teleostei ecozone both ethologically and structurally (GÜNTHER & DECKERT 1959: 38; VON WAHLERT 1964, 1968: 97).

Summing up the explanatory framework of evolutionary ecology

One task of evolutionary biology is to explain the evolution of a group and its body plan. This implies reconstructing the original circumstances, or "pre-adaptive plateau" in morphology and ecology attained by the more primitive mode of life. That reconstruction then helps clarify the prerequisites for possible changes in the stem species' mode of life. At the same time, the limitations in the organism's body construction have to be established. The transformations of features which point the way to a new body plan must be analyzed with respect to their significance as possible key innovations: did they transform the econiche in the ancestral lineage to such an extent that it opened a new ecozone?

As the Teleostei demonstrate, the establishment of a new ecozone is equivalent to a fundamental change in a taxon's mode of life. It is a transitional phase in which the stem species reaches a new stage of ecological behavior. In the teleost fishes, certain preadaptations such as the suspension of the jaw apparatus helped in reaching this stage. A change in the behavior and mode of life of a species in the ancestral lineage turned out to be the "pacesetter" of further evolution. When organisms interacted in new ways with parts of their environment, new selective forces took effect and caused changes in structures. These changes can be recorded in the ancestral lineage. Characters are based on one another and created by reorganization, new acquisition and loss of structures. Each change in morphology has to be shown as an adaptive process. Emerging features like the unique pharyngeal jaw apparatus, a skull which consists of various elements, a swim bladder and actinopterygian fins with a lightweight construction can be interpreted as adaptations to this ecozone. Although the adaptations might have occurred in different systems, in part they were either mutually dependent or one alteration in structure was the prerequisite for the next alteration.

The successful establishment of the teleost ecozone enabled further adaptive radiation. The very high number of species which resulted indicates the great success of the teleost body plan. The potential for this diversity lies in the evolution of feeding habits which focus on small planktonic organisms and epigrowth. These brought in their wake increasing ecological specialization and increasingly specialized modes of life. The numbers speak for themselves: less than 400 species of sharks still exist, while there more than 20,000 living Teleostei species. This 1 to 50 proportion illustrates that speciation and annidation (LUDWIG 1950) in hunters of large prey is more difficult than for animals which feed on small organisms. Examining different ecozones helps in understanding existing asymmetry in terms of species diversity.

Repercussions of a successful radiation

The Teleostei's staggering radiation had an effect on the outcome of earlier radiations in two ways (Fig. 7); first of all, there was a negative repercussion on other fish groups which were unable to match the bony fishes' far-reaching adaptations to a similar mode of life. Because of a higher level of achievement (discussed below) the Teleostei species were competitively superior to representatives of earlier radiations, which resulted in the extinction of all but a few groups. All species of the †"Palaeonisciformes" and most of the paraphyletic "Holostei" became extinct. Only the Lepisosteidae (*Atractosteus* and *Lepisosteus*) and *Amia* lineages managed to survive in special ecological situations. This negative repercussion is also not only plausible for other taxa in the stem-lineage. Advanced Actinop-

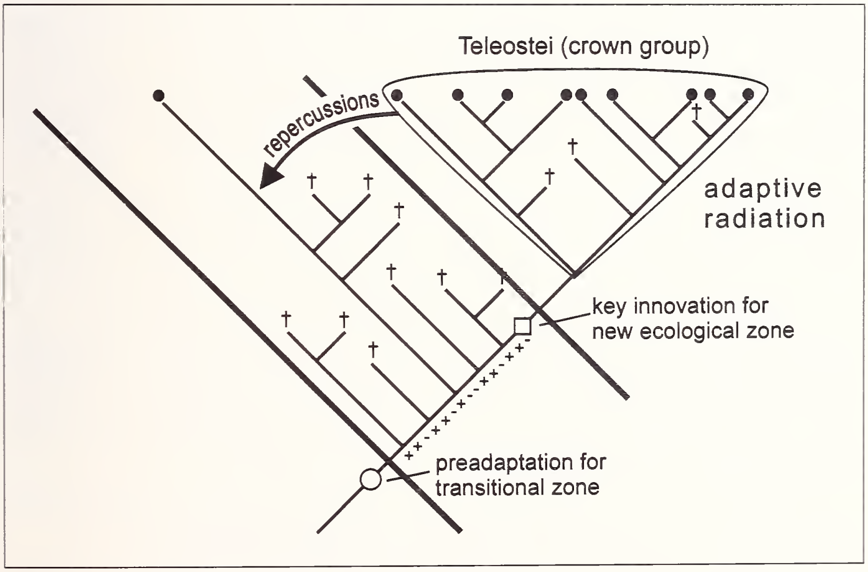

Fig. 7: Scheme illustrating additive typogenesis in the ancestral lineage of a crown group (in this case Teleostei) with acquisition (+) and loss (-) of features in a transitional zone. The opening of the transitional zone was enabled by preadaptive characteristics of an ancestral species. Key innovations during this anagenetic evolution opened the new ecological zone of the teleost stem species and allowed the succeeding adaptive radiation to make use of this zone. Earlier branches of the lineage are affected. The repercussions either accelerate their extinction by competition or support their existence by offering them new ecological licences.

terygii superiority in competition with other groups must also be considered as a possible explanation for the extinction of only distantly-related taxa like the †Acanthodii. The †Acanthodii lived until the Permian. Their feeding apparatus indicates that they probably ingested small organisms, and both the spindle-shaped body and the diminished exo-skeleton can be interpreted as adaptations for swimming in the open water. One hypothesis for the reason for the †Acanthodii extinction is that they were crowded out by pelagian species of actinopterygian fishes which were more efficient swimmers (von Wahlert 1968: 87).

This sort of synecological approach provides possible reasons for the extinction of entire groups and therefore the disappearance of certain body plans. Arriving at a possible explanation of extinction fulfills one of the tasks of evolutionary biology which were mentioned at the beginning of this essay. In some cases, all of the species which represent a specific body plan have become extinct one after the other when certain ecological licences of their zone were taken away by utilization of components by more efficient competitors.

Positive repercussions for the evolution of unrelated species can also occur. The Teleostei adaptive radiation, for example, had some positive consequences in the evolution of the sharks. While teleost fishes became abundant in the open oceans, they gave new ecological licences to the pelagic, predatory Elasmobranchii. These pelagic sharks then established a new ecozone and went through a radiation based on both an improvement in swimming efficiency and a detachment of previously close relationship to the bottom. The final step of sharks' detachment from the bottom occurred in the functional sphere of reproduction with viviparity.

While we are usually satisfied if we feel we are able to only explain some of what happened during evolution, it is also worth mentioning that such repercussions can help to at least partially explain what did not happen. By establishing an ecozone of huge pelagic predators which feed by tearing off large chunks of their prey, there were no free ecological licences available for a similar zone for the Teleostei (Günther & Deckert 1959). The well-adapted sharks effectively prevented such an evolutionary step in the Teleostei right from the start, particularly because the bony fishes' first clumsy transitional evolutionary steps would have run into entrenched competition.

Self-layering ("Überschichtung") of ecological zones and their corresponding groups of organisms

According to von Wahlert, "additive typogenesis" is not a constant steady phylogenetic process repeatedly punctuated by speciation events but is instead the result of a sequence of intermittent larger radiations from a "preadaptive plateau" (Osche 1966) which is reached before a new ecozone can be opened by a species. The new radiation which begins from this species then "overlaid" older radiations. The metaphor of "overlaying" is a state, and the process by which it occurs was called the "self-layering process" by von Wahlert (1978 a, b). This concept seeks to explain how individual groups or representatives of older radiations could survive either in spite of the emerging "anagenetic group" or alongside it. Examples of this phenomenon have already been given for the Serranidae and the flatfishes as well as for *Lepisosteus* or *Amia* and the Teleostei.

There are two situations in which one finds representatives of an older evolutionary layer:

– In geographically or otherwise separated regions that could not be reached by more efficient competitors from later radiations. There are monotremes in the Australian region which was reached only by bats and rodents of the Placentalia, for example. There are also lemurs on Madagascar, which remained unreachable for old-world monkeys.

– Remnants of older radiations can continue to exist when they exhibit a very special mode of life which could not easily be established by representatives of younger radiations when faced with competition from these specialists. Because of these specialists, there are no free ecological licences for a corresponding econiche. The jawless fish (Agnatha) fulfill these criteria because of their highly specialized way of feeding (*Myxine* or *Petromyzon*).

Such overlaid "strata" exist everywhere in nature (Fig. 5). Species of a more efficient body plan have not completely replaced the representatives of "ancient" body plans. There continue to be "reptiles" and amphibia in spite of mammal and bird radiations. Von Wahlert (e.g. 1973) generalized that "evolution is not succession, but accretion". This appears to be the case only when the newly developed ecozones are sufficiently different from earlier established zones in many ecological dimensions. If the feeding style is too similar in two groups, as it is in mussels and brachiopods, then the less effective organisms are replaced species by species.

Evolutionary detours and "over-embossing" body plans

Besides identifying self-layering as an evolutionary ecological process, von Wahlert also opened our eyes to the phenomenon that special steps in evolution and the establishment of ecozones are only possible via detours.

– Endothermous water inhabiting vertebrates (mammals, birds) could arise only via the detour of terrestrial tetrapods. They then founded new layers in marine ecosystems.

– The evolutionary loss of lungs in the now terrestrial salamanders (Plethodontidae) could only happen because the species once lived in mountain streams saturated with oxygen (von Wahlert 1957b: 274).

– Many of *Homo sapiens*' important characteristics – the prehensile hand, stereoscopic vision, spatial thinking and the fact that the young are carried by their parents – arose in evolutionary detours in primate life in the treetops.

In the morphology of such taxa, these processes lead to a situation in which properties of the body plan which are adapted for an older ecozone are superimposed and combined with adaptations to a younger ecozone. At one point I called this "overlapping" of body plans (Überlagerung, SUDHAUS & REHFELD 1992: 197). Now, however, I'm convinced that "over-embossing" (Bauplan-Überprägung) is a better description of what actually occurs. During a lecture in Berlin (27.1.1995) VON WAHLERT called it "internal self-layering" (innere Überschichtung). As an example ROMER discussed that in the vertebrate history a filter feeding chordate organism evolved an efficient locomotor apparatus, and the visceral and somatic components of the body "became more broadly overlapping and coordinated with one another" (ROMER & PARSONS 1977).

The synecological approach in evolutionary ecology

VON WAHLERT's ideas, which resulted from concrete analyses done in particular on vertebrate evolution, can be summarized in a few sentences (1965, 1971, 1972 etc.):

– The evolution of the niche is the central process of all evolutionary change, and is the ultimate reference basis of evolutionary studies.

– New habits evolve in old habitats and open new ways of life, which determine the path of evolution.

– The reaction of the organisms depends upon the available preadaptations. Preadaptations provide the internal possibilities for fundamental changes, whereas the external conditions of the environment are decisive if they are realized.

– The origin of a group must be explained by a change of the mode of life in the ancestral lineage which became possible because of preadaptations, and by morphological changes as adaptations to the changed mode of life. Therefore, a good method for understanding ecological evolution is to search for the "ethological key innovations" which opened up a new way of life and stimulated and determined the formation of the group's "morphological key innovations".

– The history of a group of organisms can not be described or even explained in isolation. Some of the prerequisites for a species' evolution originate in the evolution of other groups. Evolving groups that offer new licences for others have been called "pacesetter groups" (Schrittmachergruppen). For example, terrestrial plants were pacesetter groups for the evolution of all terrestrial animals, and terrestrial arthropods were pacesetter groups for carnivorous vertebrates on land (tetrapods).

– Each result of an evolutionary sequence becomes both a condition and a prerequisite for the evolution of these organisms and also for organisms of other groups. It opens some new possibilities and at the same time excludes others.

– In a "phylogenetic sequence" each evolutionary step must be described as a consequence of a preceding step and as a prerequisite of a subsequent one. The evolutionary step must be shown to be adaptive. In other words, one must put things in terms of a "historical narrative".

– The result is a new group of life forms with a higher energetic level and a greater physiological (metabolic) and ecological efficiency, achieved with the properties of a new body plan that overlays the life forms which have existed up until then.

– Evolution thereby manifests itself as accretions, not as a series of successions.

– The "environment" is also subject to evolution (biosphere-based perspective). During the evolutionary process, both the biomass and its productivity increase as well as the variety of the biosphere and the number of life forms.

What can finally be observed in a holistic view of the history of the biosphere as addition of output, capacity and diversity might sound too general, too global or too seemingly trivial. However, it implies a concrete research program for detailed investigations. No species lives on its own. To the contrary, there are manifold interrelations between organisms with differing degrees of ecological interdependency and interaction. In mutualistic relationships these are very close when compared with those between any other members of a biocenosis. We call it "co-evolution" when different evolving species interact more or less in concert throughout the course of evolutionary history. If the ecological relationships between representatives of two groups of organisms are close, then they can mutually influence each other's evolutionary steps over a very long period of time. Examples for mutualistic relationships are the co-evolution of flowering plants and pollinating insects, for parasitic relationships that of mammals and fleas, and for predator/prey relationships that of pelagic sharks and teleost fishes in the oceans.

Every change in an ecological niche also has an influence of some kind on other econiches. From that point of view, "everything is co-evolution" or "co-evolution exists everywhere" (von Wahlert 1978a). No taxon represents a "closed system". The history of a group or the extinction of all of the species in a group cannot be understood by an investigation of those organisms alone. The task of evolutionary ecology must be to accurately analyze existing connections and dependencies and to elaborate evolutionary interactions when actually working with individual taxa. In order to accomplish this, different cladograms have to be correlated and the interrelations between different representatives investigated in all their details. As von Wahlert (1978a) said, the long-term objective is the reconstruction of the history of ecosystems.

Epilogue

In the 1950's and 60's, evolutionary biology in Germany rushed ahead of the pack and "answered questions that nobody had dared to ask before" (as A. Kaestner commented in a lecture from G. Osche), long before sound ideas about the phylogeny of respective taxa had been worked out. This was made up for in the seventies and later, based on the method of Hennig. The "phylogenetic period" continues. It appears that for some investigators, the reconstruction of cladograms has become an end in itself, especially since the break-throughs in the nineties both in sequencing techniques and in computer methods for analyzing sequence data. It is now high time to again pick up the thread of the "period of evolutionary ecology" which was molded by VON WAHLERT and OSCHE in Germany, although that approach must of course always go hand-in-hand with cladogenetic analysis, because it will then be based on more firmly founded phylogenetic hypotheses. It is certainly promising ground to till in the future.

Acknowledgments

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Gerd VON WAHLERT's Contribution to a Comprehensive Evolutionary Biology

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1. Introduction

"Evolution" can – and may be – defined in several ways. Students at the beginning of their scientific career are frequently irritated by the fact that there is more than one definition in use, not just of "evolution" but also of other terms central to biology, as e.g., "homology", "ecological niche", or "polymorphism". This picture of laissez faire and vagueness is certainly in part responsible for the poor reputation of theory amongst empirical biologists. However, a multifariousness of competing concepts is a clear indication of vividness and the capacity to improve.

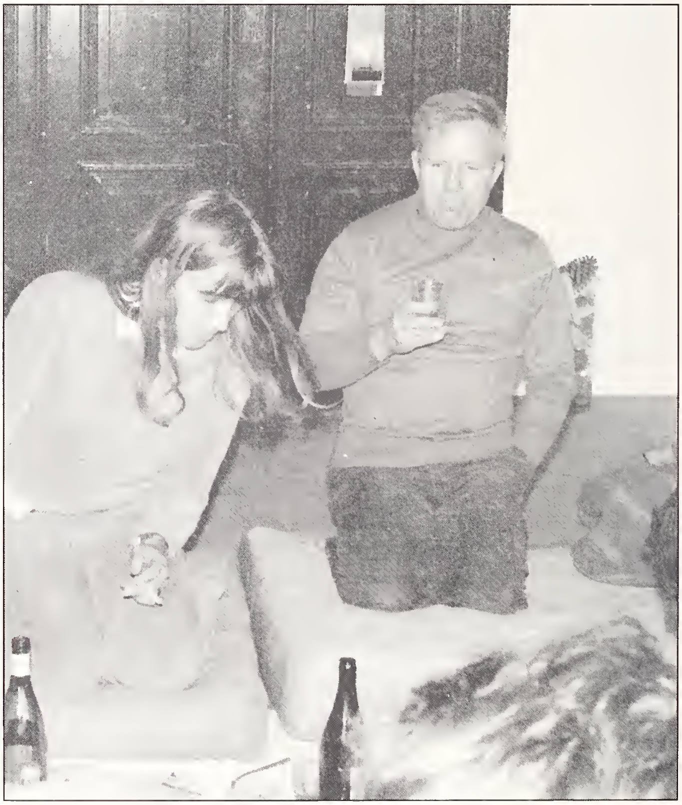
Adding a new definition or concept to those already existing could lead to the impression that confusion increases. To avoid this, I try to show the benefits and advantages of the new idea.

In Gerd VON WAHLERT's teaching at Freie Universitaet Berlin as well as in his publications of the 1970's, "evolution" was nearly necessarily "co-evolution". We, his students of this period, started under Gerd's supervision from the simple fact that no organism lives in a manner isolated from others. All life processes lead – directly or indirectly – to interaction with other organisms, be it reproduction or self-maintenance, let alone social behaviour or colonial modes of life. Therefore, it would be quite implausible to assume that synecological interaction were meaningless in the course of evolution (SCHMITT 1997). Consequently, we learned from Gerd VON WAHLERT that "evolution" always means "history of an organismic lineage" (as to discriminate from "evolution of a trait"), and since all lineages are more or less interdependent, "evolution" in its most comprehensive meaning is the "history of the biosphere". This conception of "evolution" was clearly not covered by the consensus of the synthetic theory of evolution, as it was in the end of the 1960's. Consequently, Gerd VON WAHLERT's view can – and perhaps must – be regarded as an extension of the evolutionary synthesis (SCHMITT 1994).

2. Gerd VON WAHLERT as an academic teacher

In 1969, Gerd VON WAHLERT received the venia legendi – the right to teach – from Freie Universitaet Berlin under special promotion of Klaus GÜNTHER. After Klaus GÜNTHER retired in 1969, Gerd VON WAHLERT became his temporary replacement in the summer, 1970. He gave a graduate course on the comparative anatomy and evolutionary biology of "lower vertebrates" (which meant in fact: on fishes). This course marked the beginning of a series of lectures, seminars and practical courses in which he taught not only a number of "normal" students but also stimulated a handful of highly motivated ones who became true VON WAHLERT addicts through the following six years (Gerd VON WAHLERT left the Berlin teaching staff in 1976).

We were fascinated by this unconventional teacher who occasionally sat on the desk and dangled his legs while lecturing on "recent developments in evolutionary biology" or "aims and way of searching in evolutionary ecology" (Ziele und Frageweisen der Evolutionsbiologie). To end our practical course on evolutionary



Gerd VON WAHLERT at the joint dinner after a practical course on "lower vertebrates" at a private home where we prepared and ate specimens of most of the species we had earlier as course subjects (left: Wiebke BERKING. M. SCHMITT phot.)

biology of lower vertebrates (*vulgo* fishes) in 1975, we had a joint dinner at a private home where we prepared and ate specimens of most of the species we had earlier as course subjects (Fig. 1). In his seminar discussions, he respected us as equal partners, which was far from common, even at the Freie Universitaet of that time. We were most impressed by the wide breadth of Gerd VON WAHLERT's scientific interests and his intellectual horizon. We discussed ARISTOTLE's categories as compared to KANT's as well as war and peace from a biological perspective. He sprinkled his lectures with remarks on characters and events, and he made science an entertaining adventure by his humour and his countless amusing stories.

Although we laughed a lot during these lectures and seminars, we also learned a lot about science as a social matter as well as evolution as the history of life on earth. First of all, we learned that the material basis of life is most important, that means: first comes food, then comes moral (freely after Bertold BRECHT's „Dreigroschenoper"). That is, we learned that viviparity cannot be regarded as the initial constituent of the evolution of the mammals: "By means of viviparity, no taxon changed its nature. This may have come on top of the rest and made – on my account – life more enjoyable, but nobody could live on that" (Vom Lebendgebären wurde keine Gruppe anders. Das kam noch dazu und machte meinetwegen das Leben schöner, aber leben konnte davon keiner. 30.09.1976). Or, we heard that "Birds are simply not strict lovers of flight, this all had to come first into existence historically" (Vögel sind doch nicht kondensierte Fluglust, das mußte alles erst historisch entstehen. 01.10.1976). Lessons like these sharpened our insight for the dependence of evolutionary changes in an organismic lineage upon changes in its relations to its environment. These changes had not necessarily to be provided by the abiotic conditions but could as well consist of improvements of intraorganismic processes or, more often, by transformation of the relations to other organisms. The only thing that counts is producing more viable offspring per energy input. This led to the theoretical foundation by BOCK & VON WAHLERT (1965) who emphasized that the interrelations between an organism and its environment (or rather „Umwelt"), the "synergs", can be optimized by improvement of the organismic as well as of the environmental side.

BOCK & VON WAHLERT (1965) called the sum of all "synergs" (units of interaction between organism and umwelt) the "ecological niche". This definition was at odds with common usage but agreed completely with Klaus GÜNTHER's (1950) concept of "niche". Here, "the niche" is constituted where two dimensional systems cover: the "autozoic" dimensions of a species and the "oecic" (i.e. environmental) dimensions of a biotope. Thus, a "niche" is a system of relations rather than a space which can be occupied. Consequently, empty niches are logically impossible (SCHMITT 1987).

In Gerd VON WAHLERT's view, evolution is – first of all – a historical process. From there it follows necessarily that "laws of evolution" are meaningless, as are "laws of history". They are fictions produced by the human mind, and the same applies to "evolutionary rates" (are there "rates of history"?). It also means that evolution cannot be explained by stressing "laws", i.e. by means of "nomological-deductive" explanations (BOCK 1991, the concept based on NAGEL's, 1961, differentiation between nomothetic and ideographic sciences, which itself refers to WINDELBAND's terms "nomothetisch" and "idiographisch", 1904). Second, "evolution" was nothing an organism could produce on its own. Rather, it was a collective act, performed by changing niches, i.e., interaction systems of organisms and their environment which includes naturally also other organisms. In total, evolution had to be seen as the history of the biosphere, the living world. And third, "evolution" is characterized by an increase of possibilities to exist and an increase of biomass production.

Independent of the question whether or not these statements can be tested in a Popperian sense, or whether or not they hold true in the light of traditional theories on evolution as well as new evidence, they directed our thinking. They were unorthodox and inspiring, they were plausible and – in a way – "politically correct", they met our desire for new and dynamic approaches. Observing real interaction between organisms, interpreting their features in terms of ecological roles, searching for the biomass production of a newly evolved ecosystem as, e.g., a marine reef community, seemed much more rewarding to us than memorizing "evolutionary rules" or dental formulae.

On the other hand, we realised from time to time that we were fascinated by Gerd VON WAHLERT's ideas but could not defend them against objections from a "traditional" view. That means, we were persuaded by his brilliant rhetoric but had some difficulties in internalising his ideas. In addition, we had not the informational background our professor had. And much later we learned that Gerd VON WAHLERT's convincing visions not infrequently suffered from a certain lack of clear and sharp definitions. That is, if an ecological species is defined as the collective of organisms establishing an ecological niche, and the ecological niche is defined, in turn, as the sum of all synergs of a species, then how to avoid circularity? Even defining a niche as a "not yet split ecological zone" (VON WAHLERT & VON WAHLERT 1977: 215) does not remedy this weakness, since a zone is thought to be the sum of the interactions between the environment and a group of species (l.c.). To us, the limitations of Gerd VON WAHLERT's concepts did not lessen their inspiring power.

In discussions, we regularly heard him speaking ready for the press, and we were deeply impressed by his ability to produce perfectly long and complicated sentences using foreign words from several living and dead languages. However, we made the experience that his performance became even more exciting and convincing when we opposed him. And so we did, as often as we could. Not just that we learned a lot from these discussions, we also enjoyed them. In part, they eliminated our uncertainty when arguing with other students and professors on Gerd VON WAHLERT's ideas.

Through Gerd von Wahlert, we students came into contact with the ideas of Klaus Günther and Willi Hennig and had, consequently, a much shorter way to evolutionary ecology and phylogenetic systematics than students just completing the normal academic curriculum. At that time, Klaus Günther and Willi Hennig were still alive but poorly acknowledged by contemporary colleague professors.

Klaus Günther had his office still at the Institute of Zoology but did rarely show up. Before learning a different story from Gerd von Wahlert, we had the impression – nurtured by the narrations of older students and younger professors – that Klaus Günther was an odd fellow whose great merits lay far back in the past and who then was just remarkable because of his English gentlemen-like outfit. Gerd von Wahlert told us many a story about Klaus Günther's stunning abilities, his fantastic memory, his admirable knowledge in so many fields of science and literature, his sharp intellect and his extraordinary rhetoric art. Moreover, we heard about the important contributions Günther made to evolutionary ecology, first of all through his concept of "ecological niche", but also – and perhaps much more recognized by the scientific community – by his review papers of 1956 and 1962.

In contrast, Willi Hennig was sketched as an important German scientist who was widely ignored by "the Americans," but his method was rarely explained in a competent way, let aside applied. Although Gerd von Wahlert was certainly not the most prolific phylogeneticist, he fairly taught us about the theoretical background and the practical application of Hennig's concept (e.g., 1950, 1966).

Since Gerd von Wahlert did not only talk about animals and plants when teaching evolutionary biology, we learned a lot from other fields of knowledge. Most impressive was his advice for discussions with opponents who adhered to a hermetically-closed philosophy of life, e.g. fanatic communist fellow students who tried to convince us of their political goals. Gerd said: There is only one solution if you cannot beat the logic of your opponent - attack the premises. This lesson held true not only during our student days and when discussing with political opponents but is very useful in all fields of social life up to the present.

Another aspect worth mentioning is Gerd von Wahlert's basically philanthropic religious attitude which influenced also his scientific thinking. In the 1960's and 70's, "critical" was the general device for all our approaches towards everything, be it authority or theory. Nearly inevitably, we heavily criticized Konrad Lorenz's theory of aggression (Goldau et al. 1974; to be certain: I still stand by our criticism). Under these conditions, Gerd von Wahlert wrote an article on Lorenz's ideas which he described as an apologetic attempt (1974). I admit that I had to look up "apologetic" in my dictionary but then I learned that it is not only fair but also clever to approach an idea you do not know in a way that warrants first to understand what is meant before criticizing it. At that time, I developed a deep respect towards this attitude which has a strong affinity to Gadamer's "hermeneutics" (1965).

3. "Evolution" as taught in the 1970's

Conventionally, "evolution" was seen as a process caused and steered by the interaction of approximately five so-called factors (mutation, selection, isolation, recombination, and genetic drift, sometimes also "annidation", e.g. SAVAGE 1963; STEBBINS 1966; REMANE et al. 1973). "Annidation" was introduced by Wilhelm LUDWIG in 1950 as "a fifth evolutionary factor" (ANTONOVICS 1990). The basic conception behind this list of factors seemed to be that an inert mass – the organisms – had to be moved by external forces – the evolutionary factors.

Gerd VON WAHLERT drew a picture of the organism as an autonomous being, bringing about the necessary events and forces for evolution by themselves. He put emphasis on the synecological relations between the organisms, underlining that all organisms are part of the environment (or rather "umwelt") of others. It has to be mentioned that Gerd VON WAHLERT did not ignore the importance of abiotic environmental factors. He did not even intend to show them as less powerful. He just wanted to make clear that a picture of evolution ignoring or underestimating the power of biotic environmental factors is incomplete, if not false.

In our genetics courses we learned that evolution is "change of allele frequencies". At that time, molecular techniques were in their beginnings. Thus, allele frequencies could only rarely be demonstrated directly. In most cases, one had to infer them from the frequencies of phenotypic characters that were inherited according to MENDEL's rules. Consequently, the strength of the conviction that evolution is change of allele frequencies stood on a rather weak empirical basis and depended nearly exclusively on general deductions from the concept of an "ideal" population, ruled by the Hardy-Weinberg formula. "Evolution" was caused by deviation from the "ideal" conditions (absence of mutation, absence of selection, infinite population, panmixis). Therefore, "evolution" was a mechanical process that could be described and explained, in principle and quantitatively, by using the methods of population genetics.

In Gerd VON WAHLERT's view, change of allele frequencies was a corollary or a prerequisite of evolution but does by no means allow to see and explain the whole of evolution. Why did some characters act as key innovations leading to a larger adaptive radiation while others did not, although the genetic mechanism behind is the same in both cases. How are the assumed genetic changes connected to the (quasi-) observed ecological changes (In fact, only ecological differences can be observed, the changes leading to the observed status are inferred). Questions like these were much more intriguing to Gerd VON WAHLERT and to us than fitness coefficients or calculated "rates of evolution".

While in traditional German textbooks "evolution" looked like a mere series of transformations of the organisms' exterior through the ages, Gerd VON WAHLERT described evolution in terms of production of biomass under most economic use of resources. From here, it was only a minor step to the human management of natural resources, especially in mariculture, a field where Gerd VON WAHLERT worked for many years (VON WAHLERT 1992).

4. Explaining and understanding evolution

The central theme in Gerd von Wahlert's publications is to explain and to understand evolution. How one evaluates Gerd von Wahlert's attempts at explaining and understanding depends on one's claims to a satisfactory explanation and one's conception of "understanding". To answer the questions: "Why are there no diurnal prosimians on mainland Africa' by the statement that "the adequate mutations did not occur"; or "How did mammals evolve" by the conclusion "through mutation and selection," may be correct, but will not satisfy most students and lay people. Equally, it might be flawless to explain why there is light in my room by the physical details of electricity and theory of light emission. However, this is not the only possible explanation, and it could be far more important to know that the light is on because I switched it on since otherwise it would be too dark to see what I write.

Gerd von Wahlert clearly regards the latter type of explanation adequate for the interpretation of evolutionary events. He introduced the principle of causality into evolutionary biology by his claim that an evolutionary history is regarded explained if the emergence of one group of organisms from an older one can be interpreted as a change in the mode of life and if the morphological transformations can be shown to be adaptations to this change in the mode of life („Ein Evolutionsschritt wird als erklärt angesehen, wenn die Entstehung einer Gruppe aus einer älteren durch eine Änderung der Lebensweise gedeutet werden kann und die dann erfolgten morphologischen Änderungen als Anpassung an die Änderung der Lebensweise dargestellt werden können." 1968: 115). Such a set of statements was called "phylogenetic sequence" by von Wahlert (1968: 115), or "phyletic sequence" by von Wahlert & von Wahlert (1977: 23). Bock (1991) calls this type of explanation "historical-narrative" and deems it as different from the "nomological-deductive" type.

I leave the question open as to whether or not the difference between "historical-narrative" and "nomological-deductive" explanations is real in principal. Likewise I do not discuss whether "historical-narrative" explanations are proper explanations or mere "descriptions" (Mahner & Bunge 1997: 111). As long as we find an explanation satisfactory, it may be a "subsumption" or a "description" or an "explanation proper" in the terminology of Mahner & Bunge (1997). Since all explanations can be questioned regardless of their type by asking for an explanation of their *explanans*, none of the above types is a priori more satisfactory than an other. In part, it is a matter of personal preference at which level one stops further questioning.

As with the example of the burning light, most people are regularly more satisfied by historical-narrative explanations than by nomological-deductive ones if unique historical events or processes are considered (cf. Schmitt 1997). Just therefore, historical-narrative explanations are legitimate, notwithstanding possible theoretical flaws. Even if we call a historical-narrative explanation a "description", it differs from countless descriptions of evolutionary histories in traditional papers on evolutionary biology (e.g., REMANE et al. 1973) in that it asserts a cause-effect relation, while the latter do not. Thus, as BOCK (1991) pointed out, also historical-narrative explanations are causal explanations.

Gerd VON WAHLERT's papers on the evolutionary history of certain taxa (e.g., on flatfishes in 1961, *Latimeria* and the vertebrates in 1968, insects in 1975, the animals in 1977 and 1981) or on phylogeny as an ecological process (1973), on co-evolution (1978a), or on evolution as the history of the biosphere as an ecosystem (1978b) are models of the use of historical-narrative explanations. Always in these papers, evolutionary processes are explained by demonstrating that every step is the consequence of a preceding one and the prerequisite of a following one. The pictures of these chains of events appear plausible and informative. As long as they are based on sound phylogenetic hypotheses on genealogical relations and on pertinent nomological-deductive explanations, they are "scientific under the criterion of demarcation for scientific explanations advocated by Popper" (BOCK 1991: 11). Even if in some cases Gerd VON WAHLERT's "narrations" do not take all available data into account and are therefore weak or definitely false, they show the line one should follow in attempting satisfactory explanations.

Quite often Gerd VON WAHLERT emphasizes that consideration of synecological interaction as well as historical coherence is necessary for a comprehensive understanding of evolution (e.g., repeatedly in VON WAHLERT & VON WAHLERT 1977). This could be irritating because the concept of "understanding" as a scientific method was worked out by DILTHEY (1910) as a possibility to establish the role of the humanities (Geisteswissenschaften) as sciences (*sensu lato*). According to DILTHEY, the central aim of the sciences (*sensu stricto*) is to explain their subjects, while the humanities seek to understand them. Here, "understanding" means to find out the sense in an observed phenomenon. Hence, one can only understand a phenomenon if there is sense in it. Since in modern science we agree that there is no "sense" in nature, the concept of "understanding" *sensu* DILTHEY is irrelevant in evolutionary biology. However, MAHNER & BUNGE (1997: 105) state that "Like every other scientific discipline, biology aims at understanding its subject matter", and they continue "In any of its modes understanding involves systematizing, that is, we either fit the given item into our preexisting cognitive or epistemic framework, or we transform (e.g. expand) the latter to accommodate the new item".

In following Gerd VON WAHLERT's approach, we find that his perspective on evolution as the extension of synecological interaction into geological time, i.e., "co-evolution" reveals a meaning of every evolutionary event within a broader framework. Every feature, every organism, every species, plays a certain role in an ecological and evolutionary network (similar to MAHNER & BUNGE's outline of the relations of different concept of function, 2001: fig. 1). This role can be regarded as analogous to the "sense" which can be traced. Therefore, Gerd VON WAHLERT's approach to explaining evolution can legitimately be termed "understanding evolutionary biology" (verstehende Evolutionsbiologie).

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An Outline of an Explanatory Life History

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1. Of Fish and Men

In the invitation to this symposium I am called an outsider. That brought to mind the caption of a cartoon I once saw in, I think, The New Yorker. The drawing showed an office and the text read: "Yes, we are a Non-Profit Organisation. We hadn't planned it that way but that's how it turned out". I did not plan to leave the well trodden paths more than any other young and enterprising scientist does. But, with a family tradition of not accepting an opinion just because it was widely held, after five attempts (four failures, one hit) to get formal entry to university lecturing and about ten consecutive failures to gain a professorship, I came to particularly like one poem by Robert FROST. The poem ends:

> Two roads diverged
> in a yellow wood, and I –
> I took the one less travelled by,
> and that has made all the difference.
> (from "The Road not taken" in "Mountain Interval", 1916 in 1973)

(At the invitation of Ernst MAYR, I spent the Academic Year 1957/58 as a Research Fellow at the Museum of Comparative Zoology at Harvard. During this time we lived at 56 Frost Street, and Walter and Kitty BOCK at 1A.)

The road I followed teaches patience and requires some stubbornness. Let me illustrate this.

In 1961 KAESTNER, at that time one of the most influential zoologists in Germany, refused to have a paper of mine published in *Die Naturwissenschaften* (the German equivalent of *Science*) which its editor, another Big Shot, had commissioned and accepted shortly before his unexpected death. In this paper I described my view on the origin of flatfish as transformed groupers. Some groupers rest on their sides when sleeping on the bottom. Flatfish have retained this habit as an ambush position on sand flats, a habitat without hiding places. I saw such a change of behaviour and the ecological relations as an "ethological key character" initiating the selection forces which resulted in the asymmetry of external and internal features. The most notable of these were the shifting of one eye and the distinct coloration of the functional upper and lower sides. This asymmetry (an intermediate stage is preserved by the Indian Ocean "Perch Founder" *Psettodes*) I described as "morphological key character." The combination of ethology, ecology and morphology applied here – at that time and for some time subsequently, they were quite separate fields – I had called "Evolutionsbiologie" (evolutionary biology). KAESTNER wrote to me, "There is a way of describing evolution which is phylogenetics, and an experimental one of explaining it – genetics. There is no room, nor need, for what you call evolutionary biology". The Bonn meeting and this volume show that there is.

The plans for the Bonn Symposium came to me as a surprise, and when it took place it was almost overwhelming. I had gone to Bonn braced for obsequies with kind eulogies which I would have the privilege to attend while still alive. Instead I found a group of colleagues and former students joyfully recounting that my work had been recognised and my ideas were being employed. This was listened to by an attentive audience drawn from the various fields in which I have been busy. When Michael SCHMITT asked for my consent to the subtitle "Understanding evolutionary biology", I was very happy with this formulation since I deem understanding to be more than explaining (the German equivalent is an adjective only, as there is no gerund). So I wish to repeat here my deep gratitude to the initiator and convener, all the contributors to and participants in the Bonn Meeting with another verse of Robert FROST:

> Lives there a bard who isn't moved
> When he finds his verse is understood
> And not entirely disapproved
> By his country and his neighborhood.
> (from "On Being Chosen Poet of Vermont" in "In the Clearing", 1962 in 1973)

As documented in this volume, Günther OSCHE has reviewed the setting in which – or against which – he and I developed our understanding of evolution, seeing us as "Evoluzzers" – revoluzzer is a German expression, slightly ironic, for revolutionaries – among initiated "Phylognostics". Walter SUDHAUS has described the contemporary scene in evolutionary thinking, footing on, but expanding, what he has said in his (and Klaus REHFELD's) textbook (1992). Walter J. BOCK has taken this opportunity to analyse interactions, a key notion in the understanding we share. Hartmut GREVEN and Klaus LUNAU testified how "the march is going on". Michael ("Theo") SCHMITT covered the personal aspects of a teacher-student relationship and set, in so doing, the tone for what I added in my response. In this written version, I have kept to a personal perspective and a lighter vein rather than attempt to produce another scientific paper - as will be quickly seen.

Here is another example of the need for the patience which I have been forced to develop. In 1967 (published 1968) I demonstrated my *Latimeria* to the Annual Meeting of the German Zoological Society, the only specimen ever supplied to a German institution for research purposes. I showed that the second dorsal and the anal fin, both "lobe fins" with an archipterygium skeleton, rested sideways in axil-like pits and that they would rotate through 90° when pulled up by hand into their working position. Some fast swimming fishes stow fins away in pits like aircraft their undercarriage wheels. So I assumed that *Latimeria* used these fins at slower speeds. Moving the fins by hand, I demonstrated that they would propel the fish, and, since the paired fins – pectorals and pelvics – were of the same anatomy, I ascribed to them all the same propelling function. I therefore called the second dorsal fin and the anal fin the "third fin pair" acting in the same way as they do in triggerfishes, trunkfishes and others. This implied that these fins were not primarily, if at all, props on which *Latimeria* rested or crawled on the bottom, as had been assumed in a rather typological backward projection from the tetrapod condition. When I had finished my presentation, my wife overheard two leading professors of Anatomy and Ichthyology respectively. "Do you believe that?" asked one. "No" replied the other, "but this Wahlert has always wildly indulged in fancies".

When I somewhat later wrote my *Latimeria*-book (1968), I could refer to a report, meanwhile published by the photographer Jacques STEVENS in the magazin LIFE. It contained photographs of a free swimming *Latimeria*. Ichthyologists at once criticized the report and denounced STEVENS' photos as faked, accusing him of having used a dead specimen or even a rubber model. I judged the photographs to be genuine. If STEVENS had made up his story, he would certainly have put his fish on the bottom resting on its fins, since this was the generally-held view of the creature. He described the same propulsive action of the second dorsal and anal fins which I had postulated, but which no-one else had even assumed. This I wrote to STEVENS and learnt from him that he had, as I and others had suspected, released a captured *Latimeria* in shallow water. The editors, however, had changed his text so that it suggested his observations and photographs had been made in the dark great depths of the ocean. STEVENS was overjoyed to receive my letter, since I was the first and only expert who did not call him an outright swindler. For my Latimeria-book I used STEVENS photographs to make a drawing of the swimming fish, and included in the drawing the skull and the fin skeletons. This drawing was used both on the cover of the book and now as the Logo for the Bonn Meeting. During his pioneering and daring dives in a submersible twenty-five years later Hans FRICKE found and filmed any number of *Latimeria* at the Comores (and recently some in Indonesia). He documented and described their locomotion exactly as I had predicted and STEVENS described it. However he claimed then, and still does, that no-one had ever thought *Latimeria* moved this way.

In our mariculture work – more about it later – the time span from snide smiles and ridicule to confirmation and general acceptance was only ten years.

2. A Living Fossil Concept

At this point I want to take up the topic Günther OSCHE has so knowingly reviewed. The subject matter for my thesis had been given to me by Professor Wolf HERRE in Kiel. He expected my research would show that evolution of the (ovo)viviparity of salamanders could not have proceeded solely by "mutation and selection" as the theory of evolution was usually presented. Was not viviparity a major achievement, as it marked out, typologically speaking, the "highest" class of animals there is, the mammals? Alas, my study showed that all the structural and functional elements for (ovo)viviparity existed in egg laying urodeles, and only needed to be extended or changed in gradual steps. These steps would be covered by the range of genetic changes which even Adolf REMANE and Wolf HERRE, both in Kiel, acknowledged as existing and being covered by the Darwinian theory.

The views on evolution of German morphologists were founded on two basic and categorical distinctions: between "microevolution" and "macroevolution", and that between "speciation" and "transformation" as the vectors of phylogenesis which together produce the branching of the phylogenetic lines and their "anagenetic" progress. The mechanisms of mutation (variation) and selection were accepted and credited with explaining microevolution, the origin of new characters and perhaps even species. But they were not accepted or credited with describing macroevolution, the process of major and constructive transformation and its most conspicuous aspect, anagenesis (the increase of morphological complexity), or with the origin of types, and hence the visible, or at least the apparent, "progress" in evolution. The geneticist Richard GOLDSCHMIDT with his "macromutations" was seen to point to that gap in our understanding but not as providing an acceptable answer. From early on, my position was that the search for morphogenetic factors, or mechanisms of a higher order, was not warranted as long as correlated or corresponding functional and ecological factors were not considered. This I had done in my thesis by simply following G. K. NOBLE who had already used this approach in 1927 in a paper on "the value of life history data..." and elaborated it in his "Biology of the Amphibia" of 1930. Although Professor HERRE owned this volume he had never employed it's course of thinking as he was, like other German morphologists, unable to translate his reservations about DARWIN and his followers into a concrete research strategy in order to overcome the shortcomings which he, and they, felt were inherent in the whole approach.

Let me illustrate this with another anecdote. Around 1960, I wrote a paper saying that the body shapes of skates and rays were not an adaptation to benthic life in general – elasmobranchs had originated as bottom living forms, their pelagic forms evolved within their suborders. Batoids, I claimed, had broadened their fins for digging up their prey and for burying themselves, and one line took to using their broadened disk for propulsion. There is a complete series of extant(!) batoid forms representing all stages of this transition, whose outcome can be seen as both a morphological series and an adaptive radiation. I sent the manuscript to my former professor, and he wrote: "Your paper is well written, easy to read, and very convincing, which is not to say that I believe you are right. I lack the detailed knowledge of fossil batoids to judge it really, but your solutions are always so simple. Exactly that startles the true biologist". And from a reliable hearsay source I learned that the same professor had said at least once: "This Wahlert always wants to explain everything".

This and similar experiences helped me to realise that this school of German zoologists did not want to have macroevolution, the greatest life phenomenon, and with it 'Life' at large, explained at all. They knew, or acknowledged, nothing beyond their science and had to satisfy whichever metaphysical demands they felt within their biology. This led to a concept of biology shielded against a rational investigation of its fundaments and basic tenets. What GOETHE had called the "secret laws" was in force and still is. In this view I have been confirmed recently by Dominique HOMBERGER. In 1999 she spent a few months in Germany, for the first time, and got to know some of our German morphologists. Being Swiss (from Zurich, where she also took her degree) she speaks German as any of us but knew nothing about the range of German mentalities. She summed up her impressions to me in much the same way as I have just outlined; views were presented not as testable hypotheses, or theories, but as having been already accepted on the a priori basis of a deeper knowledge. Understandably, this had considerably startled her. What now startled me was that my experience of long ago was being experienced forty years later by a competent and unbiased observer who had never been in direct personal contact with me before – we had previously heard of each other only through Walter J. BOCK.

I was able to put her experience into context by drawing her attention to a recent book of K. FLASCH, a German historian. The author describes and analyses the support given to the German cause at the commencement of the Great War in 1914. The openly anti-British stance taken by an impressive number of German scholars, among them well-known persons of the highest academic reputation, led to rather typical utterances such as that the „abendländische Kultur von der englischen Zivilisation genesen sollte" (the culture of Europe should recover from the English civilisation). This is exactly the anti-British sentiment which, I am sorry to say, was (?) typical of German conservatives, and was conspicuously affecting the way in which DARWIN's work, and the results of its elaboration, were presented to German students in my time. And this attitude is, in my view, the main reason why the "modern synthesis" of evolutionary theory took so long to be accepted in Germany.

Since this issue has become much debated in recent years, I wish to put on record two further observations. I do not see that German biologists can be credited with having arrived at a similar synthesis on their own, even if many of its elements were available to them. Neither do I see the Anglo-American "modern synthesis" as a true (= complete) synthesis at all because of its conspicuous lack of the ecological, ethological and morphological aspects of evolution. In his contribution to this volume, Walter J. BOCK mentions the alliance of studies in ethology, ecology and evolution. This is a welcome and timely, but recent step towards a synthesis which is truly deserving of the name.

Throughout my professional life I have tried to promote and apply the combination, or rather merger, of the approaches and perspectives of functional morphology into ecological morphology, including ethology. In this presentation I will sketch some of the main insights this strategy has yielded. But before I do so, I will say a few words on the mariculture work already mentioned, as well as some other issues.

3. Science Societal

In my second or third term at Kiel University, my professor and two other biologists together with three theologians formed a group to discuss 'Science and Faith'. With other students, I was invited to participate. I have kept up this discussion with various partners throughout my professional life in private talks and informal meetings as well as in formal assignments; these included teaching at Heidelberg School of Theology, the Graduate School of Ecumenical Studies of the World Council of Churches and Geneva University, and a host of memberships in interdisciplinary or church bodies of all kind.

In my year at the Ecumenical Institute (1972/3) near Geneva I came to the conclusion that churches and biologists can do more than talk about, or to, each other – they can work together. Following the publication, in 1972, of the report of the Club of Rome "The Limits to Growth", the churches wanted to say something on Man and Nature. They had done pioneering work in education, health and the social field, run schools and hospitals, employ educators, doctors and nurses, and social workers and thus can speak up (and do) in matters of education, private and public health, and social questions. But were there any biologists in the service of the Church? There were none.

At this time, one office of the Ecumenical Council, which was working for development aid, asked me to evaluate plans for a mariculture project submitted by a church agency in Hong Kong. On the basis of my report the plans were implemented. This was the beginning of work which led to the establishment of other projects: one in the neighbouring Shen Sen area of the People's Republic of China (at their request, and before the talks on the future of Hong Kong had even begun), Indonesia, Papua New Guinea, the Philippines and in India. Our aim was to improve the situation of village fishing people in the transition from subsistence to a cash economy. They were suffering from the impact of commercial, mechanized and industrialized fishing both on their own fate and that of the fish stocks. We took as our slogan: "You need more fish in the sea if you want more fish in nets and pans". In order to raise the number of fish in the sea and not just the catches from it, we recommended, and helped to install, man-made hides as feeding and breeding places housing both young and adult fish of some kind and attracting others. Building floating or anchored artefacts from bamboo and other bush material had been widely known on tropical coasts all over the world. However, the fishery sciences, which had originated in the Northern Hemisphere with its cold seas, were all but ignorant of this technique as they were of the biological conditions in these seas and the social conditions of the people living in the tropics.

Our mariculture work meant a change from an economic understanding of production (what fishermen catch) to an ecological one (what grows in the sea); it was based on the notion of sustainability, and it moreover asked for a widening of the concepts of development. These had been anthropocentric and focussed on economic questions and aims; churches credited themselves with advocating human development as the first goal, and hence social issues; but they also had so far overlooked ecological facts and conditions and, in their theological and clerical anthropocentrism, our responsibility for our fellow creatures. The member churches of the ecumenical movement recognized this increasingly as a genuine theological challenge. We advocated a "learning by doing", calling our mariculture work a "stewardship of all creation", and the approach at large "doing theology".

Although my activities in this field were initiated by a commission from the World Council of Churches, their Ecumenical Institute, where I worked as Associate Director and Professor of the Graduate School of Ecumenical Studies, was not ready to support or even tolerate them. The Institute was headed by an Orthodox Professor of Dogmatics who recoiled from this pragmatic inroad into theology and my relational thinking. Thus my hope to establish a co-operation between the Churches and Biology in the Ecumenical Institute vanished and I had to leave. However, I was able to pursue these plans in Stuttgart and saw them come to fruition in the way I had envisioned.

To this end my wife and I conducted a feasibility study from January to June in 1978, which preceded the spread of our programme, throughout parts of Asia and across the Pacific. The study was commissioned by the Federal Government, and we were able to win the support of local and regional churches and church councils on the basis of the contacts we had made in Geneva. We visited fifteen countries where we told the fisheries administrators about our plans. We talked of fishing villages, not commercial enterprises; of extensive, not intensive "high-tech" mariculture; of fishing based on local knowledge and on the traditional understanding of the relationship between man and nature, and all that as an integral part of community development and not just a technical scheme. The usual response to outlining our programme were smiles indicating that our listeners judged our efforts to be so much ill-timed romanticism. However, in 1988 we attended an International Conference on Artificial Reefs, supported a motion renaming it as a "Conference on Artificial Fish Habitats" and voted for a declaration that the installation of these habitats was the state of the art for the enhancement of ecological diversity, animal life and fish stocks in coastal waters.

At the time of writing this paper, the call for a sustainable use of the world's fishery resources is being widely heard, but far from being heeded. Fishery development is no longer seen as just an economic issue. It is now being seen as an ecological issue with a social dimension, since it has yet to be seen who catches the fish and who gets them. The industrialised nations of the North take a disproportionately large share of world catches for their populations, who are over-fed with animal proteins. In tropical countries such as Indonesia and the Philippines, the population depends on fish for around 50% of its dietary protein. But they, along with the other non-industrial countries, get only 25% of the global cashes, of which the industrialized countries get 50%. This inequality is one outcome of the globalisation of world fisheries which was in operation well before the term became generally known. Even though this, and other, uneven and unjust allocations of global resources reached the World Economic Forum in Davos in the year 2000, there is little hope that the situation will be remedied in the foreseeable future.

During these years we had come to believe that Western Science has become, willing or not, dominant over Man and Nature, and that a good many, or rather too many, scientists were, directly or indirectly, in the pay of vested interest and part of this dominance. We allied ourselves with the little fishes, literally and metaphorically, and lent our efforts to support such organisations as the International Movement of Small Scale Fishermen and Fish Workers.This movement was founded in India and has spread across the world. This in turn helped us to find financial support from the German churches and their development services, and to use their international ecumenical links and logistics in addition to those we already had. In Indonesia we worked on islands north of Sulawesi which were all Christian, as was the case in Papua New Guinea and the wider Pacific. Apart from other reasons for working with churches this cooperation had one obvious advantage which made it nearly compulsory: churches were – and are – part of the village life in communities which governmental programmes would not reach, nor we on our own; and they were more flexible and open for new approaches, particularly in rural and community development, than government agencies were and, thanks to their international partnership and cooperation, also financially able to implement and support them.

Our work in this field was based on our observations of fish behaviour and ecology starting in the Mediterranean in 1956 and then in 1958 in the Caribbean (VON WAHLERT 1960, 1961, 1962, 1963, 1963). From 1968 onwards we worked in the Gulf of Aqaba in Eilat and along the Sinai coast (VON WAHLERT 1969). In Eilat I had found the jetty of the new yacht harbour on the North Shore already colonised by a number of corals, echinoderms and molluscs – much to the surprise of Professor Heinz STEINITZ, the founder and director of the Eilat station of the Hebrew University. I won him over for the plan to monitor the development of this artificial reef and to study other places as well, provided I could find both a suitable person and the necessary funds.

The person I found in Heidelberg – Helmut SCHUHMACHER, who was one of the students in a seminar at the theological faculty which a well-known theologian and myself conducted on ‘Creation and Evolution’. SCHUHMACHER had just finished his biological thesis on a fresh-water theme but had, as I knew, saltwater and diving experience. SCHUHMACHER accepted my proposal and obtained a post-doctoral grant. He made a thorough study of the subject and has since become the leading expert on both natural and artificial reefs. He makes his own contribution to this volume. The general outcome of these studies in the Red Sea has been the linking of evolutionary and production biology, which has increasingly gained a central role in my understanding of evolution. Our mariculture activities seemed to take me way off from my academic fields, not only geographically speaking, and appeared remote from my main scientific concerns, but they have turned out to be exceptionally rewarding and germane to these interests (see VON WAHLERT 1977, 1979, 1986, 1987, 1989, 1992).

I wish to put on record here my gratitude to my colleagues in the Stuttgart Museum for their understanding support of my work. Those in the Vertebrate Section were all experienced in field work overseas for wild-life protection and conservation. They knew that in our times museum people have a primary duty to help the conservation of animals alive, not only as dead specimens, and thus their habitats too. When I set up an "Alternative Mariculture Co-ordination Centre", I made it clear that we must gain an understanding, and win the co-operation, of the people who live near or on coral islands and such coasts if we wished to help save coral reefs. We recognised that we would not get anywhere unless we understood their needs and assisted to satisfy them. Hence we worked with and for the fishing people, and in so doing we were rewarded in what they taught us. From the outset we considered them as "resource persons" and not a "target group" as no-one can "develop" other people. (However, we did have a "target group" – the fishery and development experts). Thus our "Stuttgart Double Strategy" became: to work with the fishing people and for the coral reefs.

We already knew from experience what "ordinary" people can teach the experts. While at Harvard in 1958, I discussed with R. C. STEBBINS, at that time the leading expert on American salamanders, how little we knew of how South American salamanders reproduced. Later that year I was taken by a Catholic Priest on a field trip in Columbia, and we collected a dozen of these creatures. He gave me a copy of a Colombian journal, of whose existence we had been ignorant, in which he had described, from his own observations, their mode of reproduction. These creatures bury their eggs in the wet river banks and leave them there to develop and hatch. When we returned to our hosts, their Indian maid saw them and said: "Oh, these salamanders (she called them "Lagertos" – lizards) bury their eggs, and when the young ones come out neither father nor mother look after them". I can still hear her: "ni padre ni madre".

Even before this experience there had been a similar one. Hans HASS, the diving pioneer, had claimed that sharks can be repelled by shouting. (In 1940 I had attended, in Berlin, an event where HASS had fascinated a spell-bound audience with his tales and slides from his and his friends' first underwater adventures in the Caribbean Sea – with obviously a lasting effect.) The experts said it could not work; all their textbooks had it that sharks are deaf. I went into the exhibition halls of the Bremen Museum – a museum for Natural History and Ethnology – and patted the coconut shell shark rattle which I used to point out everytime I showed people around; Pacific fishermen use them to attract nurse sharks and others, and I had published two small papers mentioning this method (VON WAHLERT 1959, 1960). If a shark comes, the fishermen put a noose around its gill region; attached to the other end of the rope is a propeller carved from wood. As the shark swims off, the propeller turns and tightens the noose, eventually strangling the fish which is prevented from sinking by the buoyancy of the wood. "Poor things", I told the nutshells, "books say you don't work". But fishermen knew.

The full extent and weight of what fishing people knew became known to us a few years later. In the Pacific we learned that fishing ground were common property as were the land. No private person or family could be the owner of what belonged to the village. Fishing was regulated by unwritten laws, wich imposed, for instance, restrictions for when, where and how fishing was allowed. Fishing grounds within easy reach were reserved for women and children, open for men only under bad weather conditions. The "tragedy of the commons", the over-exploitation by individuals taking a disproportionate share, was thus avoided. With the arrival of cash economy and with it outboard-motors this system has collapsed. Similarly we met in Ghana with fishery regulations which also prescribed where boats were allowed at all, which gear could be used, and when a fresh water lake were open or closed to fishing. Here too such provisions to maintain a sustainable fishery are doomed - in the same time when worldwide the need begins to be felt to see the oceans as a common heritage of all mankind and to establish a regime securing its future as a common resource.

4. Science Political

This is another issue of a more general nature that I want to raise, and once again I have to start with my student days in Kiel. In 1949 the LYSENKO debate reached Germany, although it did not amount to much of a debate in East Germany and East Berlin where Lysenkoism was decreed as it was in the Soviet Union and bloc. In East Berlin, however, the geneticist Hans NACHTSHEIM protested, left his position and became one of the Founding Fathers of the Free University in the American Sector. This action was intended and taken as a demonstration that German Biologists would not again follow and support a totalitarian ideology.

In Kiel Professor HERRE wanted a discussion onT. D. LYSENKO, but did not want to lead the debate for fear of exposing himself. He argued that Russian tanks were only 80 km away! (I, on the other hand believed that the word professor was derived from the Latin *profati*, to confess, and that therefore professors should stand up for their convictions.) He told me to lead the debate since "You do philosophy and such things; don't you?" On the day of the debate I faced a full auditorium in which there were not less than ten full professors. (In those days there were far fewer professors than there are today.) Not one of the ten spoke in the discussion. I dealt with LYSENKO and Russian genetics with the help of annotated documentation and a critical review published by the Imperial Bureau of Plant Genetics in Great Britain, and used material from the East which I had purchased in Berlin; that enabled me to review also the relevant theoretical issues of dialectical materialism, and to state my views on the relation between Science, Society and the State.

In 1954, my first year in Bremen, I was asked to write an article on the educative tasks of a natural history museum. So I put into writing what I considered to be the main responsibilty in teaching biology: ensuring that it never again became misused and politically exploited. I mentioned the LYSENKO case, but referred mainly to biology's earlier and horrifying perversion in the Third Reich for which our own people were answerable. In 1963, in a small book, I developed the theme that in 1933 German Biology did not need to become ideologised, since it was already deeply embedded in, and implicated with, not only conservative, but overtly nationalistic and chauvinistic views and convictions. It is important to note that these views preceded the Nazi movement and its racism, and thus had paved the way for the criminal politics of the German government and their helpers. I added that this fellowship had never been exposed and acknowledged, let alone cleared and cleaned up. I had avoided the use of the term "Fellow Traveller" for these biologists since it implies naivety.

A few days after I had made these observations in Bonn, the Max Planck Society, successor to the Kaiser Wilhelm Society, released the first news on the findings of a Commission looking into the role played by German biologists in, and prior to, the Third Reich.The reports revealed that not only had some biologists prepared the way for Nazi racism, but had also been actively involved in the crimes instigated by the German authorities. After the war, some of these biologists took active steps to suppress or destroy the documentary evidence of their involvement. An independent, extensive report has been published recently by KLEE (1999, 2001). The author presents, and substantiates, the view that not the NS-regime had politicized German biology, but that it went the other way round: that German biologists (some, but key figures) had instrumentalized the regime for aims they had been propagating before the Nazis took over.

So let me repeat here what I have taught on three continents to students of biology, medicine and theology; Science has non-scientific presuppositions, aims and consequences. I deem it a human as well as a professional duty of biologists to recognise them, to reflect on them and to act upon them in a responsible way. I will return to this theme at the end of my paper.

It was for such reasons that my wife and I worked from 1970 onwards in the emerging environmental movement, also mainly in and through the churches. Our first aim was to put the ecological responsibility on their agenda, to have them accept their responsibility for all creation, and thus to move beyond their dogmatic and practical anthropocentrism. We quoted the ecumenical slogan of "Mission on Six Continents", adding that "development, like charity, begins at home", and used for all this the notion that development means „bewusst gemachte Geschichte". This expression translates as "history made conscious" as well as "history made consciously", and we understood its goals as to fully involve all human beings in determining the fate of their group, their nation and the world at large. Whatever the fate, it must not be at the expense of our fellow creatures and the resources of the living earth. We called this an "anthropology of sharing" as well as an "anthropology in the making" in a two-fold sense – it is never finished and it is only possible to make it by doing it – rather in the same way that we "do theology". Another way of describing our aims, in this case to fellow biologists, was to change Human Biology into Humane Biology. As mentioned, we worked in the church with its numerous institutions, but through them also reached parts of the general public (publicly) and decision makers in politics and administrations, who were quick in recognising us as competent partners since we represented no vested interest (but they mostly preferred to talk with us in closed sessions).

What I have so far related of not strictly zoological questions or academic matters was a part of my life which I wanted to put on record here for its own sake, but also because it interacted with my scientific work proper. In 1986 I presented my experiences in interdisciplinary and intercultural work to a meeting of the Commonwealth Science Council on development research in Colombo, attended by scholars from a number of Asian countries. They responded that their experience mirrored my own. We had found that we should not start such research whith deliberations which sought a common or meta-language for the joint work, or to define a theoretical methodological approach; that would result in a limitless, soon aimless, and lastly fruitless self-sustaining effort and a multiplication of the problems. The only practicable way is to agree on a practical plan for a concrete goal, and to implement it. This will provide a shared understanding and yield ways of communication that would be impossible to reach with a theoretical approach (von Wahlert 1974, 1993).

5. More Theory and Praxis

In returning to my work in evolutionary biology, I can describe it as an additive growth of insights and experiences imposing one on the other. I deliberately use these expressions because they are both the key notions of my concept of evolution and apply likewise in my work.This accord reflects my faith in the essential unity of theory and praxis, contents and methods. As I have come to see it: reflecting one’s own methodology - which every scientists worth his salt does at least occasionally - is not an isolated theoretical matter of epistemology or some other philosophical field. This said, I now proceed to proper biological issues.

The strategy in my research on lower vertebrates was to apply the concept of adaptive radiation to groups of increasing size. There are only a few hundred species of salamanders, but tens of thousands of fish - so it was to them that I turned. This was made easy: in the Bremen Museum I was in charge of the herpetological and the ichthyological collections as well as the public aquarium with a range of livings “Fish and Herps” as they are called in the United States. It was here that I observed that topes, Spiny Dogfish, and other sharks pass, or circle around, a sinking bit of fish meat more than once before they snap at it. I later found the explanation; cruising sharks open and close their jaws in rhythm with the gill slits and their heart beat. They would only take hold of a morsel of food at the right moment; as long as they are not in a “feeding frenzy” they will not bite “contre coeur”, that is to say, against the heart rhythm. I discovered this after I had looked for (and found) passive respiration in sharks – which I had expected since it was known in mackerels. Sharks do suspend gill pumping movements when they reach a certain speed. I observed this when, in 1963, I worked in Genie CLARK's Cape Haze Laboratory and visited from there the Seaquarium in St. Augustine, and saw it again on my way back to Europe in the New York Aquarium. I followed these observations with experiments on anesthetized cat sharks and skates at the Zoological Station in Naples. They confirmed that the heart and the gill basket pump rates were the same and that the time required for the breathing rhythm to slow down after a swimming phase is determined by the time it takes the heart to return to its resting rate. This is clearly a heritage from acranian times; in Amphioxus the contracting bulbs of the blood system sit in the gill vessels so that the internal and external respiratory fluids, blood and water, are pumped in the same rhythm. This relationship has been retained when the jaws differentiated and the contractile bulbs fused into a single – multi-chambered – heart (VON WAHLERT 1966, 1966, 1971).

By combining morphological with live observations in aquariums and in the field, I had studied flatfish and others. At Harvard I looked into the archipterygium problem, one of the major unsolved problems in comparative anatomy and a key issue in the classification, phylogeny and evolutionary biology of fish and their tetrapod descendants. The pivoting point in this issue turned out to be that for three generations researchers had looked at the paired fins and overlooked the median fins. The paired fins had been seen as the forerunners of the tetrapod legs and thus their proper aquatic function had been ignored. I took up these studies again when I moved to Stuttgart in 1962 and could buy a *Latimeria* when the administration of the Comores offered them for sale. The colleagues there even supplied recipes used by the fishermen for cooking the fish before science became interested and provided a marketing outlet.

In 1963, in a symposium on “The Origin of Higher Levels of Organization” organised by Bobb SCHAEFFER and Max K. HECHT at the International Congress of Zoology, I described the macroevolution of fish as an adaptive radiation (VON WAHLERT 1965). Later, in the Latimeria-book, I could sketch in more detail the conquest of the open seas by the Teleosts in three main waves. By this time, and under the influence of Homer M. SMITH, I had become convinced that chondrichthyes, sarcopterygii and bony fishes proper had originated – from one common root – and radiated in fresh water. Up to this time, all fresh-water fish were taken to have come from the sea. In my view this was a residual piece of typology which prevented the understanding of fish evolution and resulted in a collection of loose ends. When I, at first out of sheer curiosity, reversed the perspective, the loose ends suddenly connected, fell into place and yielded a coherent picture. One of its main features were the three ‘waves’ of marine pelagic teleosts. First came the plankton-eating herring fish, then the foraging cod fish and last the hunting mackerels and tunas. At that time herring fish accounted for about 30% of the world fish catch, the cod fish 20% and the mackerels and tuna 10%. The rest of the catch was supplied by the plethora of other groups not mentioned in this survey of the main groups. These percentages reflect the availability of the staple food of the three groups. Each of these groups form the core of the food chains to which they belong.

I mention this as an example of the link between evolutionary and production biology, and to honour Klaus GÜNTHER who has been my main correspondent on biological matters since we met in Berlin in 1949. He once observed, in a footnote to a joint paper with Kurt DECKERT on the functional morphology of some deep sea fish, that the functional and ensuing morphological separation of respiration and feeding has enabled bony fish to invade and feed in the open sea where they then formed a food basis for predators, bony fish and sharks alike. He added that such (syn-)ecological considerations had so far received scarcely any attention.This rather casual remark has proved to be an extremely valuable heuristic clue. Once a group originates it becomes available as additional, or new, resource for others to feed upon. The occurrence of this novel food or way of feeding frequently seems to be the very opener, or 'key license', for a new ecological zone and with it a new group. That is why I called it the "Günther-Deckert-Principle" (VON WAHLERT 1978).

I later found that the "phyletic" sequence of steps leading from reptiles to mammals, just reviewed excellently by Walter Georg KÜHNE, contained a gap. It had been overlooked that mammals were able to find a novel way of feeding and of food since they were able to chase insects at night. They were able to do this thanks to a combination of their ability to hear airborne sounds and their faster reactions, a result of homoiothermy. So mammals are not what they are just because they give birth to living young and feed them on milk. As Bertold BRECHT says: „erst kommt das Fressen und dann die Moral", – "first comes fodder and then the morality". The further evolutionary history of mammals shows how the transition to plant eating was rewarded. When ungulates radiated feeding on leaves and grass, and rodents on grain, both tapped resources of an immense extent; their numbers increased accordingly, and thus also the food basis for predators.This process contributes to the evolution of ecosystems, their increase in turnover rates and thus the growth and productivity of the biosphere.

Thus our vista on the role evolution of taxa plays for and in the history of ecosystems, reflects a clarifying light on the role ecosystems play in and for the history of taxa. The ecosystems are the place where synecological relations exist, or are established, and thus coadaptation and coevolution takes place. Where else? So ecosystems must be seen as Mutual Adaptation Societies or M.A.S's.

6. Larger Groups, Wider Scope and Deeper Understanding

In the Latimeria-book (1968) I have outlined the history of fish, about half of the vertebrate phylum. As its subtitle I had chosen „Eine evolutionsbiologische Untersuchung" (A study in Evolutionary Biology). The next book, dealing with the whole phylum of vertebrates, was subtitled as an Explanatory Natural History – („erklärende Naturgeschichte"). I became involved with this book when its initiator and prospective author, a Swiss zoologist, dropped out. The publishers in Basel, who he had talked into publishing that book, consulted Adolf PORTMANN and then asked me to take over. The main title, „Das Schädelkabinett" (The Skull

Cabinet), indicated the intention to produce a volume on vertebrate skulls which the publishers had been convinced were a worthy, if neglected subject. They had commissioned a lady of proven artistic ability to draw a number of skulls. The artist, who worked mainly as a sculptor, found the skulls to her liking and had produced a marvellous series of drawings. It was at this stage that I happily joined the project, since it gave me a chance to extend the approach of the first book to the next larger group in a book promising to become quite attractive on account of the illustrations but was, as it turned out, overlooked by my peers.

I adopted the term ‚erklärende Naturgeschichte' after long discussions with Klaus GÜNTHER who admitted that my approach was explanatory, but hesitated to accept my term. I think that it was a small book by Felix MAINX (1955) in a US series "Foundations of Biology" which helped more than my arguments to convince him of the existence of two modes of biological research, both of which provide explanations. These two modes of explanation are now known as nomological-deductive (N-D) and historical-narrative (H-N). MAINX was a geneticist in Vienna; I do not know if he ever published his views in German, nor whether they were known and accepted among English readers. For a thorough record of how N-D and H-N biology came to be discerned on the international scene, readers should turn to the publications of Walter J. BOCK (e.g. 1991).

As the historical perspective is fundamental to biology, its unique feature and thus the main argument for its autonomy *vis-a-vis* physics, Ernst MAYR has stressed its importance just recently (2002). And it was in MAYR's informal seminar at Harvard that Walter J. BOCK and I first met in 1957/58, establishing a friendship and cooperation which lasts into this present time, as this volume shows.

There were two main lessons from this second book: the first concerns Überschichtung (imposing, super-layering), and the second the confirmation of the (originally deductive) insight that "no group evolves on its own". Überschichtung denotes, like adaptation, both a process and an outcome. If a specific special adaptation results in features of a broader importance or more versatile applicability, a new level of ecological possibilities and more complex and efficient design will be reached. Evolution produces its own fresh possibilities; it is a self-sustaining, additive process. This stratification by the imposing of new levels or layers is the outcome of the same mechanisms which let adaptive radiations occur, but of another quality – as circumstances permit.

A field trip into a forest can provide an illustrative example of self-layering evolution (which highschool students understand easily as my wife can testify). At night, or on a rainy day, salamanders prowl around with their measured tread preying on worms and snails which move at a similar speed. Faster, and in day-time's sunshine which warms them up, lizards hunt their fast moving prey. Again at night, the warm-blooded shrews can chase their food on the forest floor as bats and owls do in flight. Amphibians, reptiles, birds and mammals form levels not only of morphological complexity but also of metabolic efficiency. That is to say that there are strata which differ morphologically, physiologically and ecologically, and are thus superimposed on each other. With this insight the history of tetrapods became easier to trace and turned out as a network of interactions.

When the tetrapods originated the amphibians found a vast range of ecological possibilities to exploit. The amphibians took these chances to a much greater extent than is generally realised: toads live in deserts, salamanders in permafrost regions where they freeze over winter, other salamanders live in the tropics. Some tropical tree frogs do not need a pond for breeding, since they spawn into a foam they produce themselves in the axils of bromelias or other epiphytic plants. Their tadpoles are herbivorous like those of other anurans. That makes frogs the first tetrapods to eat plants and thus to tap the largest food source available. To a certain extent the adaptive radiation of frogs can be seen as the evolution of the plant-eating tadpoles with mobile adults as their means of propagation. (In the old discussion: Which came first, the chicken or the egg? Bernard SHAW is said to have described the hen as the best means for transporting eggs.)

However, most amphibians are restricted to wet habitats. Amniotes can withstand dryness and heat and thus occupy habitats which are out of bounds to most amphibians. Reptiles can share a habitat with amphibians, but when they do so they live on a higher physiological level. Both of these poikilotherm classes have been partly superseded by homoiotherm birds and mammals. But all these layers are not completely separate. On the contrary: snakes feed on fish, frogs, lizards, birds and mammals; crocodiles grasp drinking mammals and thus provide an input of organic matter for their aquatic ecosystem. Birds of prey take their food from all classes of vertebrates as well as some invertebrates, as do carnivore mammals. There are manifold trophic interrelations between the layers which can be best described as dialectic. This is particularly true for the dolphins, which have returned to the water their distant ancestors once left. In HEGEL's terms, the original water life is a position, terrestrialism its negation, the secondary aquatic life "the negation of a negation" which is the "position on a higher level". I see this as a quite fitting, if unusual, description of the relations between sharks and dolphins.

The second lesson from "The Skull Cabinet" was: a full analysis of a group of this size has to look beyond the group. Case histories like those of the flatfish or the skates and rays, or even to some degree the bony fish at large, could be dealt with on their own without imbedding them into a panoramic view on the whole of evolution. But the bony fish history has necessarily to refer to conditions outside the confines of its own group, such as the existence of the copepods and other plankton on which herring feed. The study of vertebrates at large underpins this view. The history of reptiles, birds and mammals starts with insect eaters, and therefore the insects and their history deserve at least to be mentioned in passing, and this in turn is intimately linked with the history of plants. It was impossible to accomodate all that in a book on vertebrate skulls.

So my wife and I developed the approach just sketched in a third book (VON WAHLERT & VON WAHLERT 1977, 1981), in which we outlined the history of all living things starting with unicellular organisms and proceeding to multicellular plants and animals. We chose as the title „Was Darwin noch nicht wissen konnte" (What DARWIN could not have known), drawing attention to the overwhelming wealth of facts and insights which have accumulated since, and importantly because, he had published his "one long argument" for evolution. We completed the first edition of this book while we were distracted by our preparations for a five months mariculture study we were to conduct in a dozen countries around the world, and delivered the text poorly organised and with too many factual errors that we had overlooked. No wonder our work did not make any impact on our colleagues or the public. We could remedy the shortcomings in a second edition, but this too failed to attract attention. Despite this we believe that the conclusions we reached were, and still are, valid.

With the eminent exception of Armen Leonovich TAKHTAJAN, evolutionary thinking among botanists was, at that time, in its infancy. This is the more remarkable since DARWIN was originally, and stayed all through its life, a botanist, as Mea ALLAN has shown. The key features of plant history, however, were easy to see when one looked at them with a synecological perspective. Green plants first colonised the land with algae forming thin layers, later joined by lichens and mosses. When these enlarged their biomass, increasing their volume and thickness they required stronger tissues. These could penetrate the soil, tap ground water, and thus make their owners less dependent on surface water. The deeper the roots grew the more minerals became available to the plants for their own metabolism and thus others. Metabolic cycles have existed since life began, the exchange of energy and matter between organisms without and with nuclei has persisted up to the present, and is still indispensable for the biosphere. "Higher" organisms – in every sense – have evolved from, and become superimposed on the older unicellular organisms to which they are linked with symbiontic bonds. Ferns, trees, shrubs and grasses have not replaced, let alone ousted, the more ancient organisms, but rather offered them new opportunities and partnerships. There are places in our world where scarcely anything can live except the ubiquitous bacteria. In other places only lichens survive. But wherever climatic and other conditions permit, lower and higher organisms live together. The lichens of the tundra can live without trees, but there is no stand of trees, let alone a forest, that could exist without bacteria, fungi and other "lower" plants. Well do I remember that I once told Erwin BÜNNING, in the Botanical Institute in Tübingen – where, incidentally, my wife took her doctorate – that I did not ask who of the partners benefited most from a symbiontic relationship like that of the aspen and its nitrogen fixing symbionts, rather I wondered how their ecosystem benefited. BÜNNING replied "That is a new perspective – and looks promising". And so it proved indeed; only in these and other symbiontic partnership could the plants enact the growth of biological production which we can and must see as the main feature of the evolution of the biosphere. Animals contribute too. As long as micro-organisms and plants together transform barren grounds into fertile topsoil and humus, they are supported by a host of other creatures. This was realized by Charles DARWIN early in his life. Already in 1838 he read a paper to the Geological Society "On the Formation of Mould". The role he ascribed in it to earth worms was thought impossible by fellow naturalists. So DARWIN took up the theme again in his later years, studied earthworms alive and experimented with them – as he had done, since 1860, with sundews and other plants before he published his book on insectivorous plants in 1875. For the earthworms DARWIN found out and showed how much leaves, litter and soil they move, and published in 1881, the year before his death and as his last book, "The Formation of Vegetable Mould, through the Action of Worms, with Observations on their Habits". DARWIN did not see the relation this study had to his work on evolution, but throughout his life he was fascinated by the interrelationships between the various forms of organic being.

To-day 'synecological', 'co-adaptive' and 'co-evolutionary' have emerged as the key terms for our understanding of evolution since they encompass the central notions for the insight that "all evolution is co-evolution". No group evolves by itself, neither does it evolve only for itself. Symbioses are not exceptional; they are the rule, and they are the most visible of partnerships between living organisms. We formulated this insight after Lynn MARGULIS had already published her conclusion, long since generally accepted, that eukaryotic organisms had originated from a symbiontic merger of two kinds of prokaryotic organisms. In a more recent book, she has extended this view on symbiosis by pointing out how much evolution at large, and humans, owe to this relationship. She calls symbiosis a "motor of evolution". We could not agree more, but would rather call it a main feature.

Lynn MARGULIS focusses on intracellular endosymbiosis. Her point becomes even more weighty when we consider the whole range of endo- and exosymbioses. As far as we can see, all ecosystems contain, and depend on, symbiontic cores. Coral reefs are the work of "frame builders" and "frame fillers". The frame builders, mainly "hermatypic" stone corals, produce their lime in co-operation with their endo-symbiontic algae. Savannahs have symbioses at two positions in the recycling-chains; ungulates digest their food with the help of endosymbiontic flagellates, and leaf-cutter ants and termites house and even cultivate fungi in their nests and hills. In most, if not all, cases such symbiontic cores are protected and encapsuled under stable and optimal conditions for the speedy recycling of "minimum factors" – those substances whose shortage would limit or cut back the overall turnover rate of the whole ecosystem. The tissue of hermatypic coral polyps, the stomachs of ruminants and the fungi gardens of ants and termites meet these conditions perfectly.

The symbiosis between algae and stone-corals is well known. Since the algae take up CO_2 and give off O_2, they change the pH of the cell interior and thus enhance the precipitation of lime. When this became known, biologists were puzzled that the polyps expelled their symbionts when they were experimentally deprived of food – the algae had been considered primarily as a food reserve for the polyps and only secondarily for their role in lime production. However, it turned out that the algae must have been the initiating partner of this association which satisfies their demand for a reliable source of CO_2. This is shown by the Giant Clam *Tridacna* which also houses symbiontic algae and is likewise rewarded with an enormous lime production. With their skeletons the hermatypic corals do much more than build their own colonies; they provide, as already mentioned, the framework which is then filled by other stone and soft corals. In addition a host of other creatures from many animal phyla as well as algae deposit lime by forming crusts which cement the whole into a mass able to resist the incessant onslaught of waves and currents. When the breakers have cut a gap in the reef, it is quickly closed by fast growing soft corals until the hard stone corals have grown to a size where they can take over again. This is very similar to the way in which a windfall area in a forest is first filled by raspberries and fast growing shrubs before trees take over again.

Once we had discovered and developed this synecological perspective, it was easy to apply. The main consequences of implementing it will be mentioned below, but before that I will take another look backwards.

7. Who or What Does Evolve? What is the Subject of 'to evolve'?

In the sixties Klaus GÜNTHER and I discussed the question of what is the basic unit of evolution – or the subject of the verb 'to evolve'. (This verb has no German counterpart, but this is not missed since Germans prefer nouns anyhow. To put our question we had to use English.) Obviously organisms cannot be said to evolve, but species can. That genera and all higher taxa can be said to evolve goes without question and was no issue for us. GÜNTHER and I were not yet satisfied to see or to set the species evolving in or against a passive environment. Our understanding of life was relational. So we agreed it would be both appropriate and enlightening to see the ecological niche as the unit of evolution. We understood 'ecological niche' as the multidimensional system of the relationships between the organisms and their environments. The environment can be described without the organism under study being observed or even present; to find out those factors which are part of the ecological niche one must observe the organisms in question. (Michael SCHMITT has written enlightening papers, 1987, 1991, on the fate of the niche concepts which need not be repeated here.)

GÜNTHER (1950) called the two components of the multidimensional niche, the organisms and the corresponding array of environmental factors, "autozoic" and "oecic", and we imagined that there would be some oscillation in the links between them until a new bond of biological significance has been formed. By this time the term 'preadaptation' had been introduced and clarified, in the U.S. by Walter J. BOCK (1959) and in Germany by Günther OSCHE (1961), both of whom were present in Bonn and both of whom have contributed to this volume. GÜNTHER (1949) added to this field the term 'ecological licence' for a prospective novel way of exploiting the environment and thus altering the ecological niche. I mention all this to show that the ecological perspective was well developed at the species level before it showed its heuristic and illuminating value at higher levels of organisation.

The species are the basic units of taxonomy and ecology. The origin and history of species and the larger taxa classes is an established field of study, phylogeny (or phylogenetics), whilst the study of the history of ecosystems is scarcely recognised as such and has no name as yet. Successions, the sequence of plant associations and societies from first pioneers to the final "climax formation" typical for the respective conditions is a process in time – following well-known regular patterns – but these changes are not evolution.

Phylogenetics has a long-standing history which commenced with DARWIN's insight that living nature not only has, but is history (thus giving new meaning to the older term 'natural history'). His discovery transformed at once the existing taxonomic system from an idealistic-morphological scheme into phylogeny – firstly, and unavoidably, into provisional drafts. Ever since, phylogenetics has progressed – sometimes gradually, sometimes in leaps and bounds, but we are as yet far from a general consensus both as to its methodology and its results. The "phylogenetic tree" is still beset with uncertaincies of various orders of magnitude. But even if we cannot yet trace the course which the history of even the largest branching lines has taken as exactly as we would wish; by now it has become obvious that all groups of organisms and all ecosystems have originated and evolved in one global system as interacting components sharing, or rather making up together, the biosphere and its history. The biosphere is the highest level of organisation in the realm of the living, and the largest, if not the only true, subject of evolution.

In this perspective, plants appear as producers and animals as recyclers. Only together can they maintain or increase the productivity of the ecosystems and therefore of the biomass of the biosphere. Every species makes its specific contribution to the metabolism and to the history of the biosphere. These statements also apply to, and include, the protozoans and micro-organisms which were producers and recyclers before multicellular organisms evolved from them; they continue to serve in this role and are still indispensable both to the production and the recycling side of the biospheric metabolism. Our present purpose, however, is served by the simplified summary; plants are the producers of organic substances and animals are the recyclers.

In ecology, the trophic relationship between plants and animals is described as a food chain. What plants produce is consumed by herbivorous animals which in turn are eaten by carnivores. (As Paul COLINVAUX, 1978, has pointed out, the predators amongst them are scavengers which do not wait until their food is dead.) In the historical perspective it is clear at once that plants did not come first. In the sea the number of true herbivore plant eaters is smaller than that of detritus feeders. A more detailed analysis is not required here; it will do to mention that in insects detritus, and in tetrapodes insect feeding preceded true herbivory. And looking at present ecosystems it is safe to say; without the homoiotherm herbivores and the equally efficient carnivores, the primary producers, the plants, could not have reached the turnover rates and hence the productivity marking our ecosystems like savannahs and rainforests.

The "ecologisation of phylogeny", as some observers have called this approach, and its outcome is linked with a reciprocal understanding that ecosystems have a part, an active part, in evolution. Phylogeny seen ecologically, and ecosystems seen historically, are elements of an emerging holistic view of the biosphere as the all comprising system of metabolism, and subject of evolution. This is a holistic view. Since the term holism has become discredited or even pejorative, I have called this perspective an "explicatory holism" and will try to justify that name in the following pages.

To come back to the question at the beginning of this chapter: the biosphere has a history in which all living things, organisms and taxa, and also ecosystems, participate (not all organisms actively). With this perspective there is no need to define 'evolution' since logically, as a name, it does not require definition as it would if it were a term. Names are given to things that are evident. No biologist will doubt that the biosphere has a history. I hence feel free to call the view developed here a "biospheric perspective" which I see as a complement to the organismic perspectives we know.

A second observation may help to make this holistic view on evolution easier to accept. In the theoretical discussions in biology, the distinction between "reductionist" and "organismic" biology has played a major role. I consider the biospheric perspective presented here as a reduction. This understanding is based on the simple fact that reduction is both the aim and method of every scientific endeavour, as it attempts to reduce the descriptive and explanatory elements which it uses to describe phenomena. An extremely fruitful method of reduction in biology was, and is, to show that the innumerable, most complex structures and processes rest and depend upon the laws of physics and chemistry, and can largely be described by them. This is one way of reducing explanatory elements, but not the only way. The biospheric perspective sees all biological phenomena as interrelated and interacting elements of one coherent and all-embracing course of biological events, the origin and further extension and expansion of the biosphere. (More of this in a moment.) This is a *reductio ad majorem*, and as such an equally valid way of dealing with complicated processes in a heuristically fruitful way. After all, physicists are not only looking for smaller and smaller components of matter; they are also looking for forces of cosmic dimensions and for a unified field theory which will link both fields.

8. Life and Life

The term 'biosphere' was introduced in biology by Vladimir Ivanovich Vernadsky in 1925 but popularized only much later by Pierre Teilhard de Chardin. Vernadsky (1925, 1926) based his view on the insight that the history of the earth and the history of organisms, or life itself, cannot be separated, but must be seen as interacting aspects of a single (and, as far as we know, unique) course of events, in which the biosphere came into being, and grew. What has occurred during the history of Life has not only happened on, but also to the earth: the atmosphere, the hydrosphere and the solid globe continually changed and these changes have influenced, but also been influenced by, the history of life. The role of organisms in the chemical transformation of the atmosphere from a mixture of reducing gases to oxidising air is well known. We recognise the emerging of a state of the earth capable sustaining life as a change in quality. Vernadsky identified yet another qualitative change; he saw the origin of the human mind and its effect on the earth as requiring the new, if euphemistic, term 'Noosphere'.

VERNADSKY has founded, and left behind a school in St. Petersburg which is still active in this field. However, neither he nor his school have drawn the one conclusion which I feel warranted, logically unavoidable and hence overdue; the term biosphere does not denote a distinct portion of the earth, its covering or a location on its surface. Rather than applying to a spatial part, it must refer in a temporal and historical sense to the state of the earth since the origin of Life.

The earth is not only lived on, but the earth has become alive. I see this my view supported by J. E. LOVELOCK's Gaia theory (1979), which says the same, and consider the correspondence of our positions to be the more valuable and convincing since they rest on totally different fundaments. LOVELOCK's position is the outcome of a strictly nomological-deductive method; he is a biochemist with no experience in biological research on evolution. His view is based on the self-regulation he has observed for the earth; my view is based on a narrative historical approach. These are the two approaches to the study of biology which are recognized as valid. They complement, but cannot replace, each other, and both are needed to cover the full spectrum of biological phenomena. That both have yielded the same understanding of the "living earth" is a telling mutual confirmation.The argument which has been used against LOVELOCK is that self-regulation is a property which is only known in living organisms; but the earth is not an organism and cannot be called alive. However, a closer look reveals that the linking of the words 'life' and 'organism' is typological, essentialistic and not required by logic. As long as we feel bound to use life only for organisms and hence for it to be their exclusive property (which we are free, but not compelled to do), and define the two terms by each other, we follow a tradition which keeps us from recognising 'life' as a feature of the earth, and the biosphere as a mode of its being - and the heuristic and explicatory merits of this notion.

This understanding has the great advantage in that it makes obsolete all attempts, intentional or not, to see Life as an ontological category on its own. In traditional philosophical terms, the biospheric perspective sees Life as a property of the earth, an attribute, and not as an independent ontological substance. Those who rely on, and stick to, ontological metaphysics will not accept this argument, but doubters may be helped by it.

What, then, is the life of organisms? It is their active participation in life at large, the collective one, i.e. in the metabolism of the biosphere and their (not always active) participation in its history. The value of this understanding can be shown if we ask whether, or not, a virus is alive. The answer depends on the circumstances, since at times it is alive, and at other times it is not. With an essentialist understanding of life, this is no answer; if life is an ontological quality, it can end in an organism, but it could not be switched on and off. With a relational understanding however, the life of a virus as participation can be suspended and can be resumed. There is no contradiction in this.

The definition of instincts provides another example. In all the dictionaries we have consulted instinct is described as an internal drive, or an inner urging, or as a built-in natural response which has not been acquired. These definitions are tautological or self-referential but offer no explanation since they do not refer to anything else for a logical foothold. In the biospheric perspective, instincts are mechanisms of participation which ensure that an individual organism actively participates in the collective life of the biosphere. Instincts are coupled to, or bestowed with, positive and/or negative feelings which ensure they lead to actions required not only for the survival of the individual but also for the functioning of the respective ecosystem and, to some minute degree, of the biosphere as a whole. Hunger and thirst are physiological conditions leading to eating and drinking, which in turn maintains the fitness of an individual but also the continuity of collective life processes.

Brief reflection confirms this understanding of "Life and life". It is generally agreed that life processes proper evolved in a primordial soup, of one kind or another, in which there were reactions in, and interactions between, more or less stable macromolecules or, later, simple corpuscles which had not yet become organisms. More stable units of such interactions, "hypercycles" of metabolism and propagation, formed in discrete compartments which were separated from each other in space but not in functional interaction. (There are new data which point to the possibility that these compartments formed in "bubbles" of cosmic origin.) The units communicated as they exchanged matter and energy. This interaction can be seen as a collective 'life' process which predated organisms. That makes organisms as much a function of life as vice versa. I call this interaction a "primordial coherence" and assume that a closer reflection would show its relation to, if not equivalence, with the "universal adaptation" (BOCK & VON WAHLERT 1965) which all organisms have "in common", i.e. share. And I see this understanding as a corollary of the insight that "all evolution is co-evolution". This deepens the understanding that every progressive step, or achievement, in evolution must be credited to the collective and not just to its individual members. Mammals should not be seen as enjoying the most remarkable success in evolution, but rather to represent a spectacular success, or achievement, of evolution as a whole.

VERNADSKY and his school have described evolution as an increase in diversity and complexity of organisms in terms of their structures and physiological performance coupled with an increase of the production, and the overall productivity, of the biomass. The simple word for this is 'growth'. This characterisation is in accord with the traditional description of evolution as progressive and that of phylogeny as anagenetic, but it adds the ecological dimension which is absent from the terms progress and anagenesis. If the main feature of evolution, the history of the biosphere, is growth, all biological phenomena can be seen as having originated in and contributed to that (quantitative and qualitative) growth. With this understanding, the well known dictum of Dobzhansky can be rephrased as "ultimately nothing in biology makes sense except in the light of evolution". (Walter J. BOCK insists that it is a new dictum, but I think that this is what Theodosius DOBZHANSKY meant.)

9. The Species

What, then, are the species in the biospheric perspective? They are the smallest units of common descent which are not yet irreversibly subdivided and which occupy an ecological niche. An ecological niche is the elementary biological component of an ecosystem. Niches have to have a certain size in order for the ecosystems to function. Conservationists have observed that a population can die out even if their number is above that calculated as required for successful reproduction. Could it be that in such a case the number has sunk below the strength required to maintain its niche? In this view the species can be seen as mutual assistance societies – assistance including "co-operation" in bisexual reproduction (where required). But this concept is not restricted to bisexual organisms.

Many years ago, the German physicist and philosopher Carl Friedrich VON WEIZSÄCKER observed that one of the central concepts of biology, the species, were inadequately defined; the usual definition as reproductive assemblage only applied to bi-sexual organisms, which neither represent the original condition nor the majority of organisms. Nevertheless, he said, the pragmatic solution of using such a concept by way of an analogy for organisms where its criteria do not apply or cannot be justified, was still better than the older morphological species concept. He saw, however, a serious problem in the fact that such a gravely deficient central concept apparently did not concern biologists, and obviously did not matter for the theories incorporating, or built on, this deficient concept. And then he added the remarkable observation that most probably a solution could be expected from using ecological criteria (pers. comm. 1979). I see this prediction fulfilled and the ecological species concept as deserving truly the name 'biological'. The species concept commonly called 'biological', which is based on bi-sexual reproduction, is in my eyes a functional one.

The stability of an ecosystem requires the reliable presence of its components over time. Since the life span of an organism is limited, the species maintains this sustaining by the reproduction of its members. Seen in this way, reproduction is not an end in itself but a means. The same is true for survival. It is the role of the species in the ecosystem which is important, and the survival of the species serves to maintain the ecosystem. In the long run and in a wider context, it is the role of the ecosystems in, and for, the biosphere which is crucial. Each species makes its own specific contribution to the whole, and as long as it does so the species will survive. If another species, or assemblage of species, arrives or comes into being and makes a better contribution than the original species, this species will disappear. The term optimisation (Bock & von Wahlert 1965) used for adaptation can be applied here as well. Thus the extinction of species is covered by the very concept of their existence. No other concept of species does this. Furthermore, the understanding of why species exist, survive and disappear can also be applied to classes of higher rank. Again, I know of no other concept of species which can do this.

Reproduction and survival are not ends in themselves, neither is the increase in information – I hope we can, with this insight, dispense with the repetitive ritual recitation of the tautological mantra of adaptation, selection and the survival of the fittest as requiring, explaining and justifying each other. In my view, this has never ceased to be anything but circular, and has crept into innumerable T.V nature programmes. And genes may appear to be selfish, but do not need to be hypostasized in order to make life comprehensible. What really counts is the biosphere, and this, I believe, is a notion which may be more easily understood.

10. More Fishy Stories

The explicatory value of the biospheric perspective claimed here can be demonstrated by the following observation. It has been mentioned that the evo-lution of frogs should be considered for both tadpoles and the adult. I used to call the whole matter one of "Evolution Double-tracking". The same can be found among fish. Many marine fish produce huge to immense numbers of eggs. This is usually seen as an adaptation which ensures successful reproduction despite the dangers of the open seas and its hosts of predators. Although we can see the grave dangers which are posed to ships by the winds and waves, we must not project these risks onto well adapted-pelagic creatures. And there are other ways for fish to achieve successful propagation in the deep seas. Some pelagic sharks and rays are viviparous, their embryos and young are nourished by their mothers with structures analogous to a placenta. This achievement enables these species to breed away from the coastal waters unlike their egg-laying relatives who are bound to visit these waters in order to deposit their eggs; only there can they fasten their cleidoic egg cases. These cleidoic eggs are an adaptation for saltwater breeding as they protect the embryos against the hypersaline sea water as long as their own osmoregulation does not yet work. These mechanisms maintain the appropriate levels of urea and related compounds in the body fluids. This is an old feature of gnathostomes: aestivating lung fish use it, as do those frogs, their spawn and tadpoles, which breed and develop in slightly brackish water. Chondrichthyes can be understood as having retained or revived this ability when they entered the sea. (The lower urea tolerance in other gnathostomes must be seen as a secondary feature.)

The rosefish (*Sebastes*), a common food fish of the North Atlantic, is the best known ovo-viviparous marine bony fish. So a huge number of eggs is not the only means for pelagic reproduction. With all that we know about multiple pathways – on which Walter J. Bock has written so profoundly - the question must be asked: what else could be a possible reason for the large number of eggs?

When reading, for our mariculture work, anew about fish biology, it occurred to me that fish larvae, like tadpoles, feed on food resources – mostly minute plankton organisms – not available to their parents. On the other hand, fish larvae form the staple diet for a plethora of other fish and marine creatures, including their own kith and kin. So could it be that these vast numbers of larvae were not (only) a reproductive feature of certain species, but were rather trophic elements of whole ecosystems? I soon found this idea also expressed by a proper fish biologist (Nellen 1984). This showed me that the attentive focussing on the propagative role of reproduction could obscure other aspects worth noticing. With this observation again a question formed in my mind: could it be that the preoccupation with reproductive success reflected a mental fixation on sex of a science traditionally dominated by men? I once shared this question with a meeting of the German Society for the History and Theory of Biology and had it received with sympathy. In this context we should recall that it was a woman, Lynn Margulis, who has written books on symbiosis setting forth that mutualism and co-operation are more important than the antagonistic stance which has prevailed so far in the general understanding of evolution.

From a book on fish population dynamics, I learned that a vast amount of data exists which, however, does not support the generally held fundamental concepts of fishery biology. Consequently, an assumption I had been fostering for some time gained weight, i.e. that these concepts were questionable. Fishery biology has the task of calculating stock development in order to forecast future catches and to make recommendations for regulatory measures. The sizes of fish stocks are calculated from the anticipated population growth. The basis is counts of eggs and larvae, the monitoring of the growth rates of individual stocks and the application of Volterra's Law which predicts the availability of food. This "law" considers the interaction between the populations of prey and predator, classically hares and lynx. An increase in hares leads to an increase in lynxes, which in turn results in a decrease in hares, followed by a decrease in lynx number, and so on. This can be shown graphically, with numbers against time, as two sine curves which mirror each other and which are separated by a certain time lapse. In the biospheric perspective, hares are not only providing, or "producing", food for the lynxes, but they and the lynxes are recyclers, the primary and secondary members of a chain beginning with the feeding hares and ending in micro-organisms. A complete picture should include the plants on which the hares feed as they are the producers. This would put the hares and the lynxes on the same side of the equation. Of course a mathematical relationship would exist between the numbers of hares and the numbers of lynxes, but this would not be identical with that calculated from the incomplete data. I regret I have not had an opportunity to test this view.

With the two fundamental notions for forecasting fish-stock development now appearing somewhat shaky, I was not surprised that the theories did not fit the data. It has been said above that the fishery sciences had little knowledge of the conditions of tropic seas. I now assume that these theories do not work in cold seas either. I assume this did not matter as long as both the fishing industry and fishery politics regarded fish stocks as inexhaustible. It was not until 1984 when overfishing was recognised for the first time by the FAO at its World Fishery Conference in Rome, a dozen years after the "Limits to Growth" had been published and publicised. The International Conference of Fish Workers and their Supporters, by the way, staged a counter-meeting to the Rome conference, with a public demonstration on the Piazza Navone where delegates from all southern fishing coasts reported how long they had known of overfishing in an industry rather "satisfying the greed of the rich than the needs of the poor" as a Malaysian spokesman formulated. (The latest news at the time of writing is that experts have now recommended to ban fishing in up to 50% percent of fishing areas.)

These remarks are made to show what vast, and current, vistas are opened by the biospheric perspective. They also illustrate that a field such as evolutionary biology, not usually thought to be of much practical significance, can benefit, and benefits from the understanding of very practical issues.

11. Phylogenetic Systematics – A Fresh Beginning Frayed

The ecological species concept based on reproduction is, as I see it, compatible with the phyletic concept of Willi Hennig (1950). Hennig defines the species as the segment between two branching points of a phyletic line in a dichotomous dendrogram or cladogram. Given that the aim of such schemes is reconstructing phylogeny, I deem this definition to be logical and adequate. For phylogenetic systematics, as established by Hennig, it is useful, and for my understanding indispensable, but not for other purposes.

I do not need to describe, and I do not wish to discuss here, the fate of Hennig's approach which had been brought to international attention through the publications of a Danish and some British paleoichthyologists, as well as of a Swedish ento-mologist. After that had occurred, I told my students that the spreading of scientific theories had more to do with epidemiology than of epistemology. But during its spread (in "mouth-to-mouth-breathing"), Hennig's approach and methods became simplified in a way which destroyed their methodological coherence. This led, in turn, to a cladism and a "numerical taxonomy" which completely cut its links to phylogenetics. Although this happened without Hennig's active doing, he did nothing to prevent it or to minimize the damage. As talkative as he could be in private conversation, he was shy of addressing his peers, let alone of talking in public, and declined even the most honouring invitations to do so. He did not feel obliged to comply with the expectation that scientists should communicate in more ways than by publishing learned papers. It is to his credit that he made German and other taxonomists aware of the need for a theoretical basis for their work, but he failed to at least try to safeguard the fate of his own contribution to science.

For me, the most remarkable fact is that he had seen his phylogenetic systematics not only as a method to reconstruct the history of taxa, but, as he put it in his first book, the only promising way towards investigating the "history of all nature". In formulating his objective HENNIG had referred to a book by the botanist Erwin BÜNNING on the theoretical foundations of physiology (1948). In it the author had said that dealing with some parts, or processes, of plants always means dealing with the whole of nature. I have no doubt 'biosphere' could be used for 'the whole of nature', and I think that HENNIG's objective has been reached in so far as a promising research strategy is now available.

A personal note on HENNIG. I first met HENNIG in the Berlin Museum where I worked in the summer of 1949. We were later colleagues, from 1963 until his death in 1975, when we worked in the Stuttgart Museum (in its temporary branch in Ludwigsburg). His first book had appeared in the post-war period in East Germany and never reached much of an audience in Germany, let alone internationally. The book's style was clumsy, and HENNIG's approach was not considered to be either workable or useful. HENNIG himself never attempted to reach the goal alluded to above. On the contrary he became more and more reserved vis-a-vis evolutionary biology. It was for this reason that I once described his position as that of a Caesar fishing from the bank of his Rubicon rather than crossing it. I would visit him regularly in his office for discussions. It was during one of these visits that I called his approach a "dialectic turn in biology": The essentialistic hierarchical system of LINNAEUS. LINNÉ's "Systema Naturae" defines taxa in an essentialistic way and subsumes them under their respective higher taxa (which are abstract classes); HENNIG's method determines taxa by their sister group relations, which means they were determined in a dialectical way. He would protest at this, since for him 'dialectic' was linked to his post-war experiences in Leipzig in the Soviet Zone, where he had been exposed to dialectic materialism. I reminded him that an idealistic philosopher, HEGEL, had revived this ancient and honourable term and concept before the materialists had seized it, told him that we should not surrender dialectics to a political camp which we felt had usurped it, and added, for good measure, that his use of "reciprocal illumination" was truly dialectic on two counts; it was itself a dialectic concept, and it testified to the identity of theory and praxis, which was a classic dialectical principle. All of which he grudgingly accepted. After a while.

12. Participation in Layers

In the biospheric perspective, life of the organisms is their active participation in the metabolism and history of the biosphere: living is sharing. Their active participation ends with their death and the recycling of the dead body as a final, now passive, sharing of life at large. All organisms participate in the life of the biosphere physically, and to varying degrees sensorially and psychically. Depending on the level of consciousness some also participate cognitively. Plants take up and evaporate water; they tap ground water and aquifers, they contribute to the humidity of the air to the extent that they influence the weather and climate. While most animals have largely closed circulation systems, plants have none but are directly linked to the giant global water cycles. The gas metabolism of plants, and also animals, is both linked with and is part of global cycles. In principle, the same holds true for solid substances. In cycles of much longer duration, plants and animals can become incorporated into the crust of the earth, sink into its depth and become coal, or be elevated as mountains consisting of ancient reefs or other assemblages of marine creatures. The cycle continues as plants and animals contribute to the erosion of the mountains. I mention these facts to underline the importance they have in our context.

It is common knowledge that animals participate in this world sensorially. Most people, and all biologists, know that the same is true for plants, albeit this is less noticeable to the unskilled observer. There is a huge literature, of a not strictly academic nature, which knows, or claims to know, even more about the secret life of plants. When, as a student, I heard a guest lecturer speak on the lunar periodicity of nereid worms in the North Sea, all of us laughed. However, the synchronisation of biological processes with cyclical and acyclical physical processes on and off the earth has long since become a matter for intensive research and wide application in biology and medicine. I mention this too as a reminder.

The third level of participation is the psychic or cognitive one. It has reached its fullest and unparalleled emergence with the human mind and its self-awareness or self-consciousness. In the biospheric perspective, consciousness is not only a means we participate with, but also something we participate in; the individual mind shares the collective. This may strike us as an uncommon concept as it is all but alien to the History of Western thought. In Indian culture and philosophy, the word 'Atman' stands for both the individual spirit and soul and its collective equivalent, and is one with 'Brahma', the supreme spiritual Being. The Occident has lost this understanding, but for a handful of mystics amongst our poets and one German philosopher, SCHELLING (1754-1854), who spoke of a Weltseele, or world soul. C. J. JUNG knew at least a collective subconscious.

Unfamiliar as this view is, I have found it more readily accepted when I mention and discuss language. Without doubt, language is a social phenomenon owned by a collective. No isolated individual can have a language. Humans acquire it by doing, viz. sharing the communication network of their respective social collective. A child deprived of social contacts and thus of communication will neither learn to speak nor grasp those abstract terms which mark the human language and mind. We master language and thought by sharing a collective facility. There is another trait of human life which deserves mention. Since ERIKSON (1950) we have known that children must experience a reliable nurturing environment if they are to acquire a basic trust. On this trust rests the ability to hope, to have confidence and to love. Children who do not have these experiences during their formative years can never make good the deficit.

Memory could also be mentioned here as a third collective, or social, feature. But even so, the point seems to be clear: the traits which enable humans to be humane, loving and thoughtful are endowments to the individual by the collective. They give the individual status, quality and an irreducible individual dignity, and mark it as unique. We see all of this as being quite distinct from if not contrary to anything collective. There is a tension here that we cannot and must not deny, but rather accept. But even so, in my view there is no doubt; the understanding that our life is participation includes the psychic realm. The term "Anthropology of Sharing" expresses this understanding. This term and concept originated, as mentioned before, in the practical context of our "Anthropology in the Making". With the more theoretical considerations here I feel it is now also introduced academically, *lege artis*.

I have developed the concept of the "Anthropology of Sharing" in the early 70's in seminars at the Theolgical Faculty of Heidelberg University and the C.-G. Jung Institute in Stuttgart, a vocational college for psychologists and psychotherapists, and finally as a visiting lecturer at the Department of Psychological Medicine of the Otago University, New Zealand. With my excursions into anthropology I wanted to take up the insights of the philosophical anthropology of SCHELER (1928), PLESSNER (1965) and GEHLEN (1940) (who, each in his way, had biological aspects incoporated in their work) as well as the contributions the zoologist Adolf PORTMANN (1969) had made to anthropology, all of which stress the „Weltoffenheit" (World-openness) of humans – and to show that in our time biology could cover more aspects of human life than sociobiologists and Konrad LORENZ and his followers and other rather deterministic authors did. This, now, is the place to mention, at least in passing, what has happened in psychotherapy which I am inclined to see as an "applied anthropology" (and thus also as an "anthropology in the making" where praxis preceded theory). Psychotherapy was founded by Siegmund FREUD in the individualistic tradition which has marked the history of European thought since SOCRATES and PLATO. This rather narrow understanding was widened by C. J. JUNG who spoke of the individudal and the collective unconscious. In a recent book "Hundred Years of Psychotherapy" the authors, J. HILLMANN and M. VENTURA (1992), raise the question whether, and how, the human Self should, or could, be redefined. They call the very question revolutionary, if it would be accepted, but do have an answer: they come up with replacing DESCARTES' *cogito ergo sum* by *convivo ergo sum* – I live with others and therefore I am. I am quite happy with this.

13. "Biology" Re-instated

With the understanding presented here we gain some answers, or at least new perspectives, for some general and even fundamental questions and issues in or of the science of biology. First of all we have won back the term 'Biology' for the life sciences – to denote, as the name says, the science of life as a factual phenomenon and not merely an abstract term for linking diverse "life phenomena" on a nomological meta-level. This latter view had become customary when physiologists and biologists in the experimental branches of our science declared that the definition of life should be left to the philosophers. What may at first appear as unbiased restraint, an insight into the inherent borders of our own discipline or of uncommitted modesty, was in fact a partisanship committed to an existing philosophical tradition, viz. a metaphysical ontology. This philosophical school has in my view outlived its usefulness, as has idealistic morphology, its manifestation in the early phases of biology (where it served as a valid, and heuristically fruitful, paradigma).

In my student days, and subsequently, such questions were dealt with (in Western Germany) by reference to the distinguished biologist Max HARTMANN's book „Allgemeine Biologie" (General Biology) who in turn referred to the philosopher Nicolai HARTMANN and his Schichtstufen-Ontology – ontology of layers. Nicolai HARTMANN saw a spiritual layer of the world as a whole, which was carried by and rested on a psychic layer, which in turn was on an organic layer, and finally this in turn upon an inorganic layer. (Layer here does not include any sense of history such as there is in the "layers" of evolution. Metaphysical ontology deals with timeless qualities.) Thus these distinctions were seen as the concern of philosophers and not of scientists.

I was never satisfied with a stance denying, as I saw it, biologists a say in matters which do concern us deeply. I hoped and looked for a way of doing and presenting biology with our own means as consistent in facts and concepts and not to wait for philosophers to make our patchwork coherent, and to delineate it at the same time against other natural sciences. I found that way when I became convinced that biology was fundamentally asking historical questions which chemistry and physics do not, geophysics and cosmology nothwithstanding. Among the natural sciences biology has its own, exclusive tenet in the explanatory narrative. It shares the nomological-deductive approach with chemistry and physics, but is marked out by the historical-narrative explanations. (With time I have become familiar with the distinction, and occasional clashing, between the nomological and structuralistic versus historical approaches and concepts in linguistics, anthropology, sociology and theology, and felt additionally re-assured by the philosopher Robert RORTY (1993). And in the ongoing dialogue with theologians, I learned to see the role claimed by, and readily granted to, physics as being normative for all sciences as an alliance for the defence of essentialism between physicists and dogmatic theologians.)

The gist and goals of evolutionary biology are explanatory narratives which comprise all there is to know in coherent accounts. The material thus to be presented are the traditional objects of descriptive natural history, the organisms and the ecosystems. Their description requires the nomological-deductive biology with its own texture of facts and explanations. Nomological-deductive (N-D) biology began when physics and chemistry were applied to experimental research on organisms. This yielded theoretical insights and practical results of unexpected and unparalleled scope and weight in agriculture, medicine, and in the development of biology proper and an increasing array of disciplines such as genetics, biochemistry, biophysics and molecular biology. There is no need to elaborate here what these new disciplines have contributed to the widening and deepening of our understanding of life and its phenomena. But one voice from this field, that of the Nobel Prize winner Gell-Mann (1999), is worth mentioning in our present context. He points out that the most exact analysis of living structures by nomological means comes to an end when the exact function of genetic material is to be defined. This material contains the stored information from millions, if not billions, of years wich cannot be deciphered unless this history is analysed and described with adequate means - and these are not those of N-D biology, but of its historical-narrative counterpart.

14. Three Biologies

When I formulated and published these views, I presented these various fields as three historical phases of biology:

Biology as the study of	Organisms	Life processes	The Biosphere
is based on	Morphology	Physiology	Evolutionary Ecology
Its cognitive character is	Observing	Analysing	Holistic
affective	Enjoying/Adoring	Controlling	Partnerlike
expressive	Describing	Manipulating	Caring

I called these phases "First", "Second", and "Third" Biology and understood them as forming a "dialectical scheme" of thesis, antithesis and synthesis – as presented by Hegel. It was to my slight amusement that I found myself using a philosophical paradigm to clarify biological issues. But in so doing, I do not wish to shift competence and responsibility to a philosophy outside biology. Instead, I would rather apply dialectics to nature (as Engels has done, but not Marx), thus denoting that it covers both objective features and our subjective way of describing them. Be that as it may – in any case the three phases I have described are true historical layers. In Germany as well as elsewhere researchers in "modern" experimental biology have tended to see the older "organismic" biology as out-dated, whilst it's adherents have denounced the "modern" biologists as "reductionists" – as if not all science was necessarily reductive (see elsewhere in this text). So the relation between them can be seen as antithetic, and the third phase without doubt as a synthesis. The third biology presupposes and requires the other two phases, and it incorporates and integrates them. It does not abolish their distinctive features but overcomes their feuding as it sees them as being complementary to each other, and thus establishes a new level of understanding nature.

With the biospheric perspective we gain a comprehensive concept of biology which at the same time it clarifies its relationship to physics. The genuine subject matter of biology – evolution, the history of the earth becoming the biosphere – is the one great natural phenomenon observable on this earth which cannot be fully described by physics, chemistry and geology. If someone had or has any doubt that this determination is sufficient because it resorts to a history we have not witnessed, or because it names no prima causa for this course of events, my answer was and is quite simple. I ask of the enquirer his fundamental position regarding the nature of the world in which we live. If the enquirer has a static view, then I am unable to name a cause for the start of evolution. I see the world as dynamic, as being in motion – a term in which ARISTOTLE included changes such as the development of organisms, and evolution as one quality of the dynamics of the world at large, the universe. This is, of course, just a way of describing and explains nothing. How evolution began on this earth, the only place we know it occurs, is a question for which scientific hypotheses are available and which is likely to generate more in the future. To say that life, once established, had to grow follows from the truism that subsistence can be sustained only with some excess production to form a reserve. That is to say that once a surplus is being produced it tends to accumulate. Once coral reefs are established, they need their growth potential mainly to repair gaps as fast as possible. In other circumstances they just slowly grow outwards. I do not think that there is any philosophical argument, or speculation, which can add to this.

15. A “Unifying View” in More Than One Sense

The prevailing understanding sees evolution as characterised by antagonisms: phylogeny is the divergence of lines, selection is competition. We now realise that it is not always and only a *bellum omnium contra omnes*. Selection can be reciprocal in co-adaptation, mutualistic with the enhancement of a shared environment, and the ecosystems and their operations are the outcome of forces united . When Walter J. BOCK and I introduced the term ‘optimising’ for the overall effect of adaptation, I think we could not yet foresee the extent to which this term would be found to be true nor how much togetherness it would imply and include.

No issue in evolutionary biology will remain unaffected by this newer perspective, nor will interdisciplinary studies directly or indirectly concerned with evolution, or more general discussions at all levels whether academic, popular or ideological. Of these I want to single out just one.

Evolution is generally seen as progress. Progress can be judged using a wide range of criteria. In biology, progress was first noted in terms of morphological complexity, then in physiological efficiency including that of the senses and the brain, and finally in the ability to collect, store and handle information, both psychical and genetic. All these traits of evolution could be interpreted as symptoms, or manifestations, of a Progress - with a capital P. This Progress needed no further explication, let alone justification, once it was believed to exist as force in it's own right, inherent in this world and manifesting itself in nature and history. I see such faith and trust in progress as a projection of wishful thinking, and have avoided the word progress in my biological work. (Similarly, Walter J. BOCK and I once pledged ourselves never to use the word ‘primitive’ when comparing organisms.) Be that as it may - the concept of progress as a force of, in, or for evolution becomes superfluous when the characterisation proposed here is accepted: whatever has occurred in evolution originated in, and contributed to, the growth of the biosphere in terms of its biomass and productivity. This can be called progress, in a descriptive sense, if one so wished, but a "growth of biomass" should prove resistant to being hypostasised and ideologised.

When in a discussion of such matters participants hear that I have worked in both science and theology they usually have some more questions (as it happened in Bonn). So I will also indicate here some of the observations or notions which usually then arise. It mostly starts with an assertion: If everything in evolution can be related, in scientific terms, ultimately to productivity, this is not to say that we should or could limit our personal concerns to that growth. We are free, as we always have been, to see this growth as the way in which the human mind has evolved, or the Hegelian "abolute Geist" has made itself manifest (in a metaphysical anticipation of self-organization?) - or that it was the will and action of the biblical God. But these are existential positions and are clearly a matter of personal conviction. They can be debated, but not by using scientific terms and reasoning. In the dialogue between scientists and theologians (e.g. about "Creation and Evolution") I have found it helpful when scientists understad that religion deals with "matters of ultimate concern" (as Paul TILLICH expressed it – who in my Harvard time worked in the School of Divinity right behind the Biological Laboratories) which science as such does not even touch, and that Jews and Christians trust, and thus believe in, a God to confess but not to explain. Jews and Christians do not believe in this God because they are looking for a *prima causa*. The argument that someone must have caused or made it all is no solid basis for a personal faith. Only if a person has answered the question (as formulated by Trevor LING) "Is, what there is, personal?" with "Yes" can he or she accept, encounter, or experience Him - and than of course credit him with being the Creator. This is not (only) a matter for discussion, or of contemplation, but simply and primarily a matter of experience in one's own life. I have already mentioned a new trend in ecumenical theology which cannot – and will not, and must not – conform to essentialistic dogmatics, but instead relies on the narrative tradition in holy scriptures and speaks of "doing theology", rather than the traditional systematic approach. Need I say that this approach appeals to me?

Why our planet began and then continued to retain rather than to re-radiate a minute portion of the solar energy it receives, is an open question. The biosphere traps and stores this energy in biogenous cycles within and between organisms. There are models of how this could have evolved, and we may expect that these will be refined, or changed, or replaced by others. But answering the question what sense all this makes, and even posing it, will remain another matter, a matter of personal choice. We only know the life and mind on this planet. Even if they are confined to it, they do occur in a universe of which our planet is part, and hence we can think of them as being cosmic features. We have come to realise that the universe has a history, which some have called evolution or cosmic evolution.

It may be best if we reserve the term 'evolution' for what happened on, and to, the earth, but can and must see this "organic evolution" as a particular quality of the movement - in an Aristotelian sense - inherent in a dynamic universe. But this characterisation again provides no answer to the question "why" in its deeper meaning. I do not believe that we, the inhabitants of one particle of dust among the uncountable celestial bodies in their innumerable systems, will ever be able to grasp the totality of the universe. Our cognition is limited in quantity and, to my understanding, also in quality. I accept that limitation as the price for being sentient at all, as I live with the fact that my eyes have a blind spot.

I have included these remarks since they reflect personal experiences closely related with my own scientific work, but also because I see them as having a general bearing on science as an occupation and profession. I grew up under a political regime which misinterpreted biology, ideologised and perverted it. To-day there are again voices who see biology as a basis for explaining, dealing with, and deciding on most, if not all, questions of human life, intelligence and behaviour. That is why I wish to record and repeat explicitly that I see biology as a science only and, as such, of limited remit, and deny that biology has an unlimited competence in these other fields. However, nobody will perceive these limits unless he or she realises that there are questions and answers which cannot be covered by biological research and decided by biological expertise alone. I have been exposed early in my life to experiences which have taught me that such questions exist. I was hence not tempted to decide existential problems with the means of my science, and felt free to discuss fundamental questions of science without risking my personal convictions.

But even without discussing such personal matters any further, I feel there is a lesson here for every biologist. If the evolution of a given group is to be described as a narrative, it usually is impossible to relate, let alone to discuss meaningfully, all that has happened even if it were possible to obtain all the relevant information – which mostly will not be possible. In this case, the first task for the evolutionary biologist (as, in a comparable situation, the historian) is to select the issues to be treated, to decide which lines of development be presented, which facts are indispensable for this picture, which less so. Making such decisions is a personal matter which will depend and rely on pre-scientific notions and choices. ("Pre-scientific" only in the sense that they are basic to the professional proceeding; they do not rank in any way below scientific thinking.) This task includes a diligent review of pertinent possible positions, and the mustering and mastering of this information must include a critical review of one's own positions. No responsible scientist can avoid this reflection and decision-making. For this reason I consider reflection on "pre-scientific" issues and their interrelationship with scientific questions to be not only a human and moral concern, but also a professional obligation for a biologist - if only for practical reasons. How would papers and books look if we wrote everything we knew!

16. The Old Man of Downe

In summing up I wish to say something about Charles DARWIN and his work, and also want to record what I think has been his true achievement. While studying theology, he was influenced by the rational theology of William PALEY. He gave up his faith when the slavery in Brazil was justified by a planter, and also by Captain Robert FITZROY of the “Beagle”, with arguments which we in our time know from South Africa as Apartheid Theology. DARWIN could not associate himself any longer with a God who consented to slavery. Having lost his faith – as he saw it – DARWIN no longer felt bound to creationism as a religious and scientific paradigm. With this changed consciousness, his eyes were opened, and he saw that nature not only has, but is history. When working out his “one long argument”, he hesitated to publish it. He wrote to Asa GREY that he felt he was committing murder. Was it murder of a theory? That is a scientist's job. I think that he felt he had murdered God because he had destroyed the rational argument “proving” His existence. With the recognition that species were mutable and not constant, creation as an act of God was no longer available as the most weighty “evidence” of His existence. It was this that produced the guilt under which DARWIN laboured, since he could not do away with his irrevocable conviction that species had evolved. But DARWIN never did betray the faith he had given up; he was no Darwinist taking selection or the “struggle for existence” as justifying anything in, let alone anything outside, biology. He did not hypostasise, or ideologise, evolution or its mechanisms, as others did, but remained true to the God he believed he had lost. He obeyed the commandment “thou shall have no other gods beside me” even when he saw himself as an agnostic. He was a better Christian (and theologian) than he knew.

It is my understanding that DARWIN had no inclination, and certainly no ambition, to establish theories just for the sake of establishing theories, and had neither the need nor the interest to choose a career. He was a curious naturalist in the best meaning of both words. He felt compelled to find an explanation for what he had discovered, and to make it as convincing to, and for, himself as much as for others. With the development of genetics, the elaboration of his theory fell into the hands of nomologists who were interested in the laws of evolution and not in its course. On the other hand, those who were interested in its course studied the formal structures of morphology with little or no regard to their functions, let alone ecology or behaviour. They were correct when they argued that a theory of evolution, when mainly understood and presented as a matter of genetics, could contribute nothing to the field of comparative morphology, especially the comparative anatomy of vertebrates, which together with palaeontology provided the bulk of the material used by phylogeneticists. Even the synthetic theory of evolution was seen, with some justification, as merely a merger of genetics, population dynamics and taxonomy mainly of the lower taxa. That a real synthesis is in sight is a recent development as was indicated in Bonn by W. J. BOCK's observation on The Three ‘E’s – Ethology, Ecology and Evolution.

As my understanding of evolution developed, I enjoyed some of the tasty morsels from DARWIN's book. I found the first tidbit in the "illustrations of the action of Natural Selection" in the "imaginary illustration" of wolves with diversifying food preferences. In DARWIN's characteristic way, his illustration is followed by an observation from a Mr. Pierce on wolves in the Catskill Mountains in the United States, reporting exactly those differences in feeding which DARWIN had, as he says, imagined. DARWIN, in his chapter on instinct, deals with its role in inducing, and bringing about, what we would now call synorganization, viz. those corresponding changes in the feet and bills of titmice, which correlate with an alteration of food habits. When the role I ascribed to changes in behaviour was held against me as Lamarckism, the *pièce de résistance* of my consoling quotations was one from DARWIN's last chapter: "The most important of all causes of organic change is one which is almost independent of altered and perhaps suddenly altered physical conditions, namely, the mutual relation of organism to organism".

I have used these and other quotations – taken from an edition of the *Origin* which my father, when a medical student in London, purchased there in 1911 – to substantiate and underpin my conviction that never before in the history of evolutionary biology have we been closer to the founding father, DARWIN, than we are now. Whoever sees this as a success of a progressing science on the march should keep in mind some sobering facts. We now have a wider and deeper understanding of evolution in general, and we have an immense amount of knowledge. We know many more details than Charles DARWIN, who did not know, for example, about genetics. We can hope to include, one day, all our biological phenomena, in principle, in one coherent and consistent explanatory narrative. Physicists seek to put all cosmic phenomena from subatomic details to universal forces in a "Grand Unifying Theory" – GUT. We biologists may work towards "One Unifying Coherent History" - OUCH. But having said all this, we still cannot do better than the wise old man of Downe in understanding that "all past and present organisms beings constitute one grand natural system". Our knowledge is far from complete and will, for practical purposes, remain so. There is ample room, and need, for further research. The frame sketched here needs filling to make it solid - to borrow terms from coral reef architecture. Closing the gaps in reefs and knowledge will modify the general outlay to some degree (for the last time: dialectically). I cannot participate in this work anymore, but others can and are at work. For this I am very grateful.

I wish to express my gratitude by sharing with my readers, as I did in Bonn with the audience, the experience of how intimately and intricately the development of my scientific work in biology was interwoven with studies and work in other academic disciplines, and with quite practical assignments. My concept of "Life and Life" and the "Anthropology of Sharing" was developed in a seminars I gave in the Theological Faculty of Heidelberg University, in the C.G. Jung Institute in Stuttgart, a training centre for psychotherapists, and during my time in the Ecumenical Institute in Switzerland, and reviewed again in a lecture in the

Department of Psychological Medicine, of the University of Otago, in Wellington, New Zealand. These academic activities were combined with action work in fishery development. I also worked with the Green Movement at home on their conceptual issues. The point that I want to stress once more is not just the combination of academic and other activities, but rather its synergistic effect (or reciprocal illumination). In my closing remarks in Bonn, I stressed the gain I derived from this interaction, and in private talks afterwards some partners expressed their interest to hear more about experiences that are "never read (about) in scientific papers". By complying with this request I want to encourage others to employ the same comprehensive approach to life and work and to enjoy the same benefits that this paper reflects, and reflects upon.

Acknowledgements

The last words of this account will be my thanks. I owe and wish to express them to all those who have helped me to find and make my way. The gratitude I feel includes both my teachers and colleagues, who understood my approach and wanted to see it developed, and those who criticised or rejected it. I have always tried to learn from even the most virulent objections.

Thanks are due, and herewith rendered, to Dr. Michael (Theo) Schmitt who initiated and organized the Bonn meeting and its publication, and to the contributors who made Bonn what it was and what it meant to my wife and me. Dr. J. F. Roberts – a friend since the year both of us worked for the Ecumenical Council of Churches and still my advisor on matters psychological, and who became head of the Department of Psychological Medicine at Otago University, NZ., in 1978 - reviewed and edited the manuscript of this paper and made my English more understandable. My later additions and amendments together with the resulting final version were checked for new mistakes and ineptitudes as well as for overall coherence by my neighbour in Kleiningersheim, Dr. M. D. Adam-Larkins. My old friend Walter J. Bock (New York) did the final English editing of this paper.

The very day after I had finished – as I thought – this manuscript I received from my friend John Roberts the book "Annie's Box. Charles Darwin, his Daughter and Human Evolution", written by Darwin's great-great-grandson Randal Keynes (John is born in Shrewsbury, as was Charles Darwin, and we have been there together. So he is interested in Darwin for his own reasons.). Annie was the first daughter (and second of nine children) of Charles and Emma Darwin, and died ten years old. Keynes describes her life, "drawing on a wealth of previously unseen material" from private family papers and letters, and "reveals the personal experience from which he (Charles Darwin) drew his most deeply held ideas". As far as I can judge at the time of this writing the author documents convincingly how in Darwin's life and work personal and private experienences were interrelated with his nature studies and his scientific thinking. On the first page of his introduction Keynes states: "Charles' life and his science were all of a piece". I found this interesting enough to open my file once more for this last insertion.

My wife of 46 years, Dr. Adelheid von Wahlert, née Ruckenbrod, was at my side in Bonn as she has been since our marriage in 1955. In 1956 we conducted our first field work together on the "edge of the sea" (the title of a book of Rachel Carson she loves so much). While I was down with my diving gear, she floated, with goggles and snorkel, on the surface as my security guard and "mother ship" (called the "expectant mother"-ship for obvious reasons). The daughter she delivered two months afterwards took a diving licence 30 years later, as did two of her kids only a few years after, making us a diving family of three generations. My wife took her doctorate in plant physiology, and hence was trained in nomological biology at a time when the view was widely held that "Grandpa's Biology (the one I pursued) is dead". She shared my interest and joy in observing creatures in the field and, like me, was fascinated when in 1958 we explored our first coral reefs in the Caribbean. In due time she learned to accommodate herself to my scientific perspective and, eventually, to endorse it fully. Its elaboration benefited greatly from the critical view she applied

to a branch of biology that she had been wont to look at with some condescension. When I planned the mariculture work, she decided to join me, took leave from her high-school teaching job in 1978 for the feasibility study across the Pacific, then worked full time with me after she quit teaching and was with me again in Papua New Guinea, India and Sri Lanka. We have been mates in studying collections (starting on our honeymoon when we looked up the type of the Giant Salamander in the Leiden museum), in doing field work in the Seven Seas, in working up questions and answers and in publishing the outcome, in teaching assignments, academic and otherwise. She was at my side in the environmental work, and conducted much of it on her own. Thus she was with me around the world and during the ups and downs of my zig-zag career, and suffered from rebuttals more than I did. So, after a friendship of nearly 60 years (we first met in 1943) and unwavering support for 46, the very last word of my last professional publication is: Thank you, Heidi!

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