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Adolf Remane (1898–1976) and his views on systematics, homology and the Modern Synthesis

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Abstract

Adolf Remane was primarily a morphologist and systematist. In 1952, he published an influential book on the foundations of systematics and phylogenetics in which he advocated homology as the central concept of morphology and the basis of the natural system and discussed criteria serving to discriminate homology from homoplasy in great detail. During the decades when the Modern Synthesis of evolution was created, he repeatedly commented on and criticised the synthetic theory of evolution, which he never fully accepted. Remane disapproved of idealistic morphology and was strongly opposed to Lamarckian, saltationist and orthogenetic theories of evolution. Yet, while appreciating the synthetic theory's validity in the realm of speciation and microevolution, he rejected the claim that the current genetic knowledge was sufficient to explain complex morphological transformations on the basis of random mutations and selection. Instead, he seems to have favoured mutation pressure as the most important factor in macroevolution. Nevertheless, the sometimes vicious disputes between Remane and the adherents of the Modern Synthesis may at least partly have been brought about by personal factors rather than by scientific differences.

Keywords: Natural system; Phylogenetics; Homology; Synthetic theory of evolution

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Introduction

Adolf Remane was one of the most versatile German zoologists of the twentieth century. His main biological concerns were morphology and phylogeny but he also worked on ecology, marine biology and various other topics, covering virtually all higher groups of animals from marine invertebrates to mammals (cf. Weigmann, 1973). Outside the German-speaking countries, he is probably best known for his discovery of the interstitial fauna (meiofauna within the interstitial spaces in the sand), his research on the biology of brackish water and his theory on the origin of the celom within the Bilateria which combined the enterocele theory with the origin of metamerism (Remane, 1950, 1963a, for a review and critique see Zachos and Hoßfeld, 2001). Remane regarded the celomic pouches in archimeric organisms such as echinoderms and the gastric pouches of Cnidaria as homologous and thus derived the Bilateria from Cnidaria-like ancestors. This implies that the stem species of the Bilateria already displayed a celomate organisation and that the celoms in all subgroups of the Bilateria, specifically in the two major lineages – Spiralia and Radialia – are homologous. Elegant as Remane's views may be, against the background of modern morphological and systematic research, his theory must be considered refuted. Although Remane worked extensively on the theoretical foundations of systematics and phylogenetics his findings and theories remained widely unnoticed in the English literature, partly because he mainly published in German. Remane was not primarily interested in the study of evolutionary mechanisms because he was committed to the patterns rather than to the processes of evolution. Nevertheless, as his most productive years fell within the time of the Modern Synthesis and he was convinced that the evolutionary process should form the basis of biological systematics, Remane commented extensively on the new view of evolution. In this paper, we present a short summary of Remane's work and ideas on systematics and evolution with a particular emphasis on his views on the validity of the synthetic theory.

Biographical sketch

Adolf Remane was born on August 10, 1898 in Krotoshin (in today's Poland). After the First World War he studied biology, palaeontology, anthropology and ethnology in Berlin and obtained his Ph.D. degree with a thesis on primate skulls in 1921. In 1929, he became an extraordinary professor in Kiel. From 1934 to 1936 he was a zoology professor in Halle an der Saale, but in 1936 he returned to Kiel and became the director of the Zoological Institute and Museum, a post he held until his retirement in 1967. Also, he was the founder of the Institute of Marine Biology at Kiel University and co-founder of the *Norddeutsches Phylogenetisches Symposium* (North-German Phylogenetic Symposium).

After the fall of the Nazi regime, he was temporarily dismissed by the military government and, having been a member of several Nazi organisations including the national socialist party (NSDAP) and the SA, regarded as a nazi sympathiser (*Mitläufer*) but finally reinstated as professor. Remane was engaged in several scientific societies. In 1963/64 he was the president of the German Zoological Society and became an honorary member in 1975, one year before his death on December 22, 1976 in Plön (northern Germany).

His ca. 300 scientific publications include, among other books, his theoretical "opus magnum" *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik* ("The foundations of the natural system, of comparative anatomy and phylogenetics", 1952, second edition 1956) and, co-authored by two of his former students, two zoology textbooks which have become classical texts at German universities and have been translated into several languages. In his lectures, he covered subjects and topics as diverse as systematics and comparative anatomy, genetics and marine biology, evolution and ecology, behavioural biology, biogeography, parasitology and the history of biology.

The natural system, phylogenetics and morphology

In his main theoretical publication from 1952, Remane discusses the foundations of systematics and phylogenetics. To him, the natural system is a reference system and differs from artificial systems in its predictive power: whereas simple classifications based on single arbitrarily chosen characters are often valuable in practical questions such as species determination, only the natural system is robust beyond the set of characters used in its construction – in other words, the same groupings will be found if other traits are analysed. The primary task of systematics, according to Remane, is the distinction of essential from non-essential characters (Remane, 1952, p. 11), and the only characters essential for the natural system, and hence the only characters to be used in its construction, are homologies (Remane's homology concept is described in the next section). Against Haeckel and others, he insists on the methodological and logical primacy of systematics over phylogenetics since homologies and the natural system are the primary research results and phylogeny their secondary interpretation (Remane, 1952, p. 13, 1955). Also, he quite rightly points out that the notion of a natural system is historically older than ideas about phylogeny and evolution. The vertebrates, for example, had long been considered a natural group when, in the light of evolution, this naturalness was re-interpreted as descent from a common ancestor. Remane defends the dichotomous tree as the appropriate form of representation of the natural system as he strongly believes in the monophyly of the higher groups. Monophyly, in Remane's terminology, means unique origin (i.e. going back to a common ancestor) and must not be confused with Hennigian monophyly since Remane accepted paraphyletic groupings. Interestingly, Remane, without using modern terminology of course, already advocates many systematic principles which, through Hennig's phylogenetic systematics (Hennig, 1950, 1966) and cladism, have become important terms and tools in modern systematics. Examples include the distinction between primitive and derived characters, stem species and ground pattern, and even outgroup comparisons (Remane, 1952, p. 140, 154, 156, 159). Remane did not quote Hennig, perhaps because he had worked on or even completed the manuscript before Hennig published his ideas.

An important question concerning Remane is his attitude towards idealistic morphology. Ernst Mayr has stated that this typological tradition was far stronger in Germany than in the US and that it had a great impact on the development of evolutionary theory in Germany, particularly causing a delay in the acceptance of the synthetic theory (Starck, 1980; Mayr, 1999; Meister, 2005). Idealistic morphology, according to Mayr, "was promoted in a number of very successful books by Remane, Schindewolf, and Troll" (Mayr, 1999, p. 24). Unfortunately, Mayr does not give the title of Remane's book, but it probably was his *opus magnum* from 1952. Curiously, in this book, Remane seems to reject idealistic morphology rather vigorously. He repeatedly stressed that the philosophical core of idealistic morphology was the metaphysical interpretation of results yielded by morphology and by homology research (Remane, 1948, 1952, p. 13f.). The natural system emerging from morphological analyses was then interpreted as revealing the uniform type or *Bauplan*, in other words the idea behind the multitude of similar but different organisms. This type is a metaphysical abstraction and will never be found in nature. Remane on the one hand insists that this does not lower the value of the morphological results themselves (and, indeed, much of the pre-Darwinian knowledge on morphology and systematic relationships is still valid) but on the other hand regrets that there has been no methodological purging in phylogenetics following the introduction of evolutionary thought (Remane, 1948). Remanes views on idealistic morphology are best depicted by explaining his distinction between what he calls generalised and systematic type. This distinction is basically the same as the one between (idealistic) *Bauplan* and (real) stem species and is outlined in Remane (1948) and in the fourth chapter (*Typus und Stammform*, "Type and stem form") of his 1952 book. Remane explicitly states that idealistic types belong to the realm of natural philosophy but are useless for natural science (Remane, 1952, p. 146, footnote 1). He distinguishes four different types among which the generalised and the systematic types are the most important. Actually, what Remane calls systematic type is far from being what is normally called an idealistic type, but unfortunately he held on to this term, which may have led to some confusion about his attitude towards idealistic morphology. The generalised type aims at depicting all the traits that are shared by a group of organisms. It is an abstraction of living organisms and as such does not itself represent an actual individual (Remane, 1952, p. 151f.) but rather the idea of, say, a mammal stripped of every single trait of a *particular* mammal. The similarity to Platonic idealism is obvious. Remane rejects this idealism and even makes it responsible for "repeated crises in the realm of the theory of descent" (Remane, 1948, p. 261), citing, e.g. typostrophism as one of these crises. In contrast to the generalised type, the so-called systematic type is an explicitly phylogenetic term. Its reconstruction implies the reconstruction of the ground pattern of the taxon under study (Remane, 1952, p. 152ff.). The systematic type is not idealistic but a real organism, namely the stem species (called *Stammform*, *Urform* or *Urtyp* by Remane), and hence may actually be found in the fossil record (Remane, 1948, 1952, p. 156). Based on an analysis of the publications cited, we reject the idea that Remane was an adherent of idealistic morphology in the tradition of Johann W. von Goethe or Wilhelm Troll.[1] He should be seen as a true phylogeneticist.

The concept of homology

One of the corner-stones of Remane's work on morphology and phylogenetics is the concept of homology (Remane 1952, 1955, 1963b). A homology is generally defined as "a character shared between species that was also present in their common ancestor" (Ridley 1996, p. 381f.). Remane was aware that this definition represents the theoretical interpretation of homology rather than its quality: "Realisation of homology and natural system are logically and historically the primary research results, phylogenetic relationship and trees only their secondary interpretations. [...] *It is not phylogeny that determines homology but homology that determines phylogeny*" (Remane, 1955, p. 171f., his italics).

As a tool to identify homologies, he summarises and explains in detail three criteria which had been used by various authors before Remane and even before the establishment of the theory of evolution (Remane mentions, e.g., Goethe; the term homology was originally coined by Richard Owen, a convinced anti-evolutionist; Rupke, 1994). These criteria are: (1) position, (2) specific quality and (3) connection through intermediate forms (criterion of continuity) (Remane, 1952, Chapter 2; 1955).

According to the criterion of position, two (or more) characters or character states are homologous if they are found in the same place in comparable structures. Thus, the thighbones of humans and dogs are homologous because they both represent the first part of the hind limb in the mammalian skeleton. If this criterion is not met characters can still be homologous if they show a high degree of similarity in specific features (the more complicated these features the better). Remane exemplifies this with the notochord and the neural tube in tunicates and vertebrates. The criterion of continuity, finally, allows the realisation of homology even in the absence of equality regarding position or structure if there are intermediate forms connecting the two characters under study. These intermediate forms may be ontogenetic stages or systematically intermediate species. Using this criterion, the primary jaw joint of non-mammalian vertebrates and two auditory ossicles (malleus and incus) in the middle ear of mammals can be shown to be homologous because the transition can be demonstrated both ontogenetically (Starck, 1995) and phylogenetically (Benton, 1997).

In addition to the three main criteria, Remane also introduces three complementary criteria which may help in discriminating homology from homoplasy: (1) even simple structures may be considered homologous if they occur in many related

[1]For a thorough discussion of idealistic morphology and typology, see Levit and Meister (this volume).

species; (2) the probability of two or more characters being homologous increases with the frequency of occurrence of other similar characters in the same two (or more) species; and (3) the probability of the characters under study being homologous decreases with the frequency of occurrence of this very character in definitely non-related species.

Although Remane's criteria are descriptive, some of them – the phylogenetic (but not the ontogenetic!) continuity, and the three complementary criteria – clearly imply a priori knowledge (or at least hypotheses) about relatedness and phylogenies. These hypotheses, in order not to render any argumentation circular, have to be derived from other characters than the ones whose homology or homoplasy is to be analysed. This relativises Remane's bold claim that it is homology that decides about phylogeny and not the other way around and is reminiscent of the so-called phylogenetic or historical homology concept (cf. Patterson, 1982; Rieppel, 1980, 1992, 2005). Homology, according to this notion, is regarded as a uniquely derived character inherited from a common ancestor, in other words, a synapomorphy. The hypothesis of homology, which may be arrived at on the basis of the above-mentioned criteria, is evaluated by the congruence of the distribution of this character in a phylogeny which in turn has been derived from other characters. Employing the principle of parsimony, a character in two or more taxa is considered homologous if it appears as a synapomorphy in the phylogeny. Alternatively, it is considered homoplasious if the phylogeny suggests an independent origin of the identical character in two or more taxa. This deductive homology concept (Rieppel, 1980) is the very opposite of what Remane wanted homology to be: the systematist erects a hypothesis about homology and then corroborates or refutes it on the basis of a phylogenetic analysis. However, any phylogenetic analysis has to be based on characters or, more exactly, on character states, and in order to be able to define character states one must have an idea of what a character is, or, in other words, one must have made a choice of which structures are considered to be *comparable* and which are not. No systematist would ever interpret the reduction of teeth and the reduction of limbs as two states of one character. Thus, a priori hypotheses (those about the definition of characters) are indispensable for the deductive concept of homology as well.

Remane and the synthetic theory of evolution

Remane's reputation as a phylogeneticist is shown by the fact that he was asked to write the chapter on the evolutionary history of animals (Remane, 1959a, 1967) in the second and third edition of Gerhard Heberer's *Die Evolution der Organismen* (1954–1959; 1967–1974), whose first edition (1943) was one of the key publications during the evolutionary synthesis in Germany (cf. Hoßfeld, 1997, 1999; Reif et al., 2000; Junker and Hoßfeld, 2001; Junker, 2004). As already stated in the introduction, Remane was not primarily interested in causal evolutionary biology, and his 1952 book is explicitly dedicated to the foundations of systematics, phylogenetics and the concept of homology, but it also contains an appendix on the causes of evolution called *Die Evolutionstheorien in ihrem gegenwärtigen Stand. Das Problem der Mikro- und Makroevolution* ("The present state of the theories of evolution. The problem of micro- and macroevolution", Remane 1952, pp. 322–377). In this chapter, Remane makes a distinction between speciation and what he calls "organisational modification". From the context, it becomes clear that this distinction is equivalent to the one between cladogenesis and anagenesis *sensu* Rensch (1947). To Remane, organisational modification, or anagenesis, is equivalent to evolution, and interestingly, he believes that the problem of speciation has basically been solved by the combined work of systematists and geneticists (Remane, 1952, p. 323). He originally planned to write a second volume to his 1952 book about species concepts and speciation, but this volume never appeared. Nonetheless, Remane did not seem to doubt the validity of the synthetic theory as far as speciation and microevolution are concerned. In this context, it is interesting to have a look at the literature Remane cites in his book. In a footnote to his evolution chapter in the first edition, he explains that the text was written 7 years before its publication, i.e. in 1945, which is why he did not refer to recent works by Rensch, Huxley, Goldschmidt and Simpson. The footnote does not reappear in the second edition (Remane, 1956) but still Huxley (1942), Mayr (1942), Simpson (1944) and Rensch (1947) remain uncited. The only author commonly associated with the modern synthesis whom Remane cites is Theodosius Dobzhansky (1937, German translation, 1939) but he also refers to chapters in Gerhard Heberer's volume (Heberer, 1943) and to publications by Timoféeff-Ressovsky (1939a, b), which were integral parts of the synthesis in Germany (cf. Hoßfeld, 1998; Junker and Engels, 1999; Reif et al., 2000; Junker and Hoßfeld, 2001; Junker, 2004). Thus, despite his approval of the validity of the synthetic theory in the realm of speciation, it is not clear whether Remane really had read all the key works of the synthesis by 1956.

Remane distinguishes five theories on the causes of evolution: (1) combination theory (*Kombinationstheorie*), (2) mutation theory (*Mutationstheorie*), (3) inheritance of modifications (*Erblichwerden von Modifikationen*), (4) orthogenesis, and (5) the theory of direct adaptation (*Theorie der direkten Anpassung*) (Remane 1952, p. 323, 328). While combination and mutation theory are based on observable and testable genetic changes, which is the "scientifically correct approach" (p. 324), the other theories emphasise qualities of individual organisms (ontogenetic changes, modifications, etc.), rather than genetic changes and therefore have to be viewed very critically (p. 324). Accordingly, he rejects Lamarckism (inheritance of modifications and the theory of direct adaptation) and orthogenesis. Orthogenesis, the teleological idea that evolution is not the sum of independent accidental steps but follows a path predetermined by internal forces, was a popular theory especially among palaeontologists (e.g. Schindewolf, Beurlen and Abel). Remane explicitly makes use of selectionist arguments in the context of orthogenesis when he explains the phyletic lineages, as in the evolution of horses, and the occurrence of hypertrophic secondary sexual characters (two classical examples in orthogenetic theory) as a result of directed selection (orthoselection) and sexual selection, respectively (p. 331, 334).

As to the combination theory, which is based on the phenomenon of the recombination of maternal and paternal alleles during sexual reproduction, Remane holds that this mechanism is not powerful enough to create the variability necessary to explain evolutionary processes. It is also not applicable to taxa that reproduce asexually or parthenogenetically (p. 345f.).

The last theory which Remane deals with is the mutation theory. It is important to stress that this theory has nothing to do with De Vriesian saltationism. Remane strongly disapproved of saltationist views *sensu* de Vries or Goldschmidt and Schindewolf (Remane, 1948, 1957) but regards macroevolution as a gradual process (see below). In fact, it is quite obvious that what Remane calls mutation theory is the synthetic theory of evolution, and he refers to Fisher, Wright, Dobzhansky, Timoféeff-Ressovsky and the work of Wilhelm Ludwig who had published a number of papers on natural selection (e.g. Ludwig, 1933, 1943). According to Remane, the mutation theory tries to explain evolution through the effects of random mutations and selection and also regards population waves and isolation as additional factors (p. 349). To him, there is no denying that ''these factors, *particularly selection*'' (p. 349, our italics) indeed function as evolutionary mechanisms as shown by a sufficient amount of experimental evidence. The decisive question is whether they are able to explain evolution as a whole and Remane points out differences between geneticists and microsystematists on the one hand and morphologists and palaeontologists on the other. In other words, he refers to the question whether macroevolution should be seen as an extrapolation of microevolutionary processes or not. Starting from a statement by Timoféeff-Ressovsky, who had claimed that all character changes were explicable by mutations – a conclusion regarded by Remane as ''doubtlessly rash'' (p. 354) – he tries to examine which phylogenetically relevant phenotypic changes have an observable analogon among the mutations and which do not. These observable mutations Remane calls ''real mutations'' (*Realmutationen*, a term coined by him in an earlier publication, Remane, 1939). To Remane, this comparison of phenotypic and genotypic changes is the only way of uncovering the causes of evolution since, due to the historical character of evolutionary biology, ''a completely exact explanation of the causes of phylogenetic processes'' is impossible (Remane 1939, p. 208). In accordance with his earlier appreciation of the synthetic theory in the realm of speciation, he acknowledges that differences on the level of species and genera match well with certain mutations, e.g. wingless mutants in insects or mutations resulting in multiplications of organs or changes in proportions or floral symmetry (for a classification of the different morphological results of his real mutations cf. Remane 1949, 1952, p. 357ff.). However, he also holds that there are aspects of the evolutionary process that are not yet covered by observable mutation phenomena. These aspects are what Remane calls differentiation and synorganisation. Differentiation occurs when similar elements become different in the course of functional changes (Remane 1952, p. 233, 367), as in the evolution of different cell types in multicellular organisms, the polymorphism of polyp colonies in Cnidarians or the formation of different types of vertebrae along the vertebral column (Remane 1939, p. 367). Synorganisation, according to Remane, is the formation of a novel complex apparatus from single structures (Remane 1952, p. 253, 367). The transformation of the primary jaw joint into auditory ossicles in mammals (see above) is a good example of this phenomenon. Remane is aware of the common objection to his line of argumentation – namely, that these changes are arrived at through a number of small mutations – but in his view this would only result in an ad hoc hypothesis, and the probability of a successful formation of a new structure will decrease if it hinges on a multitude of unidirectional but independent random mutations (p. 368). Remane concludes that "the mutation phenomenon as an evolutionary mechanism is still insufficient" (p. 370) but admits that this does not mean a refutation of the mutation theory since it is possible that the missing types of mutation will be found in the future and turn out to be identical to the known real mutations. One definitive case of differentiation and synorganisation being caused by observable mutations would be enough for the mutation theory to be corroborated, but as long as this is not the case Remane rejects any claims as to its general explanatory power for the evolutionary process (p. 371, Remane quotes Bauer and Timoféeff-Ressovsky, 1943). In this context, it is of importance that some adherents of the synthetic theory shared Remane's skepticism: Baur (1919, p. 346) talks of as yet unknown categories of mutations explaining the differences between the higher categories (he removed this thought from later editions, cf. Junker, 2000), and even Rensch, in his 1947 book, which is internationally regarded as one of the core publications of the synthesis, mentions specific macroevolutionary rules or laws which cannot be derived directly from the genetically studied microevolutionary processes (Rensch, 1947, p. 1; later, having gained access to the international literature, especially by Huxley, Mayr and Simpson, he made up his mind about this issue, cf. the foreword of Rensch, 1972). Further, in his contribution to the well-known volume on the history of the modern synthesis (Mayr and Provine, 1980), Rensch, although criticizing Remane's pessimism, states that Remane "correctly claimed that geneticists should search for mutations that could particularly contribute to the understanding of the phylogenetic development of new organs" (Rensch, 1980, p. 289). It also deserves attention that one kind of the type of mutations demanded by Remane has actually been discovered – the so-called *Hox* mutations. *Hox* genes are developmental genes governing the basic body structure and the differentiation of body segments. Interestingly, analyses of *Hox* genes in mice have shown that mutations at these loci can change the identity of the vertebrae produced (Kostic and Capecchi, 1994) – one of Remane's examples of differentiation processes not yet (i.e. in 1939 or 1952, respectively) covered by observable mutations! It is now common knowledge that *Hox* gene duplications may have played a key role in the origin of vertebrates and probably, within the vertebrates, in the origin of jawed forms (cf. Carroll, 1997 for a summary). In other words, two major transitions in evolution were probably triggered by hitherto unknown key gene mutations.

Remane does not define the two terms of micro- and macroevolution as processes referring to the species level (microevolution) and to the higher categories (macroevolution), respectively, but follows Richard Woltereck in regarding micro-evolution as changes in proportion or position and reductions; and macroevolution as a change in organisation (organisation being more or less equivalent to differentiation and synorganisation, p. 373). Thus, macroevolution is the part of the evolutionary process which has not yet been explained by the synthetic theory. Remane concludes that "as yet there is only probability evidence [*Wahrscheinlichkeitsbeweise*] in support of different phylogenetic processes in micro- and macroevolution, but this evidence exists" (p. 374). Although he forcefully rejects any kind of saltationist macroevolutionary theory or macromutations and instead insists that both comparative anatomy and palaeontology show that macroevolution proceeds gradually in small steps (p. 374, Remane, 1939, 1957, 1959a, p. 417; for a general rejection of sudden typogenesis cf. Remane, 1948), this skepticism is a clear contrast to one of the basic tenets of the synthetic theory – that there are no specific factors governing macroevolution other than the processes observable in populations.

So far, the only real difference between Remane and the proponents of the synthetic theory seems to be the different views on how far mutation and selection, as they could be experimentally observed then, were able to explain the evolutionary realm beyond direct empirical observation. We doubt that, as Junker (2000) claims, Remane wanted to play down the role of genetics in evolutionary biology. In fact, Remane agreed with Timoféff-Ressovsky on the primacy of genetics in unravelling the causes of evolution (compare Timoféeff-Ressovsky, 1939a, p.161, with Remane, 1939, p. 220). But in the wake of the dispute on macroevolution Remane came up with the idea of "mutation pressure" as a possible solution: "Considering the whole situation it seems most likely to me that certain mutations occur in high frequencies and in a *largely directional manner* and that this accumulation repeats itself over many generations. The phylogeneticist thus wishes for […] *directional mutations* […] to explain evolutionary trends" (Remane, 1959b, p. 225, our italics). This mutation pressure, according to Remane, lessens or abolishes the need for intensive selection. He admits that this kind of mutation is yet unknown but hopes for its discovery (Remane, 1959b). This, of course, stands in clear contrast to the synthetic theory and contemporary genetic knowledge. Not surprisingly, given the speculative character of his conjecture, Remane does not go into further detail. Junker (2000, 2004) concludes that the main cause for the controversy between Remane and the proponents of the synthetic theory was philosophical: a clash of Remane's pantheistic ideology on the one hand and the pragmatic materialism of the synthesis on the other, but the only evidence of Remane's alleged pantheism is a former colleague's remark in an obituary. Junker even regards Remane as an anti-Darwinian because of his skepticism concerning the role of selection in macroevolution. Although this evaluation depends on the definition of Darwinism (of which there are many), it may be a little exaggerated. Yet, there is a general discrepancy between the rather descriptive and often neutral style of Remane's publications and the way he is remembered by his contemporaries. Ernst Mayr, for instance, remembering the first phylogenetics symposium in Hamburg in 1956, states that the "main spokesman of the opposition [against the synthetic theory] was Remane, who attributed everything to De Vriesian mutations, revealing that he had no idea of modern genetics" (Mayr, 1999, p. 24; Kraus and Hoßfeld, 1998). Mayr here regards Remane, Schindewolf and Troll as prominent adherents of idealistic morphology in zoology, palaeontology and botany, respectively (Mayr, 1999). While the typological (idealistic) approach in morphology had indeed been predominant in Germany since Goethe, Remane, as shown, was critical of it. Neither was he a De Vriesian saltationist. As a matter of fact, although clearly an opponent of important parts of the synthetic theory, Remane did not completely reject the synthesis but seems to have fully appreciated it in the realm of microevolution. As to macroevolutionary processes, he was very reserved and looked for alternative explanations. The debate over macroevolution, however, has been going on ever since, and the hypotheses of punctuated equilibria (Eldredge and Gould, 1972, for an exhaustive discussion cf. Gould, 2002), species selection (Stanley, 1975, 1979) and the neutral theory of molecular evolution (Kimura, 1968, 1983) have shown that, while the basic validity of the synthetic theory has not been questioned, many issues concerning selection, gradualism and macroevolution are still being discussed (see also Levit et al., 2003).

Concluding remarks

Adolf Remane was without doubt one of the most influential zoologists of the twentieth century in the German-speaking world. Outside these countries, however, he was barely noticed as far as his theoretical publications are concerned. Unlike the major works by Rensch and Hennig, his 1952 book has never been translated into English, and citations of his publications are only rarely found in the English literature. The three criteria of homology given by Remane are also mentioned by Ridley (1996) and Futuyma (1998), probably the two most widely read textbooks on evolution, but Remane is not listed in the references by either of them. Nor are any of his works cited by Gould in his recently published mammoth work (Gould, 2002). Remane is cited by Mayr in *Animal Species and Evolution* (1963, but not in the abridged version of 1970) and by Jefferies (1986). These two authors, however, are bilingual. Ernst Mayr, in a couple of letters to one of us (UH), wrote a few years ago that Remane was only paying lip service to natural selection and that, 50 years from now, he will probably be remembered for his discovery of the interstitial fauna and his theoretical views will be forgotten. We hope to have shown that Remane made valuable contributions to the theory of systematics and phylogenetics and that he should not be regarded as a completely misled theorist. How complete an adherent (or opponent) to the Modern Synthesis Remane really was remains an interesting but maybe unsolvable riddle. It may well be that he was much more diplomatic in his written contributions than in discussions and meetings with opponents, thus veiling or playing down his aversions to the synthesis (which would explain the striking discrepancy between Mayr's recollections and many of the quotations presented here), but it may also be part of the truth that the clash of such strong and self-confident characters as Remane, Mayr and Timoféeff-Ressovsky led to an artificial inflation of their theoretical differences and made them seem bigger than they actually were.

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