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Microevolution as the only evolutionary mode[1]

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Introduction

Macroevolution is usually conceived as evolution above the species level, microevolution being evolution within species inclusive of the origin of a new species (e.g. MAYR 1942, p. 291; RENSCH 1959; STANLEY 1979, p. 2). Macroevolution is thus equated with the origin of taxa of "higher categorial rank", e.g. "genera", "families", "orders", etc. Taxa are assigned a higher rank whenever their Baupläne are distinguished from those of other taxa by a considerable morphological gap. Thus, macroevolution is the origin of those Baupläne.

Due to the imperfectness of the fossil record, the mechanisms of macroevolutionary changes cannot be discovered by simply tracing the stem-lineage of species-rich groups back into the past. Thus the palaeontologist must develop theories and attempt to test them in light of the fossil record. Although there is no continuous documentation of the origin of Recent "higher taxa", it is sometimes possible to trace evolutionary change within single species in detail. In addition, there are several evolutionary lineages known which show an amount of change usually regarded as indicative of the existence of different genera (the record of these lineages is however, usually full of gaps). Such tests have gained recent importance especially during the current punctuated-equilibrium-versus-gradualism-debate.

During the 1940's and 50's many evolutionary biologists demonstrated that all major evolutionary changes can be explained by microevolutionary steps and accumulation thereof.Three points are worth mentioning. 1. Intermediates between particular taxa had existed which were once believed to be impossible constructs – e.g. early mammals with two articulations of the lower jaw to the skull. The supposed impossibility of such forms had contributed much to the idea of the so-called "Typensprünge" (evolutionary leaps leading to a new Bauplan; macromutations). 2. The origin of many organs included functional changes. For example, the wings of the Pterygota cannot have served as flight organs during their earliest evolutionary stage. 3. Complex sets of characters were once supposed to be functional only in combination. This again was seen as evidence for major evolutionary steps. Another important contribution towards the hardening of the mod ern synthesis was the demonstration that such complexes had developed through the

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accumulation of minor evolutionary changes, these being related to slow changes of the life-habits (e.g. v. WAHLERT 1961). Thus, by the end of the 1960's the major questions of large-scale changes seemed to have been answered. One aspect, however, had hardly been taken into consideration: the relationship between speciation and major evolutionary changes.

SIMPSON held the view that the main source of adaptive changes is transformation within a usually not or rarely splitting lineage – a view which found wide spread acceptance among palaeontologists (see e.g. GEORGE 1971, Fig. 18; GOULD 1980, p. 161). Species as conceived by the palaeontologist were sections of lineages, only arbitrarily delimitable as there is no objective criterion of dividing a natural continuum into units. Thus, a species was seen as an assemblage of morphologically similar individuals.

A species is however, not a morphological unit. The crucial criterion of the species as a real unit of nature is reproductive isolation, as pointed out especially by DOBZHANSKY (since 1937) and MAYR (since 1942). Thus species originate through the occurrence of reproductive isolation, and this implies a splitting process. Among the first palaeontologists to consequently accept this view were ELDREDGE & GOULD (1972) when they opened the discussion on that mode of evolution, which they called punctuated equilibria (as opposed to phyletic gradualism) (see below for qualifications).

Their ideas, essentially those of MAYR (1942, 1954), but with more weight on palaeontological data, are well known: Normally, species do not undergo considerable change because they are in an equilibrium with their environment. Evolutionary changes usually occur within an instantaneous period of time during speciation (splitting) events. As this is expected to take place mainly in small populations, the documentation of such an event in the fossil record is unlikely. Hence, species usually first appear in the fossil record when they are fully established and widespread and have nearly finished their morphological adjustments. Repeated speciations may lead to a considerable amount of divergence between closely related taxa within a short period of time. Anagenesis is thus accumulated cladogenesis (GOULD & ELDREDGE 1977, p. 141). Punctuated equilibrium is said to be "by far the most common tempo of evolution", while phyletic gradualism, slow change within one or few evolutionary lineages, is "both rare and unable ... to serve as the source of major evolutionary events" (GOULD & ELDREDGE 1977, p. 119).

The ideas of ELDREDGE & GOULD were most influential with regard to the origin of "higher taxa". I believe that quite contrary to the years preceding the punctuated-equilibria-debate most palaeontologists nowadays hold to the idea that such taxa do not originate through anagenesis within one or a few evolutionary lineages, but rather that their origin involves numerous speciation events and the origin of many species and species-groups.

Several points concerning the model of punctuated equilibria are the subject of a lively debate. The question as to whether "punctuated equilibria" is actually "by far the most common tempo of evolution" has been tackled by a closer inspection of evolutionary lineages. Of particular interest are questions concerning species stasis.

Species stasis

Evidence of evolutionary stasis in fossil species is of importance because stasis implies a more than merely "gradualistic" phase: Had there been no accelerated evolutionary change prior to stasis there would have been no change at all. The question is, however, whether species stasis over considerable time is a *common* phenomenon (sibling species are evidence of such a kind of stasis). There is no doubt that certain structures may remain unchanged over a long period of time. Species stasis, however, the issue of punctuated equilibria, "implies character stasis for all characters" (LEVINTON 1983, p. 113). The following paragraphs are devoted to a few critical notes concerning the recognizability and importance of stasis.

a) Stasis in fossil species must imply stasis in the visible as well as in the unpreserved structures. This however, can never be demonstrated (HECHT & HOFFMAN 1986). It is, nonetheless, known that closely related Recent species do not or hardly differ with respect to characters which might be preserved in fossils. E. g., in molluscs one might well and erroneously take the shells of several species differing only in soft-parts as evidence for stasis in one single species.

b) Most species are subdivided into several populations. Very often, each of these populations differs from the remaining ones. If these differences are due to evolutionary change (and not modifications of the phenotype due to environmental differences), and if they have occurred at various periods of time, the species has not behaved staticly. This must not be neglected if one regards species stasis as normal.

c) It has been argued that many records of stasis in fossil species are an artifact due to the tendency to subsume similar specimens under one and the same species-name (SCHOPF 1981; MAYNARD SMITH 1981; STEBBINS & AYALA 1981 and others). It should be noted that while the distribution of species in time has rarely been worked out along with careful statistic analyses, detailed investigations have repeatedly yielded unpredicted differences.

Evidence for gradualism

To GOULD (1983, p. 440) the issue concerning punctuated equilibrium is whether or not most species are stable after their origin, during which most evolutionary change occurs instantaneously.

This implies that many species did not evolve according to the model of punctuated equilibria, because they died out soon after their origin. To give an example: While HOFFMAN (1982, p. 418) considers the famous Tertiary freshwater gastropods of Kos (Greece, NEUMAYR 1880; WILLMANN 1981) to fit the model of phyletic gradualism, I am skeptical of this conclusion. Of course, they evolved continuously, and due to the perfect fossil record this can be traced in the field as if a movie were presenting the transformations. However, the changes occurred within perhaps 200,000 years, which is a short period if compared with the at least 3 my of (shell-)morphological stasis in the respective ancestors, sister-species and other relatives. Thus there is stasis in one lineage and rapid change during speciation in the other. But if punctuated equilibrium refers to a particular mode of differential behaviour of a single species, then all lineages of Kos exhibit gradualism: the in toto transformation of species during almost 100% of their existence, as the species were extinguished before they could decide to behave static. I wonder in how many species the same situation has occurred – imagine the perhaps more than

10 million extant species of insects the majority of which are but locally distributed and adapted to a narrow spectrum of environmental factors. If they are thus bound to die out soon because of environmental changes or bound to "species-dissolution" (WILLMANN 1985) due to the same reasons they would have no chance to evolve according to the model of punctuated equilibria. Taking this into accound, gradualistic change is perhaps much more common than hitherto suggested.

Another question is whether punctuated equilibrium contributes much more to major differences than change within species (decoupled from speciation), or gradualistic change. "Classical" phyletic gradualism (as apposed to the gradualistic pattern exhibited by the shortlived species mentioned above) is now known to be far from rare (see examples and discussions in HOFFMAN 1982; GOULD & ELDREDGE 1977; GOULD 1983; FAHLBUSCH 1983, 1987; FORTEY 1988; LEVINTON 1983, 1988; MALMGREN & BERGGREN 1987; SHELDON 1987 and others). In Upper Cretaceous belemnites (SCHULZ 1979) as well as in European Arvicolidae (CHALINE 1987) gradualistic evolution resulted in a considerable amount of differences. In the latter example the changes could be traced across several speciations leading to different genera. In the meantime even GOULD admitted a "high frequency of gradualism" in certain groups (1983, p. 440).

Punctuated equilibria and the relation of evolutionary change to speciation

Whether most evolutionary change is due to gradualistic evolution, punctuated equilibria or something in between is not only an empirical question. The answer depends also on the definition of "punctuated equilibrium". Of course, the model describes evolutionary stasis interrupted by short phases of considerable change. There remain, however, two possible interpretations of this model, and they both can be derived from the writings of ELDREDGE & GOULD.

a) Punctuated equilibria refers to one species only. This seems to be the intention of ELDREDGE & GOULD when they argue that a species changes rapidly as long as its population is still small and does not run into stasis until it is well established, or when GOULD says that the duration of species' changes is a certain percentage of the species' later existence in stasis. If this is true, then punctuated equilibrium is not necessarily related to speciation (which ELDREDGE and GOULD however, claim), but to bottlenecking. Bottlenecking can occur at any time during the existence of a species.

b) The model of punctuated equilibria is concerned with speciation (ELDREDGE & GOULD, numerous articles). This may also be derived from the phrase that the theory of punctuated equilibria implies "that significant ... evolutionary change happens ... not primarily through the in toto transformation of lineages" (Gould 1982, p. 137). Then, however, ELDREDGE & GOULD are wrong with the assumption that the major evolutionary changes usually occur during speciation. Speciation is the occurrence of absolute reproductive isolation, which is usually not connected with overwhelming genetic (or, the only aspect conceivable to the palaeontologist, morphological) change. On the other hand, exactly that amount of change which is related to speciation in one pair of sister-species may well occur during subspecific differentiations of other species. From this it would follow that most evolutionary transformations are not produced by punctuated evolution, not in the very moment of speciation, but within reproductively isolated units, that is, within species.

The model of punctuated equilibria is said to refer to the behaviour of species. There is however, a fundamental incongruence between species and the evidence for punctuated equilibria in the argumentation of ELDREDGE and GOULD. To illustrate this we must keep in mind that species as real units of Nature are reproductively isolated units. Thus, "reproductive isolation" (complete isolation, KEY 1981; WILLMANN 1985) is the only species criterion, and speciation "consists in the development of reproductive isolation" (DOBZHANSKY 1958) – and nothing else.

Speciation concerns two synchronous populations which become isolated from each other and thus become new species in relation to each other. Thus, a speciation event is the beginning of a *pair* of biospecies (WILLMANN 1985, 1986). This is sometimes not well understood in peripatric speciation, possibly the most common speciation mode. Here, a large and a very small population participate in the process, and it is usually only the small population which changes (MAYR 1954, 1982). However, the peripheral population becomes reproductively isolated in relation to the large one just as this population becomes isolated in relation to the peripheral one. Hence, a species ceases to exist at that moment of time at which it splits into two. There is no such thing like a species surviving speciation, which ELDREDGE & GOULD claimed (e.g. 1972, 1977, p. 35–36).

Thus whenever only one population undergoes any change in speciation while its sister-population remains unaltered a maximum of only 50% of the originating species can exhibit evolution under the model of punctuated equilibria if they really change rapidly during the very moment of the occurrence of absolute reproductive isolation, behave staticly afterwards and do not die out soon (see above). The remaining 50% of new species are not only "stable after their origin" (the relevant point to the validity of punctuated equilibria, GOULD 1983, p. 440), but they are stable during their origin as well. Thus, the relative number of possible cases of punctuated equilibria in the earliest phase of new species is reduced as compared to a typological view of the species, under which "surviving stemspecies" are accepted.

Species selection, trends, and the effect hypothesis

According to WRIGHT (1967) and GOULD & ELDREDGE (1977, p. 139) speciations as well as characters ("Wright's rule") may be random with respect to the direction of major evolutionary trends. If this is true and "if most evolutionary change occurs during speciation events ..., natural selection ... cannot play a significant role in determining the overall course of evolution" (STANLEY 1975, p. 648). If speciations are random they are comparable to the mutations on a lower level of biological organization (ELDREDGE & GOULD 1972, p. 111; cf. also MAYR 1963, p. 621). Species may then become the subject of a process called species-selection (STANLEY 1975): differential survival of species because of a higher rate of extinction among less adapted species. As the randomness of speciation generally disallows long-term phyletic trends, a trend is said to be the result of species-selection. The issue according to STANLEY is that macroevolution is decoupled from microevolution in species-selection. But if species-selection means that adaptively inferior species die out and adaptively superior ones survive, then this is a result of the differential survival or amount of successfully reproducing offspring of the individuals of the species.

Hence, species selection can be reduced to microevolution: The differential survival of species is due to the selection of individuals, there is no decoupling of micro- from macroevolution in this context, and species selection is not in itself a process.

According to GOULD (e.g. 1980) random speciation involving a rapid reorganization of the genome – perhaps non-adaptive – within small founder populations may be a basis for a decoupling of macro- from microevolution, if differential rates of such speciations plus species selection lead to trends. There is, however, no evidence for non-adaptive speciation (e.g. HOFFMANN & HECHT 1986). Moreover there is no reason to assume the truth of "Wright's rule" (MAYNARD SMITH 1981, p. 13; 1983, p. 278, LEVINTON & SIMON 1980). Why should character-change be random with respect to long-term evolution? If in a species a character had evolved which is advantageous for the species, why and how should it become reduced in one of its daughter-species and be retained or evolve further only in the other?

VRBA (e.g. 1980) argues that species can be seen as the *effect* of adaptation. Furthermore, particularly rapid speciation can be the effect of any factors which incidentally result in differential speciation rates. If an increase in the speciation rate results in a trend, this is merely an effect as well. Trends are not necessarily adaptive. If adaptations lead to an increase of the speciation rate, they were not selected for promoting the speciation rate or for avoiding species extinction in the face of future environmental change (VRBA 1983, p. 388). If "trends are effects of differential speciation rates, which themselves are effects of different degrees of environmental specializations between species, which in turn are effects of adaptations to local environments at the microevolutionary level, then microevolution and macroevolution are decoupled, because the theory of how a character becomes genetically fixed as a withinspecies adaptation clearly cannot on its own explain why a transspecific trend should evolve with respect to that character" (VRBA 1980, p. 388).

But the formation of such a trend in itself is neither an evolutionary mechanism nor due to an evolutionary mechanism of its own. Evolution is a creative process increasing the fitness of the species with respect to their actual environment. If the environment is such that the populations of a species undergo differential change (= adaptations) leading to several species, and if due to the increased survival of the adaptively superior species – which is a result of selection among individuals, see above – a trend is formed, then a trend is merely the *result* of a large amount of microevolution (see also WILLMANN 1988a).

Microevolution and the origin of species groups

Macroevolution is not only not decoupled from microevolution, in fact it does not exist.

Apart from the primarily uniparental organisms the diversity of life is subdivided into reproductively isolated units, that is, species. Thus all evolutionary change must occur within species – and intraspecific change is microevolution. Furthermore, it becomes evident that the term "macroevolution" in the sense of the origin of "higher taxa" refers to the result of a large amount of microevolution.

A result is however, not a process, while "evolution" is. Thus the term "macroevolution" is misleading and unfortunate, and it should be abandoned. Only "microevolution" is related to a causal process.

From this it follows that the observation of species must exhibit all those differences and mechanisms which in their accumulation are of importance for the origin of major differences. Had all ever existing species been preserved as fossils showing all features, there would be a visible continuum of species-differences linking all taxa, and then no one would hold to the idea that the origin of any species group – that is, any taxon of any "higher categorial rank" – is due to a process differing from that leading to the origin of two new species from one stem species.

But where does the idea of macroevolutionary mechanisms of their own come from? One reason seems to be obvious: Neontologists as well as palaeontologists have been trapped by one aspect of the current classification of organisms, namely the ranking of taxa. Following LINNÉ, the neontologists used to deal with ranks such as orders, suborders, classes, etc. Essential in ranking is the extent of the differences between the (recent members of the) groups. Fossils have often narrowed these gaps, and according to the theory of evolution originally no such gaps ever existed. The categorial ranks, however, remained. From this resulted the problem of the origin of "classes" and "orders". There are however, no "orders" or "classes", "genera", "families" or "suborders" as real units of Nature, these are artificial mental constructs dating from pre-evolutionary times. They are of no use in modern biology, mere anachronisms, not even necessary for the systematization of life (HENNIG 1969; AX 1984, 1987; WILLMANN 1987 and others). Above the species-level there is only the species-group, the monophylum, as a real unit of Nature. It thus seems medieval when STANLEY wrote as late as 1978 (p. 36) "if genera typically arise by quantum speciation" (speciation in which much evolutionary change is concentrated), "then families, orders, and classes must arise in the same manner, normally by several discrete steps".

The only process contributing to the origin of a species-group is that the latest stem-species of the group has split into two species and that the group has enlarged through further speciation events. This includes character-changes, but striking characters, which are perhaps common to late representatives of the group, may not have evolved in its early members.

The appearance of groups exhibiting in their earliest known species a Bauplan very different from that of related taxa is another reason why some palaeontologists conceive of mechanisms additional to "normal" microevolution. Obviously, I do not share this point of view. Rapid evolutionary change in small populations may be an important factor (for more details see WILLMANN 1988a, p. 158). In several instances it has become obvious that "sudden" appearances are only supposedly so – when the sister-group is known and better documented as fossils. The hitherto oldest known fleas, for example, were found in the Lower Cretaceous. But during that time, they had already left half of their history behind them. This is known because their sistergroup – either the Mecoptera, or the Diptera, or these two groups combined – originated during the Upper Permian (WILLMANN 1988b). Thus, the first ancestor of the fleas only must have originated in that period of time as well. And although there are no fleas known from strata older than the Lower Cretaceous, we can now discuss their evolution as being the result of the adaptation homoiothermic "reptile"-like mammals as early as the Late Paleozoic. The reconstruction of sister-group-relationships is thus an important means of gaining an image of the early evolution of particular groups. But the search for sister-groups is still not common in palaeontology, and often taxa are retained which are not monophyla.

This excludes a successful search. Therefore, the determination of the first appearance of many taxa in time remains still more vague than is necessary.

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