Radiation within the framework of evolutionary ecology

Walter Sudhaus

Institut für Biologie/Zoologie, AG Evolutionsbiologie, Freie Universität Berlin, Königin-Luise-Str. 1-3, 14195 Berlin, Germany

Abstract

The talks and extensive discussions on 'adaptive radiation' during the phylogenetic symposium 2002 in Bonn are summarized, and concluding remarks presented from the perspective of evolutionary ecology. Radiation is characterized as the relatively rapid origin of diverse ecological niches established by repeated speciation events within a lineage, leading to stronger evolutionary divergence and ecological diversity in a particular region. Rather than simply being multiple speciation events resulting in the formation of a monophylum, it is a concept to understand ecological divergence and biodiversity, which emphasizes diversification of ecologically relevant morphology, physiology and behaviour of the descendants of a stem species. Therefore, instead of 'adaptive radiation' it is better termed 'ecological radiation' or simply 'radiation'.

A radiation starts with the splitting of the stem species into different lineages, and ends when either a new radiation occurs within that monophylum or the monophylum becomes extinct. This leads to a hierarchical sequence of radiations, here exemplified from the phylogeny of Insecta. Three types can be distinguished: radiation after successful colonization, radiation from a survivor of mass extinctions, and radiation after evolution of key innovations. In the first two scenarios, chance is more important and the founders of a radiation might be relatively unspecialized; in the third case, the founders are more specialized and exhibit several novelties accumulated in the ancestral line. As key innovations, the role of these features is to help open a new ecozone and to recruit new resources, which is initiated by changes in behaviour or metabolic traits.

Key characters can be used under diverse ecological conditions and modes of life, and allow the establishment of various econiches. An analysis starts with the reconstruction of a phylogenetic tree based on all known characters and the reconstruction of the 'stem species pattern', followed by an analysis of transformations of functional structures to find possible key innovations. The investigation of at least nine additional points is desirable to understand radiation and thus explain diversity.
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Keywords: Ecozone; Stem species pattern; Bauplan; Colonization; Key character; Living fossils

Introduction

During the phylogenetic symposium 2002 in Bonn, Germany, zoologists, paleontologists and botanists discussed 'adaptive radiation' from their different perspectives. It was debated whether the term 'adaptive radiation' is a concept of evolutionary ecology which has heuristic value for the study of biodiversity, or whether it describes nothing but multiple speciation events, i.e. the origin of a monophylum consisting of more than two species.

When talking about 'radiation' I suggest to avoid the epithet 'adaptive', because it might imply that there is such a thing as non-adaptive radiation. However,

non-adaptation cannot be demonstrated, since it is principally impossible to show that a structure has no function. We can only investigate whether a given function is present or not, but cannot test for all possible functions. In this sense, those who claim that there is functionlessness and non-adaptation have the burden of proof. It was suggested, that we need non-adaptive radiation as a null hypothesis. Do we really, to have the pleasure of easily falsifying it? It appears self-evident that there is no differentiation of populations, and no speciation, without local adaptation. Therefore, simply 'radiation' is the more appropriate term. A possible alternative is 'ecological radiation', as it emphasizes the ecological aspect of evolution in general.

Approaches to the concept of radiation

Which phenomena of evolutionary biology do we associate with the term radiation? The most impressive examples reported in current textbooks (some of them were also discussed during the symposium) are the Galápagos finches; the honeycreepers (Aves: Drepanididae; see Lunau 2004), members of *Drosophila* (Insecta: Diptera) and the silversword alliance (Asteraceae) in the Hawaiian archipelago; *Aeonium* (Crassulaceae) on the Canary Islands; cichlid fishes of the large East African lakes and gammaroid amphipods from Lake Baikal (for both of the latter see Schön and Martens 2004); marsupial mammals in Australia; lemures in Madagas-

car; etc. For paleontologists radiation is a 'macroevolutionary' phenomenon. When looking at fossils, a new bauplan is found to be built up within a relatively short geological period of some tens of millions of years (e.g. high-rank groups of birds and presumably eutherian mammals in the Upper Cretaceous period before the K/T event, and the radiation of these groups after this period of mass extinction). Such data have led to the image of a sudden and "explosive" radiation, the "more or less simultaneous divergence of numerous lines" from an ancestor (Simpson 1953, p. 223), like exploding fireworks that suddenly and simultaneously burst in all directions. This image has become so deeply ingrained in the thinking of evolutionists that nearly no one questions myths like the 'Cambrian explosion' (Fitch and Sudhaus 2002).

When Osborn, who coined the term radiation (Osborn 1902), published his famous scheme of "adaptive radiation" of Mastodontoidea in 1933, he drew 20 independent lines arranged like the spokes in a sector of a wheel (Fig. 1). (A later paper by him was entitled: "The 39 distinct lines of Proboscidean descent …".) Although in his illustration there was no clear point where proboscideans started in the Upper Cretaceous or Lower Eocene, we can suppose that he assumed an unspecialized ancestor to be the starting point of unbranched lineages leading to the different forms which are chronologically documented in the fossil record at different geological times. He did not really think in phylogenetic trees, although in a later diagram he depicted some branches (Osborn 1936). The
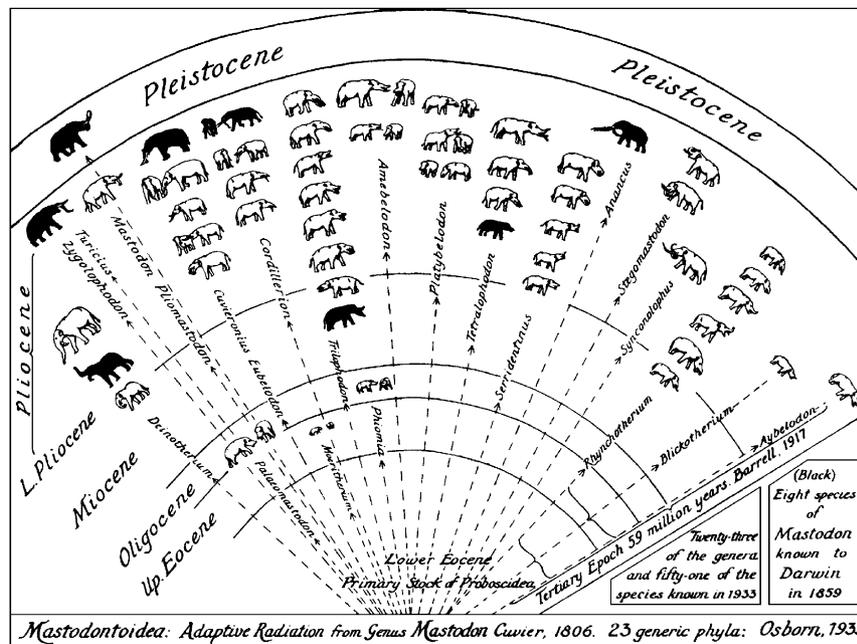

Fig. 1. Proboscidean chronology. The fan-shaped radiation of mastodonts in separate lineages from an unspecialized common ancestor in the view of Osborn (1936).

phylogenetic method of reconstructing phylogeny from the top down, starting with terminal taxa and retracing their past branching pattern by finding synapomorphies for sister taxa, was developed much later (Hennig 1950, 1966). To document the evolution of the Perissodactyla over time, Simpson (1951) arranged the different groups within concentric circles that define the boundaries between geological periods (Fig. 2). This represents a two-dimensional projection of the inner surface of a funnel in which we can look backward in time from the wide rim (today) to the narrow stem (Lower Eocene). On the microevolutionary level, the best-known example is a diagram, found in most evolution textbooks, which illustrates the radiation of Darwin's finches (Geospizidae) by arranging beak shapes in a circle, but usually lacks a phylogenetic tree. Unless the latter is added (as in the centre of Fig. 3), the diagram shows only the morphological differences that reflect differentiation in food exploitation of the 14 or 15 very closely related species, and thus resembles schemes of radially arranged variations of a 'type' (as in Fig. 4).

The few examples mentioned above illustrate the following important aspects of radiation:

- Radiation is the relatively rapid origin of diverse ecological niches established by repeated speciation events within a lineage leading to stronger evolutionary divergence and ecological diversity in a particular region. Newton (2003, p. 73) defined radiation as "the diversification of a single lineage into a range of different species in the same general region, each with distinct morphology and ecology."
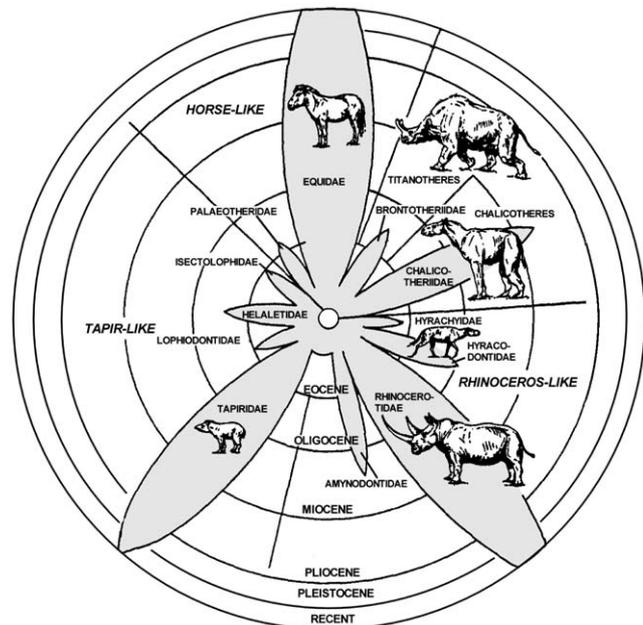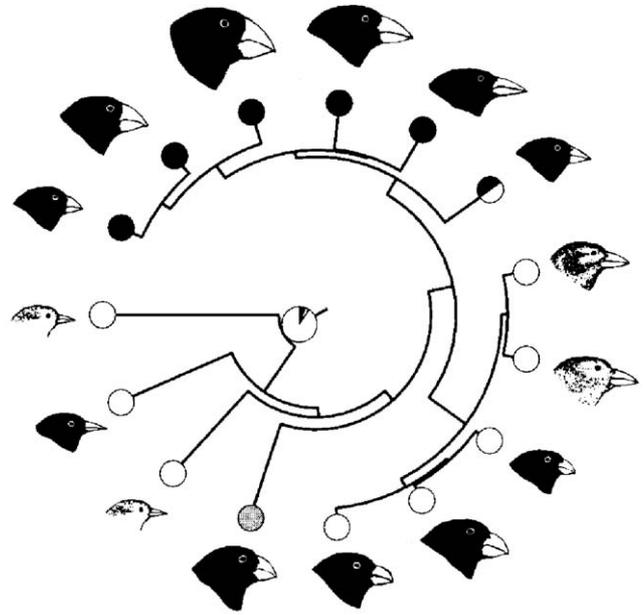

Fig. 3. Galápagos-finch radiation in beak shape and size, with underlying phylogenetic tree derived from molecular data, and indications of diets (black: seeds, shaded: vegetation, white: insects) (after Schluter 2000).
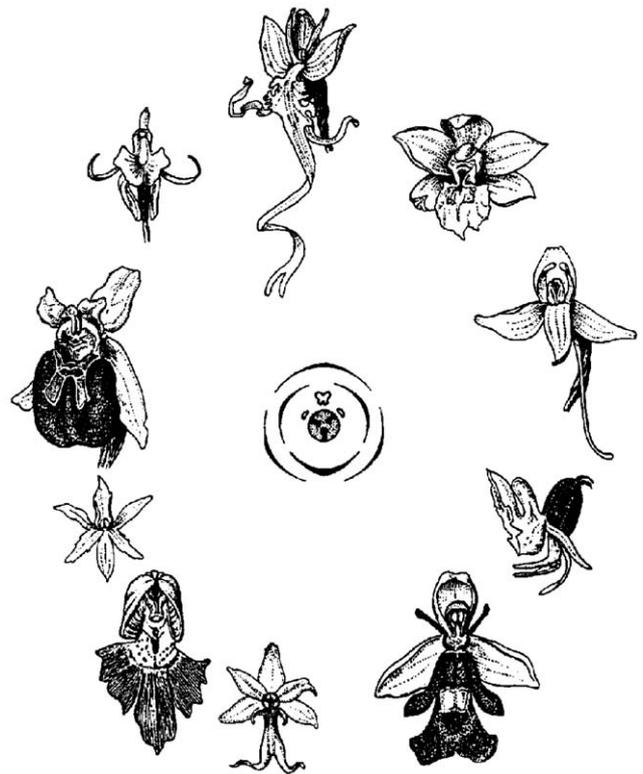

Fig. 4. Schematic flower 'type' and various flowers of European orchids (after Remane 1952).

According to Schluter (2000, p. 10), characteristics of radiation are the "appearance of new species and a concurrent increase in ecological and phenotypic diversity."

Fig. 2. Perissodactyla radiation from the ancestor in the center to a number of divergent types (after Simpson 1951).

- The radiation process begins with a species and ends when the radiating monophylum becomes extinct (like in †Ichthyosauria) or when a new bauplan is built up in a descendant lineage and a second radiation takes place, establishing a new ecological zone, or ecozone (Fig. 5). (The end of the radiation of Amniota is the beginning of radiation of crown groups like birds and mammals, but also of extinct groups like †Pterosauria.) The end of a radiation is not as sharply demarcated as the beginning, because in different lineages of a radiating taxon new radiations can take place during quite different periods of time.
- Radiation in the organismic view emphasizes diversification of morphology, physiology and behaviour of the descendants of a common ancestor. Therefore, the term brings into focus the potentials in the genotype and construction or bauplan of the stem species, its capacity or 'versatility', which was partially realized under the circumstances given in the past. As a result, we find multiple variations of the stem species pattern due to speciation events.
- In the ecological view radiation demonstrates which ways of life were ecologically licensed under the particular environmental conditions in the past.

Some points need to be discussed in more detail:

- At a geological scale, radiation appeared as a 'relatively rapid' process. In some well-studied cases (e.g. cichlid fishes) it can be shown that many species arose within an extremely short period of time. However, in most cases the period of time during which radiation took place is unknown. Therefore, speed cannot be an essential attribute of radiation.
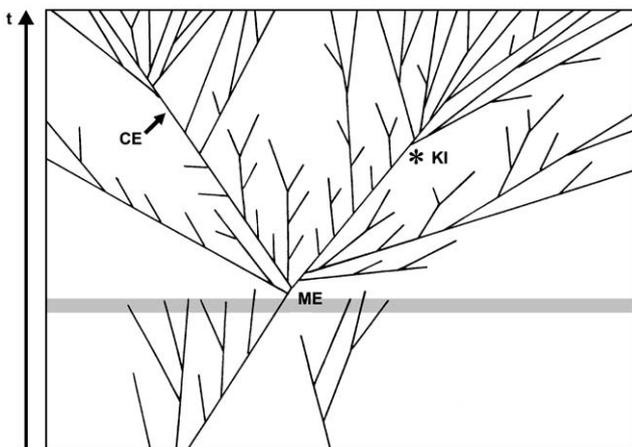

Fig. 5. Hypothetical phylogenetic tree to illustrate crucial circumstances that trigger impressive radiations starting: at ME from a species that survived a radical change with mass extinctions, at CE after a successful colonization event, at KI after acquisition of key innovations.

Nevertheless, the period of divergence in lineages near the time of their origin is quite short compared to the long periods over which basic body plans and ways of life are retained on geological time scales ('stasis').

- Even though cladogenesis was not dealt with in most of the examples mentioned, it constitutes the skeleton of radiation. Polytomies that are frequently found in phylogenetic reconstructions almost never indicate a special type of radiation (simultaneous splitting or 'explosion'). A polytomy in a phylogenetic tree usually means that we are as yet unable to resolve the dichotomous branching pattern. It does not denote a polytomous speciation event where two or more speciation processes were completed (!) at the very same moment (which is nearly impossible).
- Radiation means the formation of a monophyletic taxon of at least three species by two or more speciation events. Examples with the minimum of three (extant) species could be the iguanas of Galápagos (*Amblyrhynchus cristatus*, *Conolophus pallidus*, *C. subcristatus*) or the monotreme mammals in the Australian region (*Ornithorhynchus anatinus*, *Tachyglossus aculeatus*, *Zaglossus bruijni*). Objections against these as examples for radiation might be based on the very low species number and the considerable divergence between the two types of monotremes, the platypus and echidnas. This suggests a very large number of extinct species, which—if they were known—would represent the real radiation.
- Do we need the special term 'radiation' if it only describes a successional process of multiple speciation events? The term also implies diversification by establishment of new ecological niches. It thereby means ecological differentiation combined with phenotypical diversity (see Claßen-Bockhoff et al. 2004). For example, regarding marsupial mammals most people only think of their radiation in Australia, where marsupials attained a much higher diversity than in South America. Therefore, I think, we would hesitate to use the label 'radiation' if we were to talk about very similar forms like the five species of the cephalopod *Nautilus,* the three species of kiwis (*Apteryx*) or the seven species of the *elegans*-group in the nematode taxon *Caenorhabditis*. In the case of *Salvia*, Claßen-Bockhoff et al. (2004) do not consider 'adaptive radiation' as the only appropriate expression, even though there are about 920 species in this taxon and evolutionary divergence is found in the flowers.

Radiation should mean qualitatively more than multiple speciation events. However, it might depend on the sensitivity of the observer whether existing differences are realized. It is when we find a number of

distinct species which exhibit very different forms and lifestyles, that our thoughts about something beyond speciation within a group are inspired. The concept of radiation serves to investigate a diversity of forms originated by centrifugal evolution. Starting from one species, evolution is driven in different directions. This view underlines the significance of interspecific resource competition between members of a radiating taxon, which drives the establishment of very different eco-niches.

The three types of radiation

Regarding the circumstances and a given geographical region, three main types of origin of a radiation can be distinguished (Fig. 5): (1) after successful colonization of a new region where species with a similar mode of life are missing, (2) from a survivor of mass extinctions in the main area, and (3) within species-rich communities in the area of origin after the evolution of key innovations. A combination of these types within a radiation process is possible.

Radiation after successful colonization

Occasional dispersal events across a pre-existing barrier into a fragmentated area (e.g. an archipelago) can lead to colonization and speciation, depending on the features of the invaders, the ecological opportunities and the existing competitors. The process starts with the accidental dispersal of individuals of a certain species to a different area, or to a new host species in the case of parasites. The ability to survive and propagate in the new area and to eventually colonize it depends largely on the physiological and resource-utilizing capabilities of the newly arrived individuals. It also depends on other organisms already present in this area, which may either leave sparsely utilized ecological licences available or act as serious antagonists or competitors. The ecological niche of the invading species can be realized if all of the ecological demands of the individuals of this species during their entire life cycles are satisfied by the environment (Sudhaus 2002). The formation of an econiche is favoured if a similar life form or ecomorph does not already exist in the area. Under the pressure of new conditions a change of econiche will occur in the sequence of generations, which is the adaptation process. A rather rapid divergence from the initial stage might be the result of a founder effect, genetic revolution (e.g. changes in regulatory genes), and different ('natural' and sexual) selective pressures caused by different ecological factors and a different species community. In fragmented areas like archipelagos the process of separation of populations and their evolu-tionary divergence towards new species can be repeated several times within a few million years. There is colonization and back-colonization. Thus, it is not surprising that the most impressive examples for radiation are found on remote island groups.

In the case of radiation following colonization the starting point of a radiation is very clear. Whereas various accidental circumstances have great impact on this process, special constructions or abilities of the ancestor do not matter as prerequisites for radiation. However, opportunities for evolution are required, offered by unutilized ecological licences and a fragmen-ted area that favours separation of populations. These requirements were fulfilled for the finches which colonized the Galápagos archipelago, but not for the sister population on the mainland or the colonists on Cocos Island. On the mainland a comparable radiation was prevented by competitors of the same guild. The lone Cocos Island is too remote for multiple coloniza-tion events and too small to set up exogenous barriers impeding geneflow between populations of the only species (*Pinaroloxias inornata*) on this island. On the other hand, a similar radiation as in the Galápagos finches would probably have occurred if a warbler-like bird instead of a *Tiaris*-like bird had colonized the archipelago about 3 million years ago.

Radiation from a survivor of mass extinctions

Scopes for evolution can be given for a species if during a period of mass extinctions most serious competitors and antagonists disappeared. Whereas in scenario (1) above the initiator of a radiation needs characters enabling it to survive dispersal and colonize the new area successfully, in scenario (2) the species needs special characters to survive a rather apocalyptic period (like the Cretaceous-Tertiary transition) during which many species in the same area go extinct. As stated before, most radiations require geographical circumstances that promote allopatry, a fragmented situation, or successional separating events.

Radiation after evolution of key innovations

Whereas in both above scenarios the founders of a radiation can be regarded as relatively unspecialized, in the present third case they are specialized.

If the econiche of a species is 'surrounded' by those of competing species and interlocked with them in many dimensions, a radiation cannot be initiated until one or usually several key innovations have evolved which then offer advantages over competitors and thereby open a new ecozone. In their contributions to the Bonn symposium, Claßen-Bockhoff et al. (2004), Lunau (2004) and Wägele (2004) are searching for candidate

key innovations in their respective groups. A key innovation is an apomorphic character—a new structure, a new function developed for a plesiomorphic structure, or a changed behaviour which integrates or links (synorganizes) some plesiomorphic structures and puts these into a new ecological context. It usually is followed by the evolution of other characters in a plausible sequence. An example is the fundamental transition in a lineage from a free-living lifestyle to parasitism, which requires a set of preadaptations linked by key characters. The complex of key innovations which favour a whole new mode of life and allow a new ecozone to be established can evolve in the old environment (Simpson 1953; von Wahlert 1965). In several examples from the animal realm the opening of an ecozone started with a changed behaviour that brought about an extension of function and was a precondition for an ecological change of function (Sudhaus 2002). In other organisms there were changes in physiological, metabolic traits that facilitated a different use of resources.

Phylogeny is a sequence of radiations on different evolutionary levels

Phylogeny can be reconstructed without thinking about radiation. This has been demonstrated in many cladistic analyses and tree reconstructions using molecular and morphological data. However, radiation cannot be studied without a clear image of the course of phylogeny and of the transformations of functional structures, which in the ideal case should be founded on a phylogenetic tree that includes all characters. The 'development' of a group over time is characterized by radiations at each level of the hierarchy (Fig. 5). In the hypothetical example illustrated, speciation and radiation constantly occurred during the evolution of a monophylum. Only some of the new species generated longer-lasting lineages that founded new monophyla. Most of the species did not leave a trace in the fossil record or even continue until today. Radiations are prominent in special sections of the tree where new sets of characters (not only key innovations) had evolved. When several important characters had accumulated in a typogenetic phase, a species in the ancestral line reached a new level and became able to establish a new ecozone and start a more prominent radiation. In this way the radiation process is connected with additive typogenesis, the formation of a new bauplan. The result of repeated radiations are grades of qualitative changes ('macroevolutionary steps'), although the transformations proceeded gradually within populations of species.

One example for such an hierarchical succession of radiations is the phylogeny of Insecta, first leading to distinct, wingless taxa of the insect bauplan, then to the radiation of the Pterygota after invention of the flight apparatus, to the Neoptera with their special basal articulation and pleating mechanism which brings the wings into the resting position, and to the radiation of Holometabola after one lineage evolved endopterygote instars and the pupa as a transitional stage between the morphologically and ecologically completely different larva and adult. At each of these evolutionary levels a new major radiation arose, enabled by novelties of high ecological relevance, offering new organismic licences which transformed the niches of the descendants of this lineage. For each novelty, its possible role as a key character has to be considered. Also, it must be kept in mind that different radiations occurred in the same period of time, e.g. the radiation of Holometabola in parallel with the radiation of Paraneoptera and Paurometabola. Interrelations during the radiations were possible (co-radiations: see Lunau 2004).

Key innovations and the analysis of radiation

In order to analyse radiation, we first need a cladogram that reveals the apomorphies. Next, we must reconstruct the character set of the common ancestor, which I call the 'stem species pattern' (instead of ground pattern, which has various meanings in different disciplines of biology and should better remain a word of colloquial language). Using this basis the evolutionary biologist must attempt to work out crucial stages in the history of the group, that is, to find key characters (key innovations). As defined above, the term 'key character' does not denote a character in an identification key, nor just any important apomorphy at some point in the phylogenetic tree of the group. Also, key characters do not only offer organismic licences for special transformations in further evolution (like the increase to gigantic body size made possible by increased metabolism and growth rate after the evolution of a bird-like lung in the ancestor of sauropods: see Sander et al. 2004). Key characters are characters of fundamental ecological significance for coping with the environment (as was gigantism). Features that can be used in many ways under diverse ecological conditions and modes of life (like avian bill structures, or the chelicera of mites) are particularly likely to become key innovations. Significant for rodents, for instance, were "persistently growing, chisellike incisors" and "correlated characters, as of jaw musculature and digestive system" (Simpson 1953, p. 346).

Considering the proximate and ultimate aspects of species (Sudhaus 2002), it has been debated whether key characters for radiation could be certain mechanisms of

mate recognition and mate choice, or other reproductive mechanisms (see Reinhold 2004), which in their wake cause reproductive isolation of the species. The alternative view (which I prefer) is that key characters are innovations that allowed the establishment of various econiches, and that recognition mechanisms and reproductive communities were necessary for maintainig these econiches. In evolutionary ecology the term key innovation means that a character—synergistically with other key characters—helped to create a new ecozone and to exploit resources that would not have been available without these characters (see Lunau 2004). The ecological implications of these key innovations have to be worked out in order to understand the evolutionary events which promoted a new radiation (in the above example of insects, this has to be done for instance for mouthparts, the ovipositor, active flight with wings, the folding of the wings back along the abdomen, and metamorphosis via a pupa). In addition, the 'overembossing' of body plans (where properties adapted for an older ecozone are superimposed and combined with adaptations to a younger ecozone) has to be worked out in connection with the ecological "self-layering process" (von Wahlert), in order to explain the survival of representatives of older radiations despite or alongside with the new groups (Sudhaus 2002).

The breakthrough to establish a new ecological zone appears as a 'key event' in the phylogeny of a group. It depends on the unlikely coincidence of two things: (1) an exceptional geographical, historical and ecological constellation, and (2) unique physiological and morphological features conditioned by a special genotype which allowed a species to take advantage of this "evolutionary situation" (so termed by von Wahlert 1965).

When a new radiation is just being initiated, the key characters as well as the potential for radiation cannot be recognized a priori. There might be one strange species realizing an econiche rather unusual for the group it belongs to, or two such species after a first split. Every systematist knows such examples from 'his/her' group. Concrete examples are the fish-eating rat *Anotomys leander* (Rodentia), Striped Possums (*Dactylopsila*) with a *Daubentonia*-like lifestyle, the dippers (*Cinclus*, Passeriformes) with their underwater foraging, the Shovel-billed Kingfisher (*Clytoceyx rex*) ploughing the ground, the seaweed-eating marine iguana *Amblyrhynchus cristatus* (Squamata), the Water Spider *Argyroneta aquatica* (Araneae), the aquatic moth *Acentria ephemerella* (Lepidoptera, Pyralidae), or the nematode *Koerneria pararmata* (Diplogastridae) feeding on benthic diatoms. In some cases, the study of such 'strange' extant species may provide hypotheses for key characters which in the past facilitated the evolution of a group that is 'successful' in species number and divergence of forms.

A study aiming to analyse radiation and thereby explain diversity could have the following objectives:

- To search for the colonization event and the starting point of a new radiation in a remote area, or for the scope of evolution in a depauperate community of the main area after mass extinctions. Alternatively, to search for ethological, physiological and morphological key innovations that were powerful in an apparently saturated species community. Which characters constitute key innovations can possibly be elucidated after a meticulous reconstruction of the stem species pattern. As a test for key characters in a lineage, a comparison of speciation rates with the sister taxon has been suggested (see Lunau 2004; Wägele 2004). This method, however, falls short. It does not take into account the evolutionary divergence from the stem species, the rate of ecological and phenotypic diversification of the related species, the different potentials of the two ecozones, and the necessity for a functional and explanatory analysis of the characters in relation to the ecozone. The test also ignores that a new ecozone can be established by few or even only a single species. It is worth looking for key innovations in species like *Homo sapiens* or *Daubentonia madagascariensis* as well, not only in groups like rodents which exhibit a wide array of ecological types.

- To reconstruct the organismic preconditions in the stem species in order to find the structural components that are flexible enough to allow divergent transformations. The decisive question is which unconstrained potentials exist in the construction inherited from the stem species that can be realized in centrifugal evolution of the different lineages.

- To quantify the phenotypic differentiation in comparison to other radiations.

- To reconstruct the initial environmental situation and all relevant changes of the ecological conditions (in geology, climate and the species communities) in the course of co-evolution (in the broad sense). Change mainly results from continuous repercussions of collateral contemporaries of the parallel radiations. This aspect is taken into consideration under the heading "co-radiation" (see Lunau 2004).

- To reconstruct the sequence of niche differentiations of the different stem species.

- An attempt to explain the higher pace of species formation during some episodes.

- Implying allopatric speciation, the separation event must be searched for each point of ramification (node in the tree). An allopatric mode of speciation must be tested first, though under exceptional conditions within very special taxa parapatric or sympatric speciation (without exogenous separation at any time) appears to be possible (see Reinhold 2004; Schön and Martens 2004).

- To reach a deeper understanding of a radiation process under investigation it should be compared with the sister taxon or parallel radiations of other closely related taxa. Sometimes these radiations are symmetrical, as in the four parallel clades of *Cicindela* tiger beetles (A. Vogler, oral presentation at the phylogenetic symposium in Bonn, 2002). However, in most cases the radiations are asymmetrical (5 species of *Tiaris* compared with 15 of Geospizidae), and the phylogenies have a pectinate appearance with a number of branches with extant taxa or representatives of the stem lineage lying serially along a single stem (Fig. 5). In a few cases the recent sister taxon of a high-ranked taxon is represented by only one species (e.g. *Amia calva*, *Latimeria chalumnae*, *Sphenodon punctatus*) which is often called a 'living fossil'. However, in the future these 'living fossils' might be the starting points for new radiations (such a phenomenon was underlying some of the so-called 'iterations' documented in the fossil record).

- While thinking about favourable organismic and environmental circumstances for radiation, we also have to contemplate the inverse. For the 'living fossils' mentioned before, we must try to find out which circumstances prevented further speciation in these lineages for a very long time. Also, in groups known only from fossils we must try to find at least partial explanations for why the rate of extinction in a group exceeded the rate of speciation, such that the group diminished and finally became extinct with the end of its last member. For the time being this is the end of the tale, but the discussion has to continue.

Acknowledgements

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