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Major Patterns and Processes in Biodiversity: taxonomic diversity on islands explained in terms of sympatric speciation

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Summary

The history of life on earth is characterized by biodiversity, which is not limited to taxa, geological ages nor regions. Pandemic biodiversity is due to evolutionary processes in which every species is supposed to have evolved from another species through natural selection in a broad sense. Selection is mainly initiated and directed by availability and character of ecological niches. This is true for all taxonomical and phylogenetical levels, and is time independent. As a rule, radiation within a taxon takes place as soon as a new, free ecological niche is entered successfully, in other words, after an innovation of this taxon or after a mass extinction of other, competitive taxa. For example, the development of jaws (innovation), and later fins, in the agnatha was followed by a large-scale, long-term radiation into numerous groups of fishes during the Devonian. A similar pattern is seen in amphibians in the Carbonian (innovation: land dwelling), the amniota in the Trias (innovation: egg with membranes), sauriers in the Mesozoic (survivors of mass extinction), and mammals in the Kenozoic (survivors of mass extinction; innovation: versatile dentition). The same is seen in lower phylogenetic levels, resulting in medium-scale, medium-term radiations, e.g. ungulates (innovation: stilt-like limbs to run the plains), mainly in the Miocene.

Each newly evolved taxon displays a minor change from the innovative ancestor, and as a specialist occupies a part of the total newly entered niche. Thus, after each innovation, sympatric speciation events take place, later followed by dispersals and allopatric speciation events. The speciation leads to homochronous specialists, each adapted to a subniche of the main niche that was originally occupied by the innovative pioneer or colonizer.

The above observation leads automatically to the solution of the small-scale, short term radiation seen in endemic insular taxa. On islands, biodiversity within one taxon is the rule, and the most parsimonious explanation is to consider this diversity, too, as determined by availability and character of ecological niches, as on the mainland. The colonizers have no competitors, so have the unique possibility to radiate beyond the degree seen on the mainland, where close niches are always already occupied. Island species, depending on plasticity of functional structures, will enter all possible niches, and adapt to all available niches. In a way, the colonization on itself can be considered equal to the situation met with after a mass extinction on the mainland, which is also usually followed by a radiation within the surviving taxon. Clear examples are the large continental islands in sensu lato: the carnivorous marsupials and herbivorous mammals of South

America during the Tertiary, and the marsupials of Australia during the Cenozoic were able to radiate into a huge variety of taxa after colonization. But also small, true islands can be considered examples of sympatric radiation, as shown by the deer of Crete in the Pleistocene, and Darwin's finches of the Galapagos, and the haplochromine cichlids of East African Great Lakes of modern times. The biodiversity as seen in endemic insular monophyletic genera in the form of adaptive radiation is based upon sympatric speciation, in complete accordance with the major patterns and processes that gave rise to the long-term, large-scale and the medium-term, medium-scale biodiversity on the mainland.

Introduction

The history of life on earth is characterized by biodiversity through all taxonomic levels. Since Darwin's publication (1859), there is a general agreement that this biodiversity is caused by evolution through natural selection, although there is a discussion if this evolution is gradualistic (Makurath & Anderson, 1973; Makurath, 1974; Gingerich, 1974, 1976; Bookstein *et al.*, 1978; Chaline & Laurin, 1986), punctuated (Eldredge & Gould, 1972, 1988; Eldredge, 1974; Stanley, 1975, 1978; Gould & Eldredge, 1977, 1986), or both, depending on the functional structure studied (Spaan *et al.*, 1994; Sondaar, 1994). The end result, however, is the same: new taxa.

On earth there are several ecosystems, which comprise communities of several organic species and their environment (biotic and abiotic factors). These ecosystems are recognized on different levels, such as micro- (e.g. a tree trunk), meso- (e.g. a forest), and macro-ecosystems (e.g. an ocean or continent). In each ecosystem a species will occupy a particular niche. When one of the biotic and/or abiotic factors changes, the habitat may change, impelling the organisms to adapt to this new environment. If this environment contains free ecological niches, taxa appear to occupy as much niches as possible. As a result, natural selection on different changes in the locomotory and digestive mechanisms will take place, resulting in an adaptive radiation, and thus a sympatric speciation into a vast range of species or morphotypes. If the variety is large, and the genetic distance small, the term flock is sometimes used (e.g. Greenwood, 1974; Echelle & Kornfield, 1984, and references therein).

Depending on the level of taxonomical, or phylogenetical, organisation, the observed biodiversity is a large-scale (continent), medium-scale (mainland) or small-scale (island) adaptive radiation, and depending on the end result, the radiation is of long-term (resulting in families), medium-term (resulting in new genera) or short-term (resulting in species or morphotypes). Large-scale, long-term radiations are the most conspicuous of all macroevolutionary phenomena (Carroll, 1997) and here the adaptive radiation is strong: the radiation of metazoan phyla during the Cambrian, that of primitive fish and early vascular plants in the Palaeozoic, of dinosaurs and flowering plants in the Mesozoic, and of mammals and birds in the Cenozoic. In small-scale, short-term evolution the radiation will be weaker. The most famous examples of this is the adaptive radiation of the Darwin's Finches.

The radiation as observed in endemic insular taxa is usually explained in terms of allopatric speciation. In actual fact, this implies the existence of an archipelago, e.g. Darwin's Finches on the Galapagos Islands. The Pliocene island Monte Gargano (Italy) has been considered part of a larger archipelago (Apulo-Dalmatic Realm) in relation to the micromammals (De Giuli & Torre, 1984; De Giuli *et al.*, 1985, 1987) and the ochotonid *Prolagus* (Mazza, 1986a, 1986b) to explain the presence of several sister taxa, evolved in a relatively short time. Another explanation is the occurrence of more than one invasions, e.g. as suggested for the deer *Candiacervus* on Crete

(Kuss, 1975; De Vos, 1984, however cf. De Vos, 1996, 2000; Capasso Barbato, 1992; Caloi & Palombo, 1996) and the rodents on Monte Gargano (Freudenthal, 1976). In the latter case, it is no explanation as to where and why this new sister taxon evolved. In the former case, it does not explain sufficiently why sister taxa are found together on one and the same island. In both cases it is not clear why the sister taxa wait with migration until full speciation has taken place.

The end result of island evolution is always a range of taxa, closely related, which in a way can be compared to the medium scale, medium term radiations, and on its turn with the large scale, long term radiations as well. In this paper we compare these three types of radiations for the major vertebrate classes, to demonstrate that the processes of biodiversity are the same for all scales and all terms. The main driving force in all cases is the urge to occupy free ecological niches. In our opinion, the resulting speciation can be explained best in terms of sympatric speciation.

Class Pisces

Large scale, long term radiation

During the Ordovician-Silurian, a rapid dispersal of Ostracodermi took place, after a long period of relative stability in the omnipresent Agnatha. Later, at the end of the Silurian, the Placodermi with their primitive jaws underwent a major adaptive radiation, and the first predators arose. The more derived Actinopterygii and Sarcopterygii also radiated in many taxa, each of them in a different ecological niche. In addition, the Actinopterygii with their swimming bladder entered the deeper waters of the ocean, and occupied the available deep sea niches. Gradually, all modern osteichthyes evolved from this order, and took over all available aquatic niches in salt, sweet and brackish waters. The Sarcopterygii with their primitive lungs never radiated to the degree seen in the other order. Nowadays, the only descendants are the coelacanth, and the Dipnoi, who are restricted to tropical regions with periodical dry seasons.

Small scale, short term radiation

In the East African Great Lakes, the haplochromine cichlid fishes went through a rapid speciation (adaptive radiation), resulting in a wide range of trophotypes (Fryer & Iles, 1972; Greenwood, 1974; Barel *et al.*, 1977; Witte, 1981; Keenleyside, 1991). Initially they differed little from their immediate reverine ancestors, and there is no evidence of significant new morphological changes that facilitated their differentiation into many trophic levels; rather they capitalised on a biological versatility already present (Liem & Osse, 1975). The cichlids were obviously capable of a much higher rate of speciation than were other fish in the East African Great Lakes, and were able to differentiate into many different trophic levels with a minimum of morphological change (Carroll, 1997). It resulted mainly in differences in the mouth, which gradually became adapted to different types of food: detritus, fishes, shells, crabs, insects, phytoplankton, zooplankton. For taxonomy, such radiations are a disaster, as taxonomy deals with fixed, clearly defined subunits of the observable world, whereas in reality such a species flock approaches a continuum. The taxonomical problems become evident through the many revisions and reconsiderations of the classification of the haplochromine cichlids (e.g. Greenwood, 1981; Witte & Witte-Maas, 1981; Hoogerhoud, 1984; Van Oijen, 1991).

Mechanism

In all cases, the fishes encountered free ecological niches. In the Ordovician Ostracodermi the first pair of gills had been transformed to an opening at the head side between the eyes, through

which opening water could be let in, without mud coming between the gills. The result was a rapid dispersal of Ostracodermi. Later, the Silurian Placodermi had developed innovative structures: jaws and fins. The fins made these fishes independent of the mud, so that they could enter a vast scala of free ecological niches, and the jaws gave the possibility to prey upon other fish. The innovations gave the Placodermi the possibility to occupy a new range of free ecological niches. Again later, the placoderm-type triangular fin evolved into two main types, the stray fin and the brush fin (Actinopterygii and Sarcopterygii, resp.). Both types of fins increased the swimming ability enormously, and with it the possible range of habitats and size of territory. Within the Actinopterygii another innovation, which further increased their swimming ability, especially in deeper waters. Primitive osteichthyes had besides gills also lungs, to be able to survive periodical dry periods, and some had even external gills during the larval stage to cope with these dryness. The Actinopterygii, however, transformed their lungs to a swimming bladder. Now that they could enter the deep waters, i.e. the ocean, a new range of free ecological niches became available to them. The subsequent adaptive radiation resulted into the vast spectrum of living modern fishes.

The Holocene cichlids entered a new and still unoccupied lake: Lake Victoria was filled about 14,000 years ago, due to the creation of the Rif Valley, which started to arise from 750,000 years ago. Immediately after the formation of the lake, a host of adaptive zones became available. The entering of a zone with free niches gave the cichlids the possibility to radiate beyond the degree seen in related cichlids. The haplochromine species flock of Lake Victoria is a good example of recent speciation, that took place in less than 200.000 years (Meyer et al., 1990).

Class Amphibia

Large scale, long term radiation

At the end of the Devonian, the Rhipidistia with their choanae were the forerunners of the amphibians. As soon as a tongue and a strong central axis had developed, an adaptive radiation took place on the land amongst the amphibians, starting with the Devonian Ichthyostega. During the Carboniferous, two amphibian orders arose: the frog-like Aspidospondyla and the salamander-like Urodela. Both orders were preserved into modern times and its as a rule small sized representatives occupied especially insectivorous and carnivorous niches.

Mechanism

During the Devonian enough oxygen had developed to reduce the ultraviolet light of the sun, but the land was still unoccupied by vertebrates. At the end of this period, the first amphibians appeared. Due to a combination of innovations (the development of choanae and lungs in the adult, crawling ability, tongue to swallow food), they were able to explore the available niches on land. The Labyrinthodontia had complicated enamel patterns on their molars, which gave them the possibility to occupy different trophic niches. The adaptive radiation of the amphibians, however, never reached the extent of that of the fishes, as amphibians are dependent on sweet water for their reproduction and dry up easily. This might also be the explanation why amphibians hardly reach islands (salt water barrier) or isolated areas (dry land barrier).

Class Reptilia

Large scale, long term

At the end of the Carboniferous, the first amniotes, representatives of the Anapsida, laid their eggs on land. This was followed, during the Permian, by a quick radiation of these reptiles over the vast continental regions, which were still relatively empty after the drying up of marshes. Later, at the end of the Permian (250 Ma), a mass extinction occurred (Sepkoski, 1989, 1990; Raup, 1991), the nature of which is still unclear, though most likely it had to do with relatively sudden major changes in the positions of the continents. After this mass extinction, the sea and the continents were "empty" once more. During the Mesozoic (era of the reptiles), an explosive radiation of saurians took place, which gave rise to many orders: dinosaurs, ichthyosaurs, plesiosaurs, mesosaurs, and the flying pterosaurs. Within the Upper Triassic, the dinosaurs diverged further into three major groups: the bipedal carnivorous theropods and herbivorous ornithischians, and the quadrupedal sauropodomorphs.

Medium scale, medium term

Still during the Mesozoic a further rapid radiation took place among secondarily aquatic groups of saurians: nothosaurs, ichthyosaurs, and mosasaurs. They all occupy complete different ecological niches. Later, the same occurred within the major dinosaur groups. During the Jurassic and Cretaceous, the theropods, the ornithischians and the sauropodomorphs each evolved into a succession of divergent families.

Mechanism

At the end of the Carboniferous (280 Ma), the marshes disappeared. Simultaneously, most of the amphibians became extinct, due to their dependentness on water. This was the change for the reptiles, with their innovative amniotic eggs and protective skin, to explode into a radiation. Their eggs were independent of the water: a large yolk to provide food, an amnion around the yolk to prevent dehydration, an allantois to respire, a chorion to hold germs and chemicals outside, and a calciferous shell for mechanical stability. The fact that the amphibians had disappeared gave the reptiles the possibility to enter free ecological niches that were once occupied by amphibians. The innovation in reproduction, however, made them able to explore even more ecological niches than the amphibians could, as the distance to water became a minor factor. The keratinisation of the skin, the development of complicated lungs, and the homeothermy, as well as other innovations, made them even much more adapted to a terrestrial life than the amphibians.

But also the sea was available, as there were no fish as large as a saurian. The secondarily aquatic forms had no aquatic enemies either, because of their size, thick skin and advanced dentition. After the innovation of a hydrodynamic body, the aquatic saurians were able to occupy all available ecological niches.

The most remarkable innovation is seen in the pterosaurs: the development of wings. The air was almost free, except for some, much smaller sized early birds.

Class Aves

Large scale, long term

The modern bird orders are almost entirely restricted to the Cenozoic. Numerous specimens from the late Mesozoic have been described as possible ancestors, but none of them with conclusive evidence. Three orders can be distinguished during the Cretaceous (Hesperornithiformes, Ichthyornithiformes, Enantiornithes), all three not related to any of the now living birds (Chiappe, 1995a). Feduccia (1994, 1995) has recently suggested that nearly all of the Cretaceous bird lineages became extinct at the end of the Mesozoic, at the same time as the dinosaurs. The almost complete absence of ancestors of the modern bird orders in the Cretaceous is not the result

of an incomplete fossil record, but because they had not differentiated until the early Cenozoic. Feduccia (1994, 1995) argued that nearly every type of modern bird evolved within about five to ten million years, most of them from an assemblage termed the transitional shore birds. All modern bird orders had diverged by the Eocene, including the passerines (Boles, 1995).

Medium scale, medium term

Radiations within bird families are also known. The result of these radiations is a number of monophyletic genera or species that differ in ecological niche. They share the same habitat, but occupy a different niche. For example the flamingoes in the brackish Nakuru Lake in East Africa, where the small flamingo (*Phoeniconaias minor*) and the pink flamingo (*Phoenicopterus roseus*) live together, each with their own trophic niche, respectively algae and salt-water crustacea (Grzimek, 1968).

Small scale, short term

The finches from the Galápagos archipelago are remarkably similar in plumage, but differ in beak shape and size (Lack, 1947), whereas in continental passerine birds closely related species tend to differ from each other in plumage, whereas they are usually similar in beak and other structural characters. Differences in beak more usually characterize the broader units, the different genera. In Darwin's finches the opposite seems to be the case. A further unusual feature in Darwin's finches is that some species are highly variable (Lack 1947: 12).

The differences in beaks indicates an adaptation to different habitats. It became clear that islands had species which were different from the mainland and were adapted to the different habitats of islands.

Six genera and about fourteen species are recognized on the basis of bill size and shape and body size (Grant, 1986). They are mostly sparrow-sized, and are all dull in colour. All these species are adapted to different habitats and occupy different niches. Patterson (1978: 112) recognizes .. trophic groups: the seeds and insects eating ground finches (coastal zone, lowlands) with one cactus flower eating exception, the seeds and insects eating tree finches (forest zone), the insects eating warbler finch, the fruits, buds and soft seeds eating tree finch (forest zone), and the insects eating woodpecker-like finches (forest zone, including mangroves).

The variation within one species can be large. For example, the *Geospiza fortis* of Santa Cruz shows a clear bimodality in the bill depth of the male medium ground finches, measured at the Bahia Academia. As in this area there is a wide range of floral taxa (Abbott et al., 1977), it is suggested that *G. fortis* is in the middle of a process of fission, due to disruptive selection in a heterogeneous environment (Ford et al., 1973), but others (Grant, 1986: 276) have a different explanation.

Congeneric species each occupy a different niche, for example *Cactospiza* on Isabela. The woodpecker finch lives in dry territories and mesic woods, the mangrove finch in the mangrove woods at the coast, strictly separated from the rest of the island by a zone of bare lava (Grant, 1986: 274), although the woodpecker finch is found brooding in the mangroves at the east side of the island (Gifford, 1919).

Besides the Darwin's Finches there are more such cases of passerine birds known: the honeycreeper finches of Hawaii (Drepanididae), and the birds of paradise of New Guinea (Paradisaeidae). There is even more differentiation in morphology in the Hawaiian finches (nine genera, twenty two species) than in Darwin's Finches. Diets consist of honey and small seeds (e.g. Palmeria), hard seeds and nuts (e.g. Psittirostra, Chloridopa, Pseudonestor), and insects (e.g. the woodpecker-like Hemignathus), and the types of beak range from short and slender to the robust parrot-like beak of Pseudonestor. However, although these differences in diet are huge, other

differences are much less. For example, they are all medium-sized (10-20 cm), and have a monochrome plumage (olive green, yellow, red or black), without distinct pattern, except for the tufted honeycreeper *Palmeria dolei*, who is grey with red spots and stripes, and has a short tuft above the nasal openings (Burton & Friedhoff, 1975).

The radiation is so extreme that it is not possible anymore to tell which group is the ancestor: a finch, a honeycreeper or a tangare. The fact, however, that the variation in colour and size, in type of nest, and in number and colour of eggs, is so small is highly indicative for a monophyletic origin of the Hawaiian honey-creepers. The time range of their isolation might be long, as they are all highly specialized. Major changes in their environment, mainly of a human nature, nowadays leads to their rapid extinction, as they are not able to adapt themselves easily.

Mechanism

After the extinction of the pterosaurs, the air was free for the birds. They were more advanced than the pterosaurs as they had developed feathers, an aerodynamic beak, and a crop plus stones in their first stomach to postpone mastication. However, they could take their change only when the dominant pterosaurs disappeared.

The extreme adaptive radiation as seen in the passerine island birds is caused by the total lack of competition by other land birds, and led to the occupation of all imaginable trophic niches. Sometimes the principle of fissions might apply. Fissions occur essentially when the habitat becomes overpopulated, absolutely or relatively. An example is provided by the cactus finch *Geospiza conirostris* on Genovesa (Grant, 1986). Two types of males occur in one and the same population, with a different song and a different bill. In dry seasons they have a different diet and different eating methods, but in good seasons there is no such dietary differences. Adult males prefer to sit next to a neighbour with the other type of song, which results in a mosaic pattern of songs. In good seasons, females seem to have no preference, although they choose a mating partner of the song type opposite to that of their previous partner when their 'broedssel' failed (Grant & Grant, 1983). In dry seasons with food shortage on the contrary, fission occurs as a result of disruptive selection by the females (Grant, 1986:279; B.R. Grant, 1985). Now the population is instable and oscillates between fission and fusion (Grant & Grant, 1983), but it can be easily imagined that a series of dry seasons will induce a complete, irreversible fission yielding two different species. In Grant's opinion (1986: 279), only an extreme reduction in population size, giving change a role to play, could induce such a reproductive isolation, and thus speciation, but in our opinion, it is the relative overpopulation that is the drive behind the selective mating behaviour. Positive assortative mating is the only strategy to cope with a shortage on food in order to enter new ecological niches. Reduction in population size is not a strategy: it is a symptom of being unable to cope with the unfavourable situation.

Class Mammalia

Large scale, long term

During the Triassic, the cynodonts, a group of advanced, mammal-like reptiles, developed into several families of small and medium-sized carnivores and two families of herbivores. Some of the later members of the group are almost indistinguishable from the first mammals, which can be distinguished from reptiles by the fact that the jaw joint shifted from one position to another, and that the old jaw joint was still present in the form of three middle ear bones (malleus, incus, stapes) inside the ear (Benton, 1991). The best known is the adaptive radiation of placental mammals in the Early Cenozoic. Within ten million years, from 65 to 55 million years ago, nearly all the modern placental orders had appeared (Carroll, 1997; MacFadden, 1992; Szalay, Novacek & MacKenna, 1993; Prothero & Schoch, 1994).

Marsupials also radiated rapidly at the beginning of the Cenozoic. They were moderately diverse in North America at the end of the Cretaceous but were reduced to a single lineage following the end-Cretaceous extinction. Later, they also dispersed to the Palaeartic, but these lineages all became extinct with little further radiation. On the other hand, the lineage that entered South America, radiated extensively in that continent, spread to Antarctica, and from there extended its range into Australia as these continents first came in contact with one another and then drifted apart between the end of the Cretaceous and the beginning of the Eocene. They radiated rapidly in both South America and Australia (Woodburne & Case, 1996).

Medium scale, medium term

The first horses (Hyracotherium, Meshippus) were forest animals, with lophodont molars and subungulate, tridactyl, padded foot. In the Early Miocene, a new group enters the fossil record in North America: the grazing horses. They are recognized by an elongated first phalanx, and a true unguligrade tridactyl foot. Soon after their occurrence, a radiation took place, starting with Parahippus, who had still lophodont molars, though more complex, and later the rather hypsodont Merychippus. The lateral toes were still functional, and touched the ground during maximal dorsiflexion, resulting in a more allround locomotion (Renders, 1984; Renders & Sondaar, 1987). Its diversity is at its top in the Late Miocene, at which time about thirteen different genera of grazing horses can be distinguished, amongst others the tridactyl Hipparion and the first monodactyl Dinohippus, ancestor of Equus, both hypsodont grazers living at the same time, but in different niches. In the forests, the padded tridactyl horses such as Anchitherium and Hypohippus remained occupying the ancestral niche, without further major innovation and without remarkable radiation. On the plains, the degree of hypsodonty increased progressively and gradually in all lines, whereas the change in locomotion occurred punctuated and restricted (Spaan et al., 1994).

The artiodactyls also radiated, and to much larger extent than perissodactyls: giraffids, deer, bovids, tylopods. Within these groups, smaller radiations occurred, for example within the antlered deer. As a result, in habitats suitable for deer, two or three species or genera live in the same habitat but differ considerably in size. As a rule, in each deer-suitable habitat we find a small, medium and large deer-like species together, providing the habitat is rich enough to support more than one species. There are exceptions to this rule, for example Rucervus duvauceli and Rusa unicolor in some parts of India, who have the same size, but in this case the species occupy different ecological niches or a slightly different habitat (Van Bemmelen, 1973: 295). Quite probably, this is true for all similar cases.

Small scale, short term

The Pleistocene deer Candiacerus of Crete show a large variety. No matter how the final genera and species are placed into a taxonomical framework (for a complete overview, see Dermitzakis & De Vos, 1987 and De Vos, 2000), six size groups (De Vos, 1979), and in one of them three morphotypes of skulls and antlers (De Vos, 1984), can be distinguished, based on biometrics of cranial and postcranial materials from different sites (De Vos, 1979, 1984). These eight taxonomic units most likely all belong to the monophyletic genus Candiacerus (De Vos, 2000), or alternatively, to two paraphyletic genera, be it Megaloceros and Cervus (Capasso Barbato, 1989) or Megaceroides and ?Pseudodama (Caloi & Palombo, 1996). Irrespective of the taxonomical problems, the eight Cretan deer types in any case differ clearly too much to assume a similar ecological niche; more likely is the hypothesis of different niches. On the ground of body proportions, molar morphology and wear pattern, the specialist trophic niches occupied by the eight taxa might, tentatively, be summarized as follows: grassy food or prickly bushes on a rocky

hill (*C. ropalophorus*, *Candiacervus* spp. II), grasses on a steppe-like plain (*C. cretensis*), leaves and branches in a forest, like red deer (*C. rethymnensis*), leaf-like food and soft bushes in a forested terrain with many obstacles (*Candiacervus* sp. V and *C. sp. VI*).

A rather similar situation is met on Mallorca. The Pleistocene endemic goat *Myotragus balearicus* exhibits a great size variation, far exceeding that of mainland relatives. The largest metatarsal is three times the smallest from the same cave (e.g. Muleta) and the same level, and all intermediate sizes are also found. Grouping of bones into different size ranges or morphotypes is not possible (Sondaar, 1977).

Also the Pleistocene deer from the Ryukyu Islands (Japan) seem to follow the same pattern. On Kume Island four size-groups of metacarpal bones of *Cervus astylodon* can be distinguished (Matsumoto & Otsuka, 2000).

Mechanism

At the end of the Mesozoic (66.5 Ma), there was again a mass-extinction, the nature of which is not yet fully understood, but which surely had a huge impact on life in the seas as well as on land (Smit, 1989). Most of the Mesozoic reptiles disappeared, and the environment was "empty" again. All kinds of niches became available and the mammals could take their chance. The most primitive members of the derived mammalian groups initially show relatively few changes aside from dental specialisation. The success of the placental mammals is often attributed to the versatility of their teeth. It is true that mammals have been more adaptable and successful in their range of diet than any other amniote group: insectivores with small, sharp teeth, carnivores with enlarged canines, herbivores with blunt, grinding molars and huge tusks, piscivores with peg-like teeth, plankton-eaters with palate-born baleen sieves, and anteaters without teeth (Benton, 1991). As in the cichlids, there is no evidence of significant new morphological changes that facilitated their differentiation into many trophic levels; rather they capitalised on structural and behavioural flexibility that was evident in their ancestors.

During the Miocene and Pliocene (24-2 Ma), the climate gradually became cooler and drier worldwide, due to continental movements and the development of an ice cap at the South Pole. The main global effect was the spread of grasslands, and the size reduction of tropical and subtropical forests. New kinds of landscapes evolved: prairies, steppes, savannas, and pampas. These large grasslands stimulated great adaptive radiation of various ungulate groups, as a new environment is by definition 'empty'. The change in evolutionary direction from tridactyl padded feet to monodactyl ungulate feet coincides with the spread of grasses at that time (e.g. Simpson, 1951; Stebbins, 1981). The innovation consists, besides hypsodonty, of a true unguligrade foot with an elongated first phalanx (a pioneer structure according to Spaan et al., 1994, and Sondaar, 1994).

The late Middle - Late Pleistocene herbivorous macrofauna of Crete contains only cervids and elephants (De Vos, 2000, and Sondaar & Van der Geer, in press, for an overview), and its taxa are endemic to Crete. The island was submerged during the Pliocene, and got its present shape during the Pleistocene. When the ancestor of the cervids arrived on Crete, a variety of herbivore niches was available, except for those occupied by the elephants.

Discussion

The major pattern of the evolution of biodiversity, termed adaptive radiation, is recognisable on all taxonomic levels. The processes behind all these adaptive radiations appear to be the same at all levels: innovation followed by a rapid, monophyletic radiation to occupy as much available ecological niches as possible. In a broader sense, this innovation can also consist of the mere fact

that a taxa was a survivor of some kind of mass extinction caused by a natural disaster. A comparable situation is found when a taxon colonizes an empty region: an island for terrestrial taxa, an isolated lake for aquatic taxa. The end result is, however, in all cases the same, be it after an innovation, a mass extinction or an isolation: a radiation, in order to adapt to and to occupy new niches.

Although this sounds reasonably fair, and can be easily checked at the base of the fossil record as we saw above, it still doesn't explain what the biological mechanism is behind such a speciation event. Is it possible to explain the mechanism in terms of natural selection? Darwinian explanations surely fit for species that evolve from other species. But do they fit also for sisterspecies that are supposed to have evolved simultaneously from one and the same ancestor within one and the same habitat? In other words, though Darwinian natural selection is primarily meant to explain allopatric speciation events, can it be the drive behind sympatric speciation as well? If so, island chrono-morphotypes can be much easier explained by the same mechanism of natural selection as the one behind the evolution of mainland sisterspecies.

Allopatric species are by definition species whose dispersion areas are separated from each other, and who, as a result, have no possibilities to hybridize. If allopatric species happen to come into contact, there is a change of successful interbreeding, resulting in a species fusion, due to the fact that before this contact sexual barriers were superfluous as the species never met. Sympatric species on the other hand are species whose dispersion areas coincide or partly overlap, but who nevertheless do not interbreed. Sexual barriers to prevent interbreeding can be manifold: differences in behaviour, breeding season, pheromones, anatomy and so on, plus the fact that bastards are at the best less fertile (Burton & Friedhoff, 1975).

In our view, the definition of sympatric and allopatric species indirectly means that if speciation on islands would have been allopatric (archipelagos, highly mountainous islands) and they meet each other after migration, they would hybridize, resulting in one intermediate species, which is not what we observe. The trend on islands is on the contrary: the longer the isolation of the endemic insular genus from the mainland ancestral population, the more different morphotypes evolve, each occupying a different niche, and there is no such intermediate hybridizing clade to be found.

In fact, most examples to prove allopatric speciation can be as easily explained in terms of sympatric speciation. For example, white tailed ground squirrel *Citellus leucurus* and the dark tailed ground squirrel *Citellus harrisi* live in the same habitat, but occupy different niches. At the moment they are therefore sympatric species. However, it is supposed that in the past they formed one population. When the Colorado river separated them, they gradually began to differ, and formed two species, the white tailed form at the north side of the river, the dark tailed form at the south side of the river. Long after this allopatric speciation, the white form somehow reached the other side, and nowadays they live in the same habitat, in different niches. This sounds not very convincing, as the canyon got deeper in the mean time, and crossing became even more difficult in the present than in the past. Why didn't the white tailed *Citellus* cross this boundary earlier? And how coincidental that at both sides of the river there is the same habitat, but different niches. Why didn't the ancestral form expand its trophic niche already in the past? Apparently it was empty, as the white-tailed squirrel could occupy it much later, after it had evolved into a new species at the other side of the canyon. Unfortunately such questions cannot be answered anymore, and the only thing we have are the bare facts. Fact is, that along the Colorado river two related ground squirrels are found, that do not interbreed. Fact is, that these sisterspecies each occupy a different niche. Fact is, that the Gran Canyon is a clear geological barrier between the

north and the south side of the river. Fact is, that this barrier became steeper and broader in time, and thus less passable. Besides the classic explanation given above, another explanation is possible. Just because of the Gran Canyon the squirrel population could not expand its territory more, and got limited on food. It was simply urged to explore other trophic niches. The radiation into two trophic types was facilitated/stimulated/initiated by the geological barrier. The squirrels lived so to say on a peninsula.

In which way the speciation took place during the Pleistocene in the Cretan deer genus *Candiacervus* is not clear. Gradual genetic changes may have played a role. Although we cannot exclude allopatric speciation, which means nothing else but repetitive invasions, it is more realistic to suppose that the speciation took place on Crete itself. Invasions of the same trophic type would earlier lead to extinction of the resident species or otherwise to an unsuccessful colonization. Invasions of a different trophic type would, according to the characterisation of allopatric species, gradually lead to hybridization and thus to a monomorphic taxon.

Notwithstanding the different opinions concerning the number of cervid species in Crete, it is clear that the morphotypes differ in dental, cranial as well as in postcranial morphology. This makes us assume that each type must have been adapted to a different niche, and maybe even to a different habitat. Just as recent sympatric species, they all originate from one and same ancestor, which implies that there was only one successful invasion (De Vos, 1996, 2000). If by any change the large and the small-sized lineages appear to be polyphyletic, two invasions might have occurred (Capasso Barbato & Petronio, 1986; Capasso Barbato, 1992b; Caloi & Palombo, 1996), though this model is not so realistic, regarding the antler morphology (De Vos, 1996). The speciation of the Cretan cervids is a clear case of adaptive radiation, similar to that observed in Darwin's finches of the Galápagos. Here, too, it is likely that they all descended from a single ancestral species: all Darwin's finch species are more similar to each other than anyone is to a continental species, including the suggested ancestors *Melanospiza richardsonii*, *Volatinia jacarina* and *Coereba flaveola* (Grant, 1986). Similarly, for the Cretan deer also possible continental candidates have been mentioned: a megacerine deer of the *verticornis* group, *Cervus peloponnesiacus*, *Cervus* sp., *?Pseudodama*, *Allocenelaphus* - *Nesoleipoceros*, but none of these genera shares synapomorphologies with *Candiacervus* that are not shared with other genera.

Solving the problems of taxonomy for endemic, insular species is possible only when the mechanism behind their speciation is understood. This is not easy, as taxonomy and evolution are not independent (Lack, 1947). To explain the speciation of Darwin's finches, Grant (1986) discussed the different models of speciation: allopatric, parapatric and sympatric speciation, and speciation based on gradual genetic changes (genetic drift). The latter model can merely contribute to an already divergent evolution by means of new alleles, but is not considered a means of speciation on itself (Grant, 1986). Parapatric speciation cannot be demonstrated either in the case of the Galápagos, leaving open only the allopatric model, or, with reluctance, the sympatric model if a more stringent set of conditions were met (Grant, 1986). Amazing however, that examples of allopatric speciation given by Grant (1986) can be as easily explained in terms of sympatric speciation.

A possible example of sympatric speciation is the medium sized ground finch *Geospiza fortis* of Santa Cruz, Galápagos Islands. In this area there is a diverse flora, providing a wide range of diets (Abbott et al., 1977), and as a consequence, differences are found within *G. fortis*. Ford et al. (1973) found differences in beak depth of the males, resulting in a clear bimodality, which they explained as disruptive selection. According to them, the population was halfway the process of splitting.

Another, related example is provided by *Cactospiza* on Isabela, Galápagos Islands. These finches are divided in two populations: one living in the mangrove forests along the coast, and the other living in dry areas and mesic woods, sporadically nesting in the mangroves (Gifford, 1919; Grant, 1986). The populations are separated, though not completely, and it can be easily imagined that they originated from a species that comprised contiguous populations over a habitat gradient. According to Grant (1986), the populations may have been already separated geographically by the time of the fission, and thus there is not enough evidence of parapatric speciation on the Galapagos. However, separation is not strictly necessary (Endler, 1977; Lande, 1982), and partly differentiated populations can be found in adjoining habitats on other places in the world. The fact that it's difficult to find two congeneric and sympatric species in the fossil record that would confirm the possibility of sympatric speciation might be explained by the possibly rapid speciation. It appears that micromammals at least need only a few thousand years (*Clethrionomys*, *Apodemus*), or even only seventy years (*Mus*) to change substantially in size (Heaney, 1978: 40).

The ability to explore slightly different ecological niches appears only possible for clades that are not too specialized. This is why deer can change their habitats, if necessary, whereas a panda cannot. The plasticity of deer is illustrated by the brow-antlered deer: *Rucervus eldi* from Manipur, India, lives in very wet swamps and on floating grass islands, whereas the same species from Thailand lives in higher, less wet areas (Van Bemmelen, 1973). The same plasticity accounts for the easy fusion of deer species, for example, Schomburgk's deer (*R. duvauceli schomburgki*) dissolved into the herds of *R. eldi* when their swampy habitats disappeared in the nineteen-twenties and they had to flee to the higher areas.

For lower, cold-blooded vertebrates the idea of sympatric speciation seems more acceptable. In fact, there is in some cases no alternative. For example, how else can the monophyly of cichlids in the African Lakes be explained, other than by sympatric speciation (Schlieven et al., 1994; Turner, 1994), since they share a close common ancestry, as suggested by mitochondrial DNA (Meyer et al., 1990) and the fact that interspecific hybrids can be fertile (Crapon de Caprona & Fritzsche, 1984)? But why would patterns of biodiversity be different for lower vertebrates than for higher, and why would these patterns be different for small-scale, short-term radiations than for large-scale, long-term radiations? Our classifications are artificial, and nature doesn't care about our taxonomy. Mammalian cells do not differ essentially from those of fishes, nor do our genes, except for their number and their amino-acid sequences.

Recent studies, however, give increasing evidence of the process of sympatric speciation, and it appears that reproductive isolation of species may occur without physical isolation. Higashi, Takimoto & Yamamura (1999) explain the process convincingly at the basis of variation in a male secondary sexual character with two conspicuous extremes and the corresponding variance in female mating preference. It appears that in this way the modal divergence of the male and female traits increase, resulting in a bimodal distribution, pulling the population apart into two prezygotically isolated populations. Interestingly enough, sympatric speciation may occur more readily if there is a decrease in the cost of male conspicuousness, which occurs if barrier-free or predator-free conditions arise (Higashi et al., 1999). In fact, this is the situation we meet on islands.

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