



Species as the basic units in evolution and biodiversity: How to define and delimit larger foraminiferal species in respect to paleogeography and biostratigraphy.

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Many concepts have been developed for the base of taxonomy, the biological species. Still there is confusion in these concepts between the 'substance' of a species, e.g. which factors makes a species (definition) and how to detect or recognize a species (delimitation). Concepts like morphospecies and chronospecies (= palaeospecies) that are mainly used for fossil specimens, and all methods based on molecular genetic methods belong to the group of concepts for delimitating species.

The species can be defined as a pool of contemporarily interconnected genotypes. This pool can be homogeneous or be divided into geographically separated sub-pools. Interconnectivity within such pools is given by the potential to transfer complete genomes or exchange genome parts through asexual or sexual reproduction. A change in genotype frequencies over successive generations is caused by preferred or restricted genome transfer due to evolutionary factors.

After establishment of new adaptive zones, evolutionary factors leads to species differentiation. Depending on number, duration of the onset and the further role of the new adaptive zones (stable or continuously changing), various methods of speciation – grouped into split off and split up speciation – can be established. True speciation is characterized by a complete loss of the potential to transfer genomes between the new species without the possibility to fuse (hybridise) when their adaptive zones come in contact or overlap. In case of a broad geographical distribution, the area might be differentiated into several adaptive zones, where transferability between subgroups is restricted or even lost. Temporarily disconnected adaptive zones can again become combined, reinstalling transferability between sub-pools of genotypes. Genotypically and morphologically different subgroups preserving transferability are thus not species; taxonomically, these structurally distinct subgroups can be treated as subspecies. Due to this uncertainty in the transition zone, a delimitation of species in the Recent is difficult in genotypically related but geographically separated groups. This is also the case in fossil forms when regarding a single geological horizon.

A strong discontinuity in a single evolutionary line is caused when a new adaptive zone for the species opens contemporaneously with the closing of the previous adaptive zone. This type of speciation, termed 'quantum evolution' or 'punctuated gradualism', is a special form of a geologically instantaneous 'split off speciation', where the mother species becomes extinct.

Contrary to quantum evolution, an instantaneous change in the transformation rate within an evolutionary line does not lead to new species. The clear differentiation in the species transformation rates should be taxonomically treated as different subspecies.

Because the potential to transfer genomes or genome parts is a non operational criterion for delimiting species, the main criterion for recognizing species is character's homogeneity (including molecular genetic methods). Because molecular genetic methods are restricted to living organisms, morphological criteria have to be used for recognizing and delimitating species by the criterion of homogeneity, especially in the fossil record. Homogeneity (including continuity) has to be checked in the four dimensions 'shape', 'environment', 'ontogeny' and 'geological time', allowing to differentiate between subspecies and 'true' species, while preserving different generations and ontogenetic (larval) stages within a single species.