

Basic Types of Life

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Summary: The main conflict in the species discussion may be summarised as follows: the population geneticist is mainly interested in gene flow and, therefore, has to prefer a biospecies concept. On the other hand, the practising taxonomist and the palaeontologist are mainly interested in similarity and, hence, have to use a morphological species concept. This conflict is fundamental and cannot easily be resolved. It is often stated that higher levels of classification are even more problematic than the species definition. Using a genetical criterion based on interspecific hybridization, it is suggested that a systematic category above the genus level may be defined rather objectively: *two organisms belong to the same basic type if (i) they are able to hybridize or (ii) they have hybridized with the same third organism*. In principle it is possible to check experimentally by artificial insemination or artificial pollination if two biparental individuals belong to the same basic type. The basic type category thus may prove to be open to empirical validation. Advantages and problems of this basic type criterion are discussed.

A general summary follows on a few basic types of the plant and animal kingdom that have been described. Based on rather limited data it appears to emerge that (i) the basic type criterion can be applied successfully in animal as well as plant taxonomy, (ii) a clear gap of overall similarity is found between different basic types, (iii) within basic types a variety of microevolutionary processes may help to understand speciation, and (iv) the distribution of characters across different species of the same basic type may be discussed under the hypothetical assumption of a large hidden variation potential harboured by a genetically complex ancestral population.

It must be emphasized that only 14 basic types have been described to date. This number is too low to provide for a reliable basis of generalization. Therefore, the basic type concept is only suggested to serve as a preliminary working hypothesis.

I. The species problem

Currently, about 1.5 million species are binominally named. However, this is probably only a fraction of the total number of extant species. Estimates vary between 3-5 millions and 10-50 millions (MAY 1988). For four reasons, it is necessary to name the species on earth. First, only by naming is it possible for biologists to communicate on their subjects. Second, only by naming is it possible to classify. Third, only by naming is it possible to understand the mechanisms of microevolution, i.e. speciation and fourth, only by naming is it possible to protect the threatened diversity of life. Therefore, classification of organismic diversity remains one of the most important as well as most fascinating tasks of biology. (Unfortunately, there is an irritating world-wide tendency to reduce funding for such fundamental research.)

The numbers of species given above are rather unreliable estimates. In part, this is due to some uncertainty of species definitions. Very

often, systematic studies, for practical reasons, cannot else but use a morphospecies definition. The definition of the biological species (see below) is usually not applicable in field or museum studies. This causes an on-going conflict in taxonomy. DOBZHANSKY wrote: "The species problem is the oldest in biology" (DOBZHANSKY 1972). Although there is a seemingly endless discussion of the species problem in the biological literature, it is still unsolved. The discussion has a long history, which is not to be summarized in this paper (see, e.g., MAYR 1982; WILLMANN 1985). Neither shall I present the various philosophical implications of the species definition (see, e.g., SUCKER 1978; VAN DER STEEN & VOORZANGER 1986; ERESHEFSKY 1992).

Numerous species definitions (for review see, e.g., HÄUSER 1987) as well as speciation mechanisms (for review see JUNKER 1993a; OTTE & ENDLER 1989), have been and are still proposed. Often, the discussion is polarized (e.g., COYNE

et al. 1988), usually not free from subjective statements and not restricted to biology. As Jerry A. COYNE recently put it: "No area of evolutionary biology has been more beset by semantic and philosophical squabbles than the study of speciation. The difficulty of understanding such a slow historical process has repeatedly driven scientists out of their laboratories and into the arms of philosophy. From this union has sprung a bloated, quasi-philosophical literature about whether species exist, what they are and whether they differ from more arbitrary categories such as genera or families" (COYNE 1992a).

This paper has not been written in order to present a solution to the species problem. For reasons which are to be discussed below, a final solution probably does not exist. Instead, after a short introduction to the species discussion, a somewhat objective way to define a higher taxonomic rank than that of species and genus will be suggested.

Species concepts

Dependent on the way of counting, a dozen or more different species definitions exist (ERESHEFSKY 1992; LÖNNIG 1993; OTTE & ENDLER 1989). HÄUSER summarizes 15 definitions which have been proposed between 1966 and 1985 (HÄUSER 1987). In the author's opinion, all definitions fall into either one of four basic groups: ecospecies, chronospecies, morphospecies and "geno"species.

Some authors suggest that the unique role of ecological niches could be used for the description of ecospecies (SIMPSON 1961; TURESSON 1922). But what, exactly, is a particular ecological niche? Some authors feel that this species definition is open for a great deal of subjectivity (for a discussion see MAYR 1963; WILLMANN 1985). The chronospecies concept pays attention to the historical course of speciation (AX 1987; WILEY 1981; WILLMANN 1985). SIMPSON suggests that a chronospecies is a phyletic lineage, evolving independently of others, with its own separate and unitary evolutionary role and tendencies. AX and WILLMANN include all individuals, irrespective of morphological divergences, in one species if no split of lineages has

been demonstrated. Concerning species concepts in palaeontology, REIF concludes that (i) none of the proposed concepts leads to objective criteria for the diagnosis of evolutionary species and (ii) the fossil record is almost nowhere sufficient for the direct application of species-delimiting criteria (REIF 1984).

The chronospecies is defined by criteria similar to those applicable to the morphospecies. Until 1940, the morphological species definition was most commonly accepted, but it is still used frequently. CRONQUIST (1978) suggests: "Species are the smallest groups that are consistently and persistently distinct and distinguishable by ordinary means". Obviously, this definition involves subjective elements, which is nicely illustrated by the definition of GINSBURG: "A given population is to be considered a species with respect to another closely related population when the degree of intergradation (overlap of the observed samples) is not more than 10 percent" (GINSBURG 1938), cited according to (MAYR 1963). Objections against this species concept have been raised repeatedly and discussed thoroughly by different authors (for a review see, e.g., HÄUSER 1987).

Today, genetic species concepts are most popular among biologists. The idea that gene flow is an important argument for defining species has been expressed by early biologists. MAYR defined: "Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (MAYR 1940). Other biologists contributed to the development of the biospecies concept as well (e.g. DOBZHANSKY, HUXLEY, STRESEMANN, WRIGHT and others, for references see MAYR 1963; 1982; WILLMANN 1985).

Reproductive isolation of biospecies

The key issue of the biospecies concept is reproductive isolation. But what, exactly, is reproductive isolation? This is by no means a question easy to answer. In fact, one of the criticisms of the biospecies concept focuses on the definition of reproductive isolation (e.g., CRACRAFT 1983). The analysis of hybrid zones clearly shows that gene flow between "good species" is frequent (BARTON & HEWITT 1985;

1989); the more species are closely studied, the more hybrid zones are found (e.g., MOSSAKOWSKI 1990). Often, the hybrids are not only viable, but fully fertile. Nevertheless, the parental species are commonly treated as different. For example, the eastern Europe fire-bellied toads *Bombina bombina* and *Bombina variegata* (Amphibia) interbreed freely in a narrow zone that extends over 1000 km. On the other hand, they differ by morphology, ecology and genetics (SZYMURA & BARTON 1986). The straightforward solution in such cases, according to WILLMANN, appears to be simple: *Bombina bombina* and *B. variegata* should be treated as a single species (WILLMANN 1987). In other cases, stable hybrid zones are found but it seems that there exists a strong selection against hybrids, resulting in a substantial, though not absolute barrier to gene exchange over these tension zones (BARTON & HEWITT 1989) which are considered to represent stages of speciation. To what extent is gene flow between "good species" acceptable? Strict adherents of the biospecies concept would deny *any* gene flow between species. Actually, in numerous cases no hybrid zone exists ("good species") but only occasionally hybridization occurs. Hence, some gene flow exists. Moreover, the hybrids sometimes display a strongly decreased fertility. Gene flow caused by these hybridization events is very minor, but is not zero: should one define one or two species? Usually, even the originators of the biospecies concept end up with two species in such cases (BARTON & HEWITT 1989). However, if one would apply the biospecies concept consequently, two clearly separated species must be united even if a partially fertile hybrid is detected once in dozens of generations. This, however, would lead to a degree of lumping of species probably completely unacceptable for most taxonomists. Furthermore, biospecies recognition very often is difficult to test since it is extremely tricky to measure gene flow between populations if it occurs only very seldomly.

Reproductive isolation between species may comprise only certain genes. Based on a most comprehensive study on species hybridization within the plant genera *Phaseolus*, *Chrysanthemum* and *Pisum*, LAMPRECHT submitted that genes exist which may be used to define species (LAMPRECHT 1966). He suggested to discrimi-

nate between intraspecific and interspecific genes. If the maternal genotype is AA and the paternal genotype is aa, intraspecific genes would segregate as 1 AA : 2 Aa : 1 aa or, if the maternal genotype is aa and the paternal genotype is AA, the segregation will be 1 aa : 2 aA : 1 AA. However, the segregation of interspecific genes will be 1 AA : 2 Aa : 0 aa or, if the maternal alleles are recessive, 1 aa : 2 aA : 0 AA. If AA or aa occur, these hybrids are sterile in case of interspecific genes. One interpretation of these data is that paternal alleles of interspecific genes cannot be expressed homozygotically in the maternal cytoplasm. They do not show a mendelian behaviour. Based on this observation LAMPRECHT defines: "All biotypes carrying the same alleles of interspecific genes belong to the same species." An advantage of such a species definition would be that it might be subject to empirical validation. An extensive discussion of this concept is given by LÖNNIG (1993).

It appears, therefore, that the biospecies concept does include serious problems and is not as objective as some of its proponents would suggest. Basically, it is an operational and conceptual tool to describe the process of speciation. For this purpose, no viable alternative seems to exist. This is not to say that the mechanistic basis of speciation has been unraveled. DARWIN considered speciation the "mystery of mysteries", FUTUYMA (1983) lamented that speciation is "more thoroughly awash in unfounded and often contradictory speculation than any other single topic in evolutionary theory" and COYNE concluded that "speciation is still a little-understood area of evolution" (COYNE 1992b). Nevertheless, it seems very unlikely that speciation, which obviously is at work through different mechanisms (COYNE 1992b; JUNKER 1993a; OTTE & ENDLER 1989; ZWÖLFER & BUSH 1984), can be described adequately without using the biological species concept.

Some causes for the species conflict

What are the causes for what has been called the "species plague" (VAN DER STEEN & VOORZANGER 1986)? First, given the problems described in the previous paragraph in using the

biological species concept, it has been admitted quite frankly that the biospecies concept was not developed for practical application, that is to recognize species in nature, but for theoretical reasons, i.e. to understand the role of species as natural units of microevolution (DE JONG & GOODMAN 1982; WILLMANN 1987). It is thus understandable that most practical taxonomists prefer the morphospecies concept over the biospecies concept.

The morphospecies concept, in contrast, considers only characters to describe the basic units of life. Therefore, there is a clash between these two views of species: one is based on gene flow, the other on the maintenance of a cluster of phenotypes. Sometimes, both the morphospecies and biospecies concept may lead to similar results. In these cases, reproductive isolation is coupled with morphological and, most often, genetic distance (SPERLICH 1984). However, there are puzzling examples to the opposite: it was possible to demonstrate that speciation events (using the biospecies concept) can happen by changing only very few genetic characters (COYNE 1992b). In extreme cases, even single-gene speciation is possible (ORR 1991). It has been shown that sibling species, which can be almost indistinguishable morphologically, are also virtually identical alloenzymically (JOHNSON et al. 1986), but nevertheless provide an excellent example for "good species" which are reproductively completely isolated. Reproductive isolation may even be due to microorganisms residing in the cytoplasm of eggs, but not in sperm cells, thus causing cytoplasmic incompatibility. This results in sterility of crosses between two otherwise very closely related species (BREEUWER & WERREN 1990). Another example for sterile hybrids of genetically otherwise closely related species are transposable genetic elements (P-elements), causing incompatibility when a sperm cell carrying the P-element fertilizes an egg cell without P-element (for review see KIDWELL & PETERSON 1991). On the other hand, morphologically quite dissimilar individuals may be nearly identical genetically (for a recent example see FORD & GOTTLIEB 1992).

The second reason for the conflict, therefore, may be summarized as follows: The population geneticist is mainly interested in gene flow while the taxonomist is mainly interested in the degree of similarity (i.e., differences). In order to understand speciation, similarity can be almost neglected, but for classifying organisms, similarity is one of the key issues. The biospecies concept does not allow one to decide whether two species are "closely related" while the morphospecies concept does not allow one to know whether gene flow exists. It does not seem that an easy solution to this fundamental conflict exists.

Do different disciplines need different species concepts? Perhaps a variety of views of the species is appropriate in order to describe the complexity of nature (MISHLER & DONOGHUE 1982)? However, this would be likely to generate considerable confusion. A clear consensus is needed on what units one is talking about. In the writer's opinion, the observation that organisms form populations which may become separated, thus evolving independently, is a basic phenomenon of microevolution and, therefore, should be applied whenever possible in order to define biospecies. If no data from field studies are available (this is found in most cases), there will be no other choice than to use a morphological species concept. In case such data become available, one should give priority to species definitions based on gene flow. In doing so, over-all similarity will be excluded from the species definition but still is an important piece of information: Overall similarity, in these cases, might be used to delimit different genera. If different biospecies are readily discernible, they may be assigned to different genera. Since this latter procedure includes some subjectivity (see below), it would be desirable to have a taxonomic category available above the genus level which harbours all genera with the same overall similarity as well as the same basic genetic pattern. It would be further desirable to define such a category with some objectivity. It is suggested in the following paragraph that such a category indeed may exist.

II. Categories above the species level

A review on the history of the understanding of higher categories in taxonomy can be found elsewhere (BARLETT 1940; MAYR 1982; MORTON 1981; SINGER 1962). Often, it is held that higher categories are completely artificial (AX 1987; MAYR et al. 1953; PETERS 1970). However, due to some classification models, higher categories can be viewed as natural if they comprise only and all living species which descended from a single ancestral population, i.e. are monophyletic (MAYR et al. 1953; SCHAEFER 1976). Although there is a consensus among all authors that higher categories cannot be defined objectively, some agreement on practical rules to set these categories exist, at least among phylogenetic systematists: higher categories (i) need to be monophyletic and (ii) should be separated by a clear gap when compared to other groups closely related. (It is not intended here to compare the cladistic, numerical and evolutionary approach to classification, for a short review see MAYR 1990.)

What is a genus?

When compared to the species discussion, only very little work has been devoted to the definition of the genus (for a detailed review see DUBOIS 1988). It has, for instance, been suggested that the number of species to be included in one genus should have an upper limit of 40 (ROSS 1975). MAYR et al. (1953) proposed that the number of species in a genus should be inversely correlated to the morphological gap between genera. They define: "A genus is a systematic category including one species or a group of species of presumably common phylogenetic origin, which is separated from other similar units by a decided gap." According to CAIN (1956), a genus is "monophyletic, but purely positional in rank, and a collection of phyletic lines. . . . Only comparative criteria are applicable at the level of the genus (and other higher categories)". In a discussion of the genus concept MICHENER concludes that "a category such as genus, as it is ordinarily used, can only be defined as a monophyletic unit of one or more species, differing in some ways from other such

units" (MICHENER 1957). SIMPSON suggested that genera are "the most definite and permanent unit of modern classification, to such an extent that the genus may be considered the basic unit of practical and morphological taxonomy, although the species is the basic unit of theoretical and genetical taxonomy" (SIMPSON 1945). Probably, he was led by the experience that a well-trained specialist of a particular group is able to integrate a vast array of features of a group, thus developing a reliable "feeling" for relatedness. However, this feeling cannot be strictly defined, a genus "has no single, crystallized, idealized pattern or morphotype" (SIMPSON 1953).

Interspecific hybridization has been proposed as a criterion to define genera (VAN GELDER 1977, DUBOIS 1988). This interesting approach will be discussed below in more detail.

What is a family?

The definition is often quite similar to that of the genus. "A family is a taxonomic category containing a single genus or a monophyletic group of genera, which is separated from other families by a decided gap. It is recommended, as in the case of the genus, that the size of the gap be in inverse ratio to the size of the family" (MAYR 1969). The family level is sometimes chosen in a way that "the gaps within the family are small enough so that the relationships are readily evident, but gaps between families are so large that the relationships can be discerned only by detailed study" (EDMUNDS 1962). Adaptive features have also been used for discerning families: "A family-group seems to be a group of species adapted for a broadly similar mode of life. This mode cannot be narrowly defined - it is not solely a means of food-getting, or of reproduction, or of food-type but rather a new combination of these and other adaptations" (SCHAEFER 1976).

Since both genus and family definitions are clearly arbitrary, SIBLEY et al. (1990), based on DNA-DNA hybridization, proposed a quantitative measure for defining family and genus rank within birds: they suggested to use the

term family if the differences in $\Delta T_{50}H$ values (these are measures of homology between DNA sequences) between individuals are not greater than 9-11 while they use the term genus if these values are lower than 2.2. However, it does not appear obvious why these authors chose exactly those numbers and not, for instance, 14-16 for the family and 3.1 for the genus. Most probably, they calibrated their numbers by referring to preexisting taxonomic rankings. If so, this would be an example of circular reasoning, not adding any objectivity to the problem.

Interspecific hybridization

One aspect of similarity can be measured precisely these days by sequencing genes. But the information provided by gene sequences must be interpreted and may yield different classifications for different genes. More important, the most interesting differences between organisms are found in the genetic program package which leads to the formation of morphogenetic pattern during ontogeny. But this program cannot be localized in sequences of structural genes. It is also unlikely that mere sequences of various regulatory genes as such provide the basis needed in order to understand morphogenesis of an organism. It would seem that a complex interaction of a variety of regulatory genes with numerous structural genes, intimately bound to a specifically structured three-dimensional space of the zygote must be known in order to describe pattern formation during ontogeny. However, we are very far from understanding such processes and, therefore, cannot use them for classification. But it is obvious that successful hybridization is a clear indication that the species from which the germ cells are derived from are closely related. Can this important piece of information be used for classification?

CLAUSEN et al. proposed the taxonomic categories of ecospecies, coenospecies and comparium (CLAUSEN 1951; CLAUSEN et al. 1939). An "ecospecies" has its own genetic system sufficiently differentiated and distinct from the genetic systems of other ecospecies to produce only hybrids with reduced fertility or viability. The ecospecies often corresponds to the species

rank in common classifications. A coenospecies comprises ecospecies displaying the ability for restricted interchange of genes in spite of partial hybrid sterility. The comparium, finally, comprises coenospecies which are capable of producing sterile interspecific hybrids. There have been a number of approaches to use intergeneric hybridization as an argument to lump species from different genera into one genus (ANSELL 1971; BUETTNER-JANUSCH 1966; SIMPSON 1961; STAINS 1967; STEBBINS 1956). VAN GELDER suggested that "species in one genus should not be capable of breeding with species in other genera" (VAN GELDER 1977). In other words, if interspecific hybrids are observed (irrespective of whether they are fertile or sterile), the parental species should be included into one genus. Consequently, VAN GELDER lumped 42 mammalian genera and created 17 genera instead; STEBBINS (1956) suggested that it might be appropriate to merge 20 genera of Triticeae into a single genus. Probably, genus numbers would be reduced further if systematic cross-fertilization experiments were undertaken. The genus definition of VAN GELDER corresponds closely to the comparium of CLAUSEN et al. (1939). VAN GELDER (1977) even wrote: "It seems to me that if the chromosomes of two taxa are compatible enough to develop a foetus to term, then the parents would seem to be more closely related than generic separation would suggest."

More recently, DUBOIS (1988) also suggested to use interspecific hybridization as a taxonomic criterion. He proposed that "whenever two species can give viable adult hybrids, they should be included in the same genus; if other valid criteria had led them previously to be placed into different genera, these must be merged." This approach corresponds closely to VAN GELDER (1977). However, for the following reasons such a definition for a genus is probably not useful. First, the information storage capacity of biosystematic classifications is severely reduced since a variety of morphologically extremely different as well as highly similar species would be lumped together in one genus, comprising a large number of species. For instance, geese, swans and ducks would be members of the same genus (SCHERER 1993b). Over-all similarity, which is the basis for most classifications, even at the species le-

vel, would be excluded as a criterion. This is highly undesirable for the practical taxonomist. Second, it would dramatically change the nomenclature currently in use and, therefore, cause tremendous confusion. These two consequences must result in the rejection of such a genus definition by most taxonomists.

The basic type criterion

Definition of basic types

A taxonomic rank termed "basic type" or "baramin" by Frank L. MARSH (1941; 1976) comprises all individuals which are able to hybridize and, therefore, appears to be related to the genus definition of CLAUSEN, VAN GELDER and DUBOIS discussed in the previous paragraph. Building on CLAUSEN'S, MARSH'S, VAN GELDER'S and DUBOIS' work, it is submitted here that hybridization data be used by the following primary membership criterion:

Two individuals belong to the same basic type if (i) they are able to hybridize.

Additionally, a secondary membership criterion is proposed which greatly facilitates basic type recognition:

Two individuals belong to the same basic type if (ii) they have hybridized with the same third organism.

For practical reasons one may substitute the term "individual" by the term "species", although in a strict sense only individuals are able to hybridize. Note that it is neither considered to be important whether hybridization occurs in nature or in captivity, nor if it is induced by artificial insemination or artificial pollination. Note further that fertility or sterility of the hybrid is not used as a criterion of relatedness since sterility can be caused by rather minor genetic changes. In contrast, if hybridization is possible, morphogenetic programs of the parents obviously are highly similar, warranting the inclusion into one basic type.

In order to indicate basic types without confusing currently accepted taxonomic nomenclature, they will be labeled by adding the prefix *bt* to the acknowledged latin name of the group.

Advantages of the basic type definition

The basic type definition has several advantages. *First*, the criterion provides a category whose members share the same morphogenetic pattern. This has consequences for phylogenetic interpretations concerning such groups. *Second*, a wealth of interspecific hybridization data are already available (see section III of this article), which have rarely been used in classification. *Third*, if data are missing, one may introduce the experimental approach of artificial insemination or artificial pollination (CLAUSEN et al. 1939). Therefore, this criterion is a taxonomic category which is subject to empirical validation. *Fourth*, this approach allows one to define the basic type taxon in much the same way as the biospecies. One of the advantages of the biological species taxon is that it can be defined without any reference to other species. Definitions of higher taxa, in contrast, "can only be relative to those of other categories, specifying relative ranks in the hierarchy and set relationships to taxa" (SIMPSON 1961). This limit can be overcome by the classification criterion suggested here (compare also DUBOIS 1988). *Fifth*, SCHAEFER (1976) stated correctly that, until now, it was impossible to answer the question of how a taxonomic category in one group (for instance, birds) can be made equivalent to the same category of another group (for instance, mammals or angiosperms). The criterion suggested here provides a taxonomic rank above the species level which is directly comparable within all kinds of sexually reproducing organisms. *Sixth*, the criterion proposed leaves plenty of room for using morphological similarity in defining genera. Thus, the information storage and retrieval capacity of such a classification scheme (i.e. species - genus - basic type) remains high. *Seventh*, application of this criterion does not cause major changes in nomenclature since the binominal names remain unchanged.

Problems of the basic type definition

The basic type criterion is a wholly positive one. If hybrids are known, membership is unequivocal. However, for more than 90% of the families of higher plants no intergeneric hy-

brids have been recorded at all. If no hybrids are known, one could use selected genera and try to breed hybrids experimentally. If one fails consistently to produce hybrids, this does not necessarily mean that the two individuals belong to different basic types. It is well known that even among members of closely related species sometimes no hybrids can be formed. In this case, one has to refer to similarity criteria in asking whether the individuals under discussion are sufficiently similar to members of a basic type which are known to be involved in hybridization. If such hybridization data are also missing, an annotation to a specific basic type is only possible by referring to taxonomic rankings currently in use.

The definition given above may, however, eventually turn out to be not entirely objective. Some of the reasons have been already mentioned when the biological species definition was discussed: there exist grades in reproductive isolation at the species level and these grades exist as well at the basic type level. The primary and secondary membership criteria use the production of offspring (hybridization) to recognize basic types. However, what does hybridization mean? There are cases where hybridization occurs and the offspring is fully viable. In other cases the offspring dies before reaching maturity; sometimes, the offspring dies shortly after birth; and still in other cases, the development of the embryo is terminated at some stage during embryogenesis. What then, exactly, does hybridization mean? Is the criterion of hybridization met if, for instance, a mammalian hybrid foetus dies before birth? In order to deal with this problem, MARSH submitted the following membership criterion: "In every case where true fertilization of the egg occurs, the parents are members of the same baramin" (1941; 1976). This definition was adopted later by SCHERER & HILSBURG (1982).

What does "true fertilization" mean? Certainly parthenogenesis, induced by unification of sperm cell and egg cell followed by an elimination of paternal chromosomes, should be excluded. Concerning animals, true fertilization in the sense of MARSH means: (i) recognition of sperm and egg, (ii) sperm entry, (iii) formation of haploid pronuclei, (iv) formation of a diploid nucleus, (v) activation of the zygote,

(vi) doubling and separation of both maternal and paternal chromosomes and (vii) formation of the early blastomeres involving the chromosomes of both parents.

This criterion has been critically discussed by LÖNNIG (1993). He pointed out that during early stages of embryogenesis development including replication generally proceeds without transcription and is controlled by various cytoplasmic factors formed in the egg while it matured in the mother. According to WOLFE (1993, p. 1103), "much or all (of the morphogenetic information) of early development is stored in the egg cytoplasm, . . . early embryonic stages are under the control of maternal genes. In some organisms, such as *Drosophila*, the effects of some maternal genes are exerted through their mRNA or protein products throughout embryonic development. In others, such as mammals, the effects of maternal genes are much reduced and limited to very early embryonic stages." Only later during embryogenesis does nuclear transcription occur. What is even more important for defining 'true fertilization' is the suspicion that "the biochemistry regulating these divisions is similar, if not identical, among all the animal phyla, and that the biochemistry of cell division may be the same throughout all eucaryotes" (GILBERT 1991, p. 111). Therefore, DUBOIS (1988, p. 42) concluded: "The fact that two species may be able to give viable hybrids until the end of the blastula stage is therefore of little genetic or phylogenetic meaning and is of little interest to the systematist."

Obviously, the definition of a basic type by using the criterion of true fertilization as given by MARSH (1941) and used later by SCHERER & HILSBURG (1982) needs to be revised. Therefore, a future tertiary membership criterion could be similar to the following definition:

Two individuals belong to the same basic type if (iii) embryogenesis of a hybrid continues beyond the maternal phase, including subsequent coordinated expression of both maternal and paternal morphogenetic genes.

If one is going to perform test-tube hybridization between distantly related genera in order to define basic types experimentally, an appropriate tertiary membership criterion will

probably be indispensable. Unfortunately, almost no comparative data are known on gene expression during early embryogenesis of closely and only distantly related species including the respective zygotes. Closer investigation of transcription during early embryogenesis in such cases eventually might reveal that some functional gene complexes are basic type specific while others are not (LÖNNIG 1993, p.

13; compare also the idea of intra- and interspecific genes of LAMPRECHT 1966). Clearly, the development of a workable tertiary membership criterion is, at the best, in its initial stages.

Throughout the chapters which follow in this book, only the primary and secondary membership criteria, i.e. successful hybridization, have been used in order to delineate basic types.

III. Application of basic type taxonomy

In creating a classification system, one can use features of organisms describing their similarity, starting at the species level and working up the hierarchy. This was termed "upward classification by empirical grouping" (MAYR 1982). On the other hand, it is likewise possible to concentrate on differences of organisms starting from higher systematic categories and working all the way down to the species level. This has been termed "downward classification by logical division" by MAYR (1982) or, more recently, "discontinuity systematics" (WISE 1992). Both strategies are useful. Classification based on interspecific hybridization, like the one based on biospecies recognition, is an "upward classification approach". First, a short review of the application of this approach is given with special reference to the papers published in this book.

The data base

Usually it is widely believed that interspecific hybridization occurs only very rarely. However, the study of the literature reveals numerous hybrids observed in nature or derived in captivity which often have never been compiled systematically. For instance, in a recent paper it was stated that "approximately one in ten bird species is known to hybridize, and the true global incidence is likely to be much higher" (GRANT & GRANT 1992). Thus, from a world total of 9672 bird species, 895 species are known to have bred *in natura* with at least one other species (PANOV 1989). Not only species of the same genus are involved, intergeneric hybridization

in the natural habitat is also found. It is restricted to seven orders but is fairly frequent where it does occur (GRANT & GRANT 1992). To these hybrids, a great number of hybrids derived in captivity can be added; for instance, within the family Anatidae (approximately 150 species), well over 400 different interspecific hybrids are known (SCHERER & HILSBURG 1982). In captivity, much more intergeneric hybrids occur than under natural conditions. In a few cases, check lists of all known crossings within certain groups exist, for instance for birds (GRAY 1958), mammals (GRAY 1972) or Poaceae (KNOBLOCH 1968). However, many check lists are rather old and outdated. On a regular basis, new hybridization reports can be found, for instance, in the International Zoo Yearbook. It appears, therefore, that a good number of crosses are already known. These can be used immediately in order to discern basic types.

Basic types within plants and animals

An overview on the taxonomic ranks of basic types described in SCHERER (1993a) can be found in Table 1. Obviously, the basic type rank depends on the author having created the systematics of that particular group. For instance, according to WOLTERS (1983), *bt*Anatidae is at the family level, but could also be assigned to the subfamily level (JOHNSGARD 1978; SCHERER 1993b). Generally it appears that basic type rank is comparable with the subfamily or family level in Aves or Mammalia while it may range between tribe and family rank within plants. However, based only on a small num-

Tab. 1: Taxonomical outline of plant and animal groups which have been investigated with respect to interspecific hybridization (see different authors in SCHERER 1993a). Basic types are high-lighted by bold print. A question-mark indicates that the assignment of basic type rank to this taxonomic group is uncertain.

| P L A N T A E | | A N I M A L I A | |
|---------------|-----------------------|-----------------|---------------------------|
| | Embryophyta | p | Chordata |
| p | Bryophyta | sp | Vertebrata |
| c | Musci | c | Aves |
| o | Funariales | o | Anseriformes |
| f | btFunariaceae | f | btAnatidae |
| p | Pteridophyta | f | btAnhimidae* |
| c | Filicatae | o | Galliformes |
| o | Aspidiales | f | btPhasianidae |
| f | btAspleniaceae | f | btCracidae*(?) |
| p | Spermatophyta | f | btMegapodiidae*(?) |
| c | Dicotyledoneae | o | Falconiformes |
| sc | Rosidae | f | btCathartidae |
| o | Rosales | f | Accipitridae |
| f | Rosaceae | sf | btAccipitrinae (?) |
| sf | btMaloideae | sf | btButeoninae (?) |
| sf | Dryadoideae | sf | btAegyptiinae (?) |
| t | btGeeae | f | btFalconidae |
| c | Monocotyledoneae | o | Passeriformes |
| sc | Liliidae | so | Passeres |
| o | Poales | f | btEstrildidae |
| f | Poaceae | f | Fringillidae |
| sf | Pooideae | sf | btCarduelinae |
| t | btTriticeae | c | Mammalia |
| | | sc | Placentalia |
| | | o | Carnivora |
| | | f | btCanidae |
| | | o | Perissodactyla |
| | | f | btEquidae |
| | | o | Primates |
| | | f | btCercopithecidae |

p = phylum; sp = subphylum; c = classis; sc = subclassis; o = ordo; so = subordo; f = familia; sf = subfamilia; t = tribus; bt = basis typus. * assignment of basic type rank is based on circumstantial evidence, not on hybridization.

ber of 14 basic types described as yet, no final statement is possible. Far more groups have to be studied, especially from other vertebrate classes, invertebrates and from other plant phyla.

Data on interspecific hybridization differ widely for the plant and animal groups investigated. For instance, within **btEquidae** (one genus, 6 species), from a total of 15 hybrids theoretically possible, 14 have actually been reported (STEIN-CADENBACH 1993). In contrast, within the **bt?Accipitrinae/Buteoninae** (29 genera, appr. 150 species), only seven, including two intergeneric hybrids (between *Accipiter* and *Buteo* and between *Buteo* and *Parabuteo*) are known.

Interestingly, one of the intergeneric hybrids connects the two subfamilies. It is, therefore, obvious that this basic type cannot be defined yet on the basis of hybridization (ZIMBELMANN 1993). Although the number of intergeneric hybrids actually found will depend on the number of genera within a basic type, other parameters additionally are responsible for such vastly different sets of data. For instance, within **btAnatidae** (148 species, 40 genera), having a similar size than the **bt?Accipitrinae/Buteoninae**, a total of more than 300 intergeneric hybrids have been observed. This difference, obviously, is due to the fact that anatids can be bred easily in captivity while birds of prey can

only be bred with difficulties. If birds of prey propagate in captivity, breeders usually try to avoid any hybridization for reasons of species conservation.

From this discussion an important bias of basic type classification emerges. It is restricted to groups of organisms which are not only very well known but were kept in captivity or cultivation for some reason or the other. However, the perspective of planned hybridization, for instance by using artificial insemination or artificial pollination, should be considered carefully. First, induced by the rapid development of *in vitro* fertilization, the production of animal embryos gets easier. Second, comparatively few hybrids are necessary in order to discern a basic type. It is a general observation that species of the same genus with few exceptions will hybridize in captivity (by the way, this fact may shed some light on the “feeling” of taxonomists enabling them to assign species to a genus). Therefore, intergeneric hybrids are far more important to study than interspecific hybrids and experiments may be directed mainly to intergeneric crosses. Furthermore, it is not necessary that each intergeneric hybrid which is theoretically possible be actually achieved. The basic type definition maintains that two species are assigned to the same basic type if they are connected indirectly by hybridization. For instance, consider *btCercopithecidae* (9 genera, which gives 36 different intergeneric combinations). Only 9 combinations were actually reported (HARTWIG-SCHERER 1993) but these connect 8 from 9 genera which delimits *btCercopithecidae* quite clearly. At the minimum, in order to delimit a basic type, one would need to produce only $(n-1)$ hybrids, where n is the number of genera. This task would appear to be quite feasible, at least in case one is dealing with plants.

Basic types: Addition of supplementary membership criteria

Apart from a few examples, not all hybrids are available which would be necessary to discern the basic types (see table 1) unequivocally. Therefore, in order to reach a tentative basic

type classification, one may wish to use additional criteria, which are provided by all levels of traditional taxonomy.

As an example, consider the genus *Miopithecus* which is not known to have hybridized with other cercopithecoids. Since it is very likely based on data from morphology, anatomy, chromosomal structure and behaviour that *Miopithecus* falls well within the range of the family, some authors have suggested to abandon the genera *Erythrocebus*, *Miopithecus* and *Allenopithecus* in order to include those species in the genus *Cercopithecus*. On the other hand, the genera *Mandrillus* and *Macaca* are connected by hybridization with *Cercopithecus* but are definitively much more distant to *Cercopithecus* as is *Miopithecus* (HARTWIG-SCHERER 1993). Therefore, there is little doubt that *Miopithecus* belongs to *btCercopithecidae*.

Another example has been reported by KUTZELNIGG (1993). According to different authors, *btMaloideae* (including apple trees) comprises between 15-30 genera with 200-2000 species. If one decides to accept 24 genera, only 12 of them are connected by hybridization. Why should one include the other genera into the basic type? First, hybridizations have been derived mainly by chance. It is, therefore, very likely that a systematic crossbreeding programme would yield a wealth of further hybrids. Second, several hybrids have been reported between genera which are thought to be widely different according to other criteria. Third, missing hybrids often comprise genera which are thought to be closely related; some authors would rather unite them in one genus. Fourth, it has turned out to be impossible to divide *btMaloideae* into different subgroups without arriving at severe contradictions. So it was impossible to treat the genera involved in hybridization as a distinct subgroup, separated from the other genera. Fifth, *btMaloideae* does show clear synapomorphies. Together, these additional criteria would suggest that all genera could tentatively be considered to belong to the same basic type.

An opposite example is provided by *Anseranas semipalmata* (Australian Magpie goose, Anseriformes). Some authors have included this species into the family Anatidae while others have created a separate monotypic family for

this single species. No hybrids at all are known so far. There is an increasing number of observations based on morphology, anatomy, behaviour, biochemistry and molecular biochemistry which clearly separate *Anseranas* from *btAnatidae*. For instance, sequencing of hemoglobin placed *Anseranas* as distant from *btAnatidae* as from *btPhasianidae* (SCHERER 1993b; SCHERER & SONTAG 1986). Therefore, it is considered to be very reasonable to omit *Anseranas* from *btAnatidae*.

A yet unresolved problem is posed by the different avian families belonging to Galliformes (e.g. chicken, pheasants, see KLEMM 1993). Usually, 250-300 species in 70-94 genera are attributed to this order and divided into 1-7 families with a total of 5-15 subfamilies. 159 hybrids are known, 28% of which connect different subfamilies. Several authors would feel that the order should be divided into three families: Phasianidae (ca. 200 species in 70 genera), Megapodiidae (12 species in 7 genera), and Cracidae (43 species in 10 genera). Within Megapodiidae, no hybrids are known; within Cracidae, only two intergeneric hybrids have been reported while within Phasianidae numerous hybrids are known. It is quite likely, therefore, that *btPhasianidae* can be postulated. The unsolved question is whether to include all three families into one basic type. There have been reports on hybrids between megapodids as well as cracids with *Gallus* (Phasianidae). However, these reports are quite old, were not reproduced and, thus, cannot be treated as sound evidence. It does not seem to be possible to divide the three families convincingly by demonstrating that each owns a clear set of synapomorphies; on the other hand, preliminary molecular data seem to indicate that Megapodiidae and Cracidae are more similar to one another and somewhat distant to *btPhasianidae*. In contrast, numerous synapomorphies exist when the order Galliformes is considered which, according to WISE (1992), would be in favour of a single basic type. As long as no more data is at hand, one would tentatively assign these three families to different basic types although it might well turn out that basic type rank finally be assigned to the order Galliformes. This is an outstanding case predetermined for experimental basic type taxonomy at

the level of artificial insemination (development of embryos can be observed quite easily in bird eggs) supplemented by investigations at the molecular level.

Finally, a problematic case from the bird order Passeriformes shall be discussed. Passeriformes are considered as phylogenetically young, yet extremely diverse in terms of numerous species. Numerous hybrids are known within the finch family Fringillidae (FEHRER 1993). Two subfamilies Fringillinae and *btCarduelinae* are often proposed. Only unreliable records on crosses between these two subfamilies are known while within the subfamilies numerous hybrids were reported. Both groups share characters but are also distinctly different with respect to others. Clear synapomorphies restricted to each group seem to be absent.

Recognizing a basic type based on hybridization

Based on the foregoing discussion, the procedure recommended for delineating a basic type may be summarized as follows:

1. Collect all interspecific hybrids available within a particular group of organisms and produce a cross breeding matrix (or polygon), placing special emphasis on intergeneric hybrids. Check if any reliable report indicates that different groups (e.g. subfamilies or tribes) are connected by hybridization.
2. Determine the overall range of variance which is indicated by those members of the group which are connected through hybridization. Then, check whether other species which are not involved in hybridization, would fall within the range of that variance.
3. From these data, derive predictions on the membership of problematic species or genera and test such hypotheses by artificial hybridization.

Recognizing basic types without hybridization?

If no hybrids exist at all, one could still try to demonstrate continuity within groups or discontinuity between groups. Mentioning hybri-

| Criteria for comparing two groups | YES | NO |
|---|-------|-------|
| Hybridization fails? | | |
| Ancestral group is uncertain? | | |
| Ancestral group is uncertain when fossils are considered? | | |
| Lineage ¹ is lacking? | | |
| Lineage is lacking when fossils are considered? | | |
| Clear synapomorphies ² within <i>each</i> group? | | |
| Clear synapomorphies when fossils are considered? | | |
| Ancestral group is younger? | | |
| Stratomorphological ³ intermediates lacking? | | |
| Artificial morphological discontinuity ⁴ ? | | |
| Low frequency of synapomorphy when the two groups are compared with an out-group? | | |
| Molecular discontinuity? | | |

Table 2: Criteria to decide whether a phyletic discontinuity between any two groups of organisms exists, i.e. whether these two groups can be considered to belong to the same basic type. These questions are designed in order to be answered by YES or NO. If the answer to a particular question is YES, a phyletic discontinuity exists. Perhaps the two groups under discussion form two basic types. If the answer is NO, a phyletic discontinuity is lacking; in this case, the two groups may belong to the same basic type. For a more detailed discussion of the concept of discontinuity systematics refer to WISE (1992).

¹ A lineage is a continuous series of organisms connecting the two groups.

² Synapomorphies are characters unique to all members of a particular group.

³ Stratomorphological intermediate is a fossil form which is morphologically intermediate between the two groups under discussion as well as stratigraphically intermediate between presumed ancestral and descendant forms.

⁴ An artificial morphological continuity would be created if a hybrid between two members of one group would bridge the gap to the other group.

dization as the most important criterion, WISE (1992) suggested several additional membership criteria for recognizing basic types (“baramins” in his terminology). Expressed as questions which are to be answered by “YES” or “NO” these criteria are given in table 2. WISE applied his approach to the order Testudines (turtles, containing up to 16 families). No extensive record on intergeneric hybrids is known. The first result emerging from the study by WISE is that there exists a very clear phyletic discontinuity between Testudines and all other reptile orders. Turtles as a whole are united by an impressive array of synapomorphies; ancestral groups cannot be pointed out unequivocally both within extinct and extant groups. However, it was much less clear whether the turtles can be further divided. Based on limited data available, WISE arrives at the rather preliminary suggestion that the turtles may be divided into four basic types, i.e. the pleurodires, the chelonioids, the trionychids and the non-chelonioid, non-trionychid cryptodires. This suggestion can now be tested by designing suitable hybridization experiments. This approach certainly deserves extensive application by investigating numerous groups with no hybrids known.

Evolution of basic types

Macroevolution and microevolution

Only about 14 basic types have been investigated in some detail. However, it is a general observation that the hybridization criteria would place the basic type to a taxonomic rank which has been already recognized by traditional taxonomy. Recognition of such groups has always been accompanied by pointing out that their members share clear synapomorphies and that they are clearly separated from next closely related groups. This holds for basic types at family rank as well as for basic types at the rank of tribe. In other words, there is an undisputed gap between basic types when extant organisms are compared. In the few cases investigated, these gaps seem also to be present in the fossil record of those groups, for instance for *bt*Anatidae, birds of prey or *bt*Cercopithecidae. Is it possible that, generally, no fossil links can be demonstrated which would unequivocally connect two clearly delineated basic types? However, paleontological data have yet to be related to basic type taxonomy. For instance, the fossil history of horses certainly deserves an in-depth study concerning this question

(MACFADDEN 1993; MACFADDEN & HULBERT 1988). Based on the data at hand it might be expected that major discontinuities between basic types will continue to emerge at different levels of comparative biology. As a very tentative suggestion it is submitted that the term "macroevolution" be used to describe the formation of different basic types.

In contrast, one might wish to use the term "microevolution" for processes leading to the formation of genera and species within a basic type. It is postulated that species belonging to the same basic type form a monophyletic group. This paragraph will not deal with mechanisms of speciation, which have been reviewed elsewhere (JUNKER 1993a), but rather with the distribution of characters throughout the members of a basic type, perhaps allowing some conclusion on the nature of the supposed ancestral population.

Nature of ancestral populations

When the results of the different papers presented in this book are reviewed, some common features emerge which are found across the different groups of animals and plants.

Hybrids of two species often have morphological or behavioural features not found in their parents. Sometimes these characters were previously unknown, but quite regularly they turn out to be similar to a third species of the same basic type (compare the membership criterion "artificial morphological discontinuity", table 2). For instance, this has been demonstrated within *bt*Anatidae (SCHERER 1993b; SCHERER & HILSBURG 1982), including both interspecific and intergeneric hybrids. As an extreme, it has been reported repeatedly that a hybrid between the two European species *Aythya fuligula* and *A. ferina* was indistinguishable from *A. affinis*, a third species from North America. Further examples were reported for *bt*Equidae (STEIN-CADENBACH 1993), *bt*Estrildidae (FEHRER 1993), or *bt*Geeae (JUNKER 1993b). This means that the species involved in hybridization harbour an unrecognised potential of variability which is expressed upon hybridization. This potential of variation seems to be common to different species of the same basic type. A rela-

ted observation concerns species within basic types which are impossible to classify. In case of *bt*Anatidae, these species are termed "aberrant types", displaying a mosaic of characters usually found in quite different tribes of the anatids. KUTZELNIGG (1993) mentions monotypic genera within *bt*Maloideae: for instance, the monotypic genus *Pseudocydonia* is similar to *Cydonia*, but also to *Chaenomeles* and *Pyrus*. Hence, it is impossible to assign this genus to either one of these genera. A large number of such problematic species or genera are known. Interestingly, the oldest fossil remains of Anseriformes also display such a morphology: *Romaninivilla* definitively is anseriform, but has similarities to Anatini, Dendrocygnini, *Anseranas* and Anserini.

The same phenomenon has also been described for *Nyctereutes* (raccoon dog, *bt*Canidae). The basic type Canidae comprises three major groups: The wolf-like canids, the South American canids and the fox-like canids. The raccoon dog is similar to the wolf-like canids when its limb morphology is considered. According to its mastigory characteristics, this animal groups towards the South American canids while the over-all similarity of single copy DNA indicates that it is most closely related to the fox-like canids (CROMPTON 1993).

There are two potential explanations for such observations: it may be speculated that this be explained by the common ancestor already possessing a potential of variation (plesiomorphy). This does not mean that all characters of extant species were expressed in the ancestral population but that the genetic potential for such variation was hidden in the ancestral polyvalent gene pool. A hidden potential for variation suddenly becomes visible when different species or even races are hybridized; obviously, the genetic balance of a species which results in a continuous expression of species-specific features becomes disturbed upon hybridization, revealing an astonishing potential of variability. Another interpretation would be convergence (homoplasy). In that case, selective forces should exist which account for an independent origin of similar characters. Often, such selective forces are unknown (which does not necessarily mean that they do not exist).

It is found throughout the basic types described in this book that it seems impossible to construct a phylogenetic tree of all members of a particular basic type without numerous contradictions. Different characters yield different phylogenetic trees, for instance, when the six species of *bt*Equidae are considered (STEIN-CADENBACH 1993). This is also true for a variety of characters from other basic types, e.g. plumage pattern of anatids (SCHERER 1993b) or carduelids (FEHRER 1993), the supposedly “highly reticulate evolution” within Triticeae (JUNKER 1993c) or a variety of characters within *bt*Maloideae (KUTZELNIGG 1993). In the latter basic type, “primitive” characters are found regularly together with “advanced” characters (“heterobathmy”). However, there is no objective way in order to know which character is ancestral and which one is derived. Any such decisions are usually disputed. Characters, therefore, seem to form a network rather than a tree, when species of a basic type are compared.

Again, there are two potential explanations: plesiomorphy and homoplasy. Homoplasy requires mechanisms which evolve the same character independently. Such mechanisms (i.e. selective pressures) are yet to be demonstrated in each specific case. Application of the concept of plesiomorphy to such an extent which would

explain the very common mosaic pattern of characters within basic types would lead to the idea of an ancestral population with an extremely high degree of polyallelism and, hence, with a large potential of variability. The evolution of different species from “complex” ancestors would scatter different characters and character combinations throughout the descendant species, the process being influenced by, e.g., size of the descendant populations, migration pattern of populations, chance effects and, finally, the action of selective forces on random character combinations. Such a process might explain the network of characters without involving unknown selective pressures.

Furthermore, it is quite well-known that speciation processes lead to specialisation which means that the descendant population has lost genetic potential when compared with the ancestral population. Speciation itself would therefore appear to support the concept of ancestral populations with a large hidden potential of variation. ADLER (1993) pointed out that it is possible to interpret some characters of *bt*Funariaceae in terms of a morphologically complex ancestor. The five genera of this basic type are assumed to be reduced in morphological complexity to various degrees.

IV. Concluding remarks

The ideas expressed in this paper are certainly not entirely original (comp. CLAUSEN 1951, MARSH 1976, VAN GELDER 1977, DUBOIS 1988). In fact, they trace back to Carolus LINNAEUS who, in his later writings, departed from the idea that species do not change (LANDGREN 1993; MAYR 1982). The basic unit of his late classification system was the genus rather than the species. He believed that these fundamental units of life, through hybridization, produced the species. LINNAEUS himself did not use the category of a basic type but “. . . surprisingly many of the genera recognized by LINNAEUS consist of well characterized groups of species, many still accepted as genera or families today” (MAYR 1982). It appears, therefore, that the genera of LINNAEUS in some cases may come close to the basic types proposed in this book.

It is suggested that basic type classification is applicable to both animals and plants. This classification could comprise three main lower categories:

(i) the biospecies concept as a means to describe biodynamical processes, i.e. speciation (comprising individuals genetically related through participation at the same gene pool); (ii) the genus category as a means to describe overall similarity (comprising morphologically related forms) and (iii) the basic type category as a means to describe monophyletic, though potentially heterogenous groups (comprising morphogenetically related forms).

Basic types may be discerned experimentally by hybridization. It is now necessary to test this preliminary suggestion with as many animal and plant groups as possible. The articles

which follow are only a first small step into this direction. The results available so far seem to be encouraging. Critical test cases will be provided by groups which comprise a number of closely related families or subfamilies, such as Passeriformes. However, further work could also demonstrate that the basic type criterion submitted here will not hold up when it is put to test in daily classification work of practising taxonomists.

Typen des Lebens

Zusammenfassung

Definition systematischer Kategorien: Spezies, Gattung und Familie

Bis heute ist unklar, wie man Arten definieren soll. Zwischen 1966 und 1985 wurden 15 Art-Definitionen vorgeschlagen, ohne daß sich die Fachwelt auf einen bestimmten Artbegriff hätte einigen können. Es lassen sich zwei Klassen von Definitionen unterscheiden: Genetische Artbegriffe beruhen auf der fortpflanzungsbiologischen Isolation von Populationen; Morphologische Artbegriffe greifen auf die Bewertung von Ähnlichkeit oder Verschiedenheit von Organismen zurück. Obwohl der Biospeziesbegriff nach MAYR und anderen als weitgehend akzeptiert gilt, werden doch teilweise hitzige Debatten geführt. Die Auseinandersetzung läßt sich folgendermaßen charakterisieren: Weil der Populationsbiologe hauptsächlich am Genfluß zwischen Populationen interessiert ist, muß er mit einem genetischen Artbegriff (meist Biospezies-Begriff) arbeiten. Die Art als evolvierende Einheit steht hier im Mittelpunkt der Betrachtung. Der Systematiker und Paläobiologe ist dagegen hauptsächlich an Ähnlichkeiten oder Unterschieden interessiert, durch welche sich Organismen zusammenfassen oder gegeneinander abgrenzen lassen. Die beiden Betrachtungsweisen lassen sich kaum ineinander überführen, weil Fälle bekannt sind, in denen sich Populationen morphologisch (und teilweise genetisch) kaum unterscheiden lassen, aber doch fortpflanzungsbiologisch völlig isoliert sind. Sie sind demnach Biospezies, aber keine Morphospe-

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zies. Andererseits können Populationen morphologisch außerordentlich unterschiedlich sein, aber dennoch im Freiland vitale, fertile Hybridpopulationen bilden. Sie sind Morphospezies, aber keine Biospezies.

Obwohl der Ansatz, Arten als evolvierende Einheiten aufzufassen, attraktiv ist, läßt sich das Konzept in der weit überwiegenden Anzahl der Fälle noch nicht anwenden, weil viel zu wenig Daten über Genflüsse von Populationen im Freiland vorliegen. Dort, wo sie bekannt sind, zeigt sich zudem, daß es zahlreiche Übergänge im Grad der Fortpflanzungs-isolation zwischen Populationen gibt, was eine allgemein akzeptierte biologische Artdefinition weiter erschwert. Vertreter des Biospezies-Begriffes haben denn auch ohne weiteres eingeräumt, daß die MAYRSche Biospezies-Definition nicht aus Gründen praktischer Durchführbarkeit, sondern aus Gründen der Beschreibung evolutionärer Vorgänge eingeführt wurde. Auch der Morphospeziesbegriff leidet eingestandenermaßen an mangelnder Objektivität. Es sieht daher insgesamt so aus, als ob sich der Konflikt zwischen Morphospezies-Begriff und Biospeziesbegriff nicht leicht lösen ließe. Möglicherweise ist auch eine einzelne Artdefinition gar nicht in der Lage, die komplexe Vielfalt der Organismenwelt zufriedenstellend zu beschreiben.

Entsprechende Probleme ergeben sich, wenn die Definitionen für höhere Kategorien wie Gattung oder Familie untersucht werden. Allgemein werden Gattungs- und Familiendefinitionen noch für weit willkürlicher gehalten als Artdefinitionen. So befindet sich die Taxo-

nomie in der eigenartigen Situation, daß für Begriffe, mit denen der Biologe täglich umgeht, keine allgemein akzeptierten Definitionen existieren.

Definition von Grundtypen

Aus der Einsicht, daß sowohl genetische als auch morphologische Klassifikationsansätze biologisch begründet sind, erwächst die Frage, ob man nicht beiden Betrachtungsweisen eine möglichst objektive taxonomische Kategorie überordnen kann. Im Anschluß an Arbeiten von LINNAEUS, CLAUSEN, MARSH und VAN GELDER werden Beobachtungen über zwischenartliche Kreuzungen für Klassifikationszwecke benutzt. Als primäre Definition wird vorgeschlagen:

Zwei Arten, die durch zwischenartliche Kreuzungen miteinander verbunden sind, gehören zu einem Grundtyp.

Als sekundäres Kriterium für die Zugehörigkeit zweier Arten zu einem Grundtyp wird vorgeschlagen:

Zwei Arten, welche mit der gleichen dritten Art durch Kreuzungen verbunden sind, gehören zum gleichen Grundtyp.

Bei den o.g. Definitionen wird nicht berücksichtigt, ob die Mischlinge fertil oder steril sind oder ob die Kreuzung unter natürlichen oder künstlichen Bedingungen erfolgt ist. Aufgrund der Beobachtung, daß es auch bei zwischenartlichen Kreuzungen Übergänge im Grad der Vitalität der Embryonen gibt, wird ein mögliches tertiäres Grundtypkriterium diskutiert:

Wenn eine Zygote aus Keimzellen zweier Arten nach der maternalen Phase der Entwicklung die Embryogenese unter koordinierter Ausprägung des paternalen und maternalen Erbgutes fortsetzt, gehören die Eltern zum gleichen Grundtyp.

Dieses Grundtypkriterium ist jedoch vorläufig, weil über die Genexpression bei Hybriden derzeit zu wenig vergleichende Daten bekannt sind. Allen drei Definitionsteilen liegt der Gedanke zugrunde, daß zwei Arten ein sehr ähnliches morphogenetisches Programm haben müssen, wenn die beiden Genome bei der Embryogenese harmonieren. Alle drei Definitionsteile sind ausschließlich positiver Art. Ein Mißerfolg, zwischen zwei Arten Hybriden

zu erzeugen, läßt keine Aussage über die Zugehörigkeit der beiden Arten zum gleichen oder zu verschiedenen Grundtypen zu. Dies ist sinnvoll, weil bekannterweise aufgrund geringfügiger Veränderungen im Genom einer abspaltenden Population eine vollständige Fortpflanzungsisolation entstehen kann, obwohl die Grundstruktur der embryogenetischen Abläufe davon unbeeinflusst bleibt.

Wenn zu wenige Hybriden bekannt sind, um eine Organismengruppe zu einem Grundtyp zusammenzufassen, können aufgrund morphologischer Ähnlichkeiten Experimente zur künstlichen Besamung oder Bestäubung konzipiert werden. Hierdurch kann die Zugehörigkeit einer Art zu einem Grundtyp experimentell überprüft werden. Wenn aus methodischen (z.B. Kreuzungsexperimente mit Wälen) oder ethischen Gründen (Kreuzungsexperimente unter Einbeziehung von *Homo*, Artenschutz) keine experimentelle Prüfung möglich ist, muß auf bekannte Ansätze der Klassifikation zurückgegriffen werden. Dabei könnte ein Klassifikationssystem, welches gezielt nach Unterschieden zwischen Organismen sucht, dem Grundtypkonzept am nächsten kommen.

Anwendung der Grundtyp-Kategorie

Bei verschiedenen Gruppen des Tier- und Pflanzenreichs wurden Grundtypen beschrieben. Die bisher vorliegenden, allerdings begrenzten Untersuchungen lassen gemeinsame Grundlinien erkennen: 1. Die Grundtyp-Kategorie liegt in der Regel zwischen Gattung und Familie. 2. Verschiedene Grundtypen sind nicht nur aufgrund fehlender Hybridisierung, sondern auch durch andere Merkmale oder Merkmalskomplexe sehr klar voneinander getrennt. In den wenigen Fällen, in denen bisher die Fossilgeschichte berücksichtigt wurde, ergibt sich, daß keine unumstrittenen gemeinsamen Vorfahren verschiedener Grundtypen aufgetaucht sind. 3. Es erweist sich als schwierig, die zu einem Grundtyp gehörenden Arten im Rahmen einer "Stammbaum-Phylogenie" (Höherentwicklung) zu verstehen. Bei allen Stammbäumen müssen zahlreiche Konvergenzen angenommen werden und in zahlreichen Fällen treten "abgeleitete" und "ursprüngliche" Merkmale in der gleichen Art auf (Heterobathmie).

4. Diese Verteilung von Merkmalen auf die Arten des einen Grundtyp repräsentierenden Artenfächers läßt die Deutung zu, daß die hypothetischen Stammformen von Grundtypen genetisch polyvalent waren. Die Differenzierung dieser Stammformen in die heutige Artenvielfalt ist vermutlich durch mikroevolutionäre Vorgänge (Speziation) ohne Höherentwicklung abgelaufen. Die heutigen Arten würden demnach über ein geringeres Variationspotential als ihre Ahnen verfügen.

Eine Klassifikation, welche die Grundtypkategorie einbezieht, könnte drei Kategorien umfassen. Dabei wird davon ausgegangen, daß morphologische und genetische Klassifikationsbegriffe komplementär und nicht konträr sind. 1. Als Grundeinheit der Taxonomie gilt nach wie vor die Art, wobei die Biospezies-Definition vorgezogen wird und die Individuen zusammengefaßt werden, welche am gleichen Genpool partizipieren (*genetischer Aspekt*). Wenn für die Definition einer Biospezies nicht genügend Daten vorliegen, werden zwangsläufig Morphospezies gebildet. 2. Über der Art steht die Gattung als Zusammenfassung der Arten, welche einander ähnlich sind (*morphologischer Aspekt*). Morphologisch deutlich verschiedene Biospezies eines Grundtyps werden verschiedenen Gattungen zugeordnet. 3. In der Kategorie des Grundtyps sind alle Arten zusammengefaßt, welche das gleiche Grundmuster der Embryogenese aufweisen (*morphogenetischer Aspekt*). Keine der eingeführten höheren taxonomischen Kategorien läßt sich generell mit der Kategorie des Grundtyps identifizieren. Ein Grundtyp kann verschiedene Familien, Unterfamilien oder Tribus enthalten, während in anderen Fällen eine Familie verschiedene Grundtypen umfassen kann. Es wird vorgeschlagen, einen Grundtyp durch das Präfix *bt* für *basis typus* unmittelbar vor dem eingeführten lateinischen Namen der Gruppe zu kennzeichnen (beispielsweise *btAnatidae*; *btMaloideae*).

Bisher wurden erst 12 Grundtypen beschrieben. Diese Zahl ist viel zu gering, um als zuverlässige Basis für Verallgemeinerungen zu dienen. Das Grundtypkonzept ist eine vorläufige Arbeitshypothese, deren generelle Brauchbarkeit sich durch breitere Anwendung in der Klassifikation erst noch erweisen muß.

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