Origin and History of Some Terms in Systematic and Evolutionary Biology

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serves to verify the comment by Atchley et al. (1976) that "the vast majority of biologists are unaware of the statistical consequences resulting from compounding variables into ratios."

It is obvious that dimensionless variables have a role in scientific inquiry. Biologists should and will continue to use dimensionless variables for certain types of scientific inquiries but this use must be tempered with caution when statistical analyses are to be employed (Dinkel et al., 1965; Schuessler, 1973; Anderson and Lydic, 1977, 1978; Atchley and Anderson, 1978).

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Some of the foremost historians of science have come to the conclusion that the most important aspect of the history of biology is neither the discovery of new facts nor, as often in the physical sciences, the establishment of new laws, but the development of new concepts and the maturation or revision of existing concepts. To trace the history of concepts, however, is quite difficult, because they are often vague when they first appear, and become conspicuous only when a definite term is attached to the concept. The history of technical terms, therefore, is an important component of the history of concepts. Equally important is the history of definitions of such technical terms. The changing definition of words like *species* or *isolating mechanisms* is a good illustration of this point.

Interestingly, the coining of new terms has often been instrumental in resolving long-standing confusions or controversies. In genetics Johannsen's proposal of *gene*, and of *genotype* and *phenotype*, as well as Bateson's *allele* (originally *allelomorph*) and *genetics* are examples. In taxonomy, the availability of terms like *taxon, sympatric,* and *polytypic* has greatly simplified many discussions. Every newly developing science is in need of new terms to label newly discovered phenomena or new concepts. The recent histories of ethology, ecology, and molecular biology provide many illustrations. However, once a term has

been given, it tends to hang on tenaciously even when its underlying meaning is changing radically. The term *mutation* is a good example. As far back as the 17th century (Mayr, 1963:168) it was used either for a drastic variety or for changes in fossils and both usages were in vogue for the next 250 years. Waagen's (1869) use of this term for any sudden change in a fossil sequence was widely adopted in paleontology, but in 1901 De Vries proposed to use it for any drastic change of the phenotype (and the underlying genetic change). Such changes, De Vries thought, gave rise to new species. After 1910 Morgan used it for any discontinuous genetic change and this definition of the term mutation eventually prevailed, after some decades of terminological confusion.

A large number of technical terms is used in general and in evolutionary systematics, some of them of long standing, others introduced only in recent years, either by myself or by other authors. In recent years I have often been asked, orally or in correspondence, whether certain terms used in my books had been introduced into the literature by myself or had been taken over by me from other authors, and if so from whom. This is not idle curiosity because the history of such terms indeed often reflects part of the conceptual history of biology. It is the object of this communication to make the information more widely available which I had previously given to my correspondents. Among the listed terms 15 were first proposed by me, some of them merely as English equivalents of foreign language terms (like *sibling species*), while 15 others had been proposed by other authors. I have included them for two reasons. First because the place of their first publication is usually unknown to most zoologists and secondly because the definition has sometimes changed, indicating a change of the underlying concept. However, I have made no effort to make this list complete, since this would duplicate available glossaries.

Allopatric (Mayr, 1942:149). I said

"Two forms (or species) are allopatric, if they do not occur together, that is if they exclude each other geographically" (see also sympatric and parapatric).

Allospecies (Amadon, 1966:246). A term proposed by Amadon to replace semispecies of Mayr (1942:165), but not semispecies of Mayr (1963:501–502). A component species of a superspecies (see semispecies).

Circular overlap. I have not been able to trace the first use of this term. In 1942 (pp. 180, 198) I referred to "overlapping circles" or "overlapping rings." Other authors have referred to "ring species." Unfortunately several authors translated Rensch's term *Artenkreis* (see superspecies) also as '*ring species*' and this created considerable confusion. The terms *rings of races* or *circular overlaps* are, I believe, now used exclusively, instead of ring species. For Rensch's *Rassenkreis* see polytypic species.

Cladogram (Mayr, 1965:81; Camin and Sokal, 1965:312). It became apparent soon after 1953 that there were many different kinds of dendrograms, and Mayr and Camin and Sokal, unknown to each other, proposed on December 29, 1964 the terms cladogram and phenogram at the same meeting of the Society of Systematic Zoology, Knoxville, Tenn. A cladogram is a dendrogram depicting the branching of the phylogenetic tree without respect to rates of divergence.

Coefficient of difference (Mayr, 1943:102). This term was proposed by me in an attempt to express the overlap between samples in terms of the properties of the normal curve instead of in terms of linear overlap. It is explained in more detail in Mayr, Linsley, and Usinger (1953:146) and in Mayr (1969:189).

Deme (Gilmour and Gregor, 1939). The term was rather vaguely defined at the occasion of its original proposal, essentially as a new term for population with all the heterogeneity and ambiguity of that word. Several zoologists, for instance Simpson (1953) and Wright (1955), gave the term a more specific meaning by restricting it to the "local population," the

representatives of a local gene pool
(= the community of potentially inter-
breeding individuals at a given locality).
In spite of the acknowledged impossibil-
ity of delimiting a given local population
against others, the term deme is now
quite widely used in this sense, at least
by zoologists and geneticists. (For de-
tailed discussion see Mayr, 1963:137,
358.)

Dendrogram (Mayr et al., 1953:58). I
had long used this term, in lectures and in
manuscript, for any branching, tree-like
diagram serving to indicate degrees of re-
lationship. The term was first published
in Mayr, Linsley, and Usinger (1953:58,
175). (See cladogram, phenogram.)

Essentialism (Popper, 1950:34). A term
introduced by the philosopher Karl Pop-
per to designate Plato's ideology accord-
ing to which the variability of the world
is a reflection of a limited number of un-
derlying constant and discontinuous es-
sences. Previously in systematics and
evolutionary biology this ideology was
usually referred to as "typological think-
ing" (see Mayr, 1969:66–68; 1976:26–29).
Opposite to population thinking.

Founder principle or *Founder effect*
(Mayr, 1942:237). The genetic conse-
quences of the founding of a new popu-
lation by only a few individuals or by a
single fertilized female. The conse-
quences of such an event had previously
been pointed out by Rensch (1939).

Genetic revolution (Mayr, 1954:170).
The drastic genetic reorganization that
may occur in a small founder population.

Isolating mechanisms (Dobzhansky,
1937a:405). Factors that prevent the in-
terbreeding of species and incipient spe-
cies had been discussed since Darwin
(and even before him). Romanes and Du
Rietz were among the authors especially
interested in this subject. It was, how-
ever, not until Dobzhansky proposed the
term isolating mechanisms that their full
significance was recognized. Dobzhan-
sky included both biological isolating
mechanisms and extrinsic geographic
barriers under the same term, which re-
sulted in heterogeneity and vagueness of

definition. So far as I am aware I was the
first to offer a rigorous definition
(1963:91): "Isolating mechanisms are bi-
ological properties of individuals which
prevent the interbreeding of populations
that are actually or potentially sympatric"
(see op. cit., pp. 89–135).

Isophene (Huxley, 1938:516). Defined
as "lines of equal development [on a con-
tour map] of the character measured" (re-
ferring to clinally varying characters).

Macrogenesis (Jepsen, 1943:526;
1944:88). Evolution by discontinuous ad-
vances; saltational evolution.

Monothetic (Sneath, 1962). A group is
monothetic if it is defined in terms of a
single feature which is both necessary
and sufficient for inclusion in the group
or by a set of features which are severally
necessary and jointly sufficient for inclu-
sion; coined by Sneath to replace Beck-
ner's (1959:22) monotypic group. Ant-
onym of polythetic.

Monotypic (Huxley, 1940:10). A term
introduced by Huxley to designate spe-
cies that do not break up into subspecies.
Antonym of polytypic. Analogously used
for higher taxa.

Non-dimensional species (Mayr,
1946:273; 1949:37). This term designates
the concept of the species based on a sit-
uation of no extension in space and time.
No species taxon is ever non-dimen-
sional, but since the relational aspect is
crucial in the biological species concept,
it is best defined where it occurs in its
purest form, i.e., in the non-dimensional
situation.

Parapatry (H. M. Smith, 1955). Non-
overlapping geographical contact (conti-
guity) without interbreeding (see allopat-
ric).

Phenetics (Mayr, 1965:74). A term used
by me for that type of numerical taxono-
my in which relationship is determined
by unweighted similarity (Sokal and
Sneath, 1963). (Based on Cain and Har-
rison. 1960. Proc. Zool. Soc. London
135:3.)

Phenogram (Mayr, 1965:81; Camin and
Sokal, 1965:312). A diagram (usually a
dendrogram) representing degree of

overall similarity (usually unweighted similarity); simultaneously proposed by Mayr, and Camin and Sokal. See cladogram.

Phenon. This term was first proposed by Camp and Gilly (1943) for phenotypically homogeneous samples at the species level. Sokal and Sneath (1963:54) used the same term phenon as a measure of phenetic similarity (or difference). Mayr (1969:5) employed it more or less in the sense of Camp and Gilly "for a phenotypically reasonably uniform sample." Males and females often belong to different phena, as do also individual variants, whereas in the case of sibling species several species may belong to a single phenon. The phenon, as defined by Mayr, is a convenient unit of provisional taxonomic analysis. It corresponds to the phenetic group of Cain and Harrison (1960).

Philopatric (Mayr, 1942:195). This is the English equivalent of the German term *ortstreu*. The noun *philopatry* has been used by me and other authors for the tendency of many animals to stay at or near their place of birth or of post-dispersal settlement.

Phylogram (Mayr, 1969:256). A dendrogram indicating both cladistic branching and the relative amount of progressive (anagenetic) change that has taken place between internodes. The traditional phylogenetic tree is the most frequently used form of phylogram.

Polythetic (Sneath, 1962). A group is polythetic if it is defined in terms of features which are neither severally necessary nor jointly sufficient for inclusion in the group; instead each organism possesses a large number of the defining features, and each feature is possessed by a large number of these individuals; coined by Sneath to replace Beckner's (1959:22) polytypic group. Antonym of monothetic.

Polytopic (Mayr et al., 1953:32). A term referring to collective subspecies, consisting of "several unrelated and widely separated populations" that have acquired independently the same diagnostic characters (see also Mayr, 1969:193).

Polytypic (Huxley, 1938:219; 1940:10). To designate species that break up into subspecies. Rensch called such species *Rassenkreise*. Antonym of monotypic. Analogously used for higher taxa.

Population thinking (Mayr, 1959:2). The conceptualization according to which classes of biological phenomena are composed of unique individuals and show a characteristic variation, which has reality. The calculated mean values of these populations and of samples from them do not reflect an underlying essence. (See also Mayr, 1963:5–6; 1970:47–52). Polar opposite to essentalism (q.v.).

Program, open (or *closed*) (Mayr, 1964:939). A behavior program which when open is able and when closed is unable to incorporate additional experiential information (see also Mayr, 1974).

Semispecies (Mayr, 1940:260). Taxa that are on the borderline between subspecies and species. Qualifying as species under some, but not under other criteria (see also Mayr, 1963:501–502).

Sibling species (Mayr, 1942:151). The English equivalent of *espéces jumelles* of the French and *Geschwister-Arten* of the German literature. Defined as reproductively isolated but morphologically identical or nearly identical species.

Superspecies (Mayr, 1931:2). Introduced as the English equivalent of Rensch's *Artenkreis*. A monophyletic group of entirely or essentially allopatric species.

Sympatric (Poulton, 1908:62). A term for forms or species which coexist, that is of which the areas of distribution overlap or coincide. Poulton's term had been forgotten, except for a single use by K. Jordan in 1916, when I revived it in 1942 (p. 148). In order to permit discrimination from ecological exclusion, I later offered a revised definition of sympatry as "the existence of a population in breeding condition within the cruising range of individuals of another population" (Mayr, 1969:413).

Sympatric speciation (Mayr, 1942:189). Speciation without geographic isolation,

or the acquisition of reproductive isolation within a deme.

Taxon (Meyer-Abich, 1926). A taxonomic group that is sufficiently distinct to be distinguished by name and to be ranked in a definite category. This term, as useful as it is, was at first ignored by taxonomists, until revived by the botanist Lam in about 1948. In 1950 it was incorporated in the International Rules of Botanical Nomenclature. The first use of *taxon* in the zoological literature that I have been able to trace—I am almost sure there must be earlier ones—was by Mayr, Linsley, and Usinger, 1953:36, but still in a confusing manner.

Teleonomic (Pittendrigh, 1958:394). Redefined by me as follows: A teleonomic process or behavior is one that owes its goal directedness to the operation of a program (see Mayr, 1976:383–404).

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Generalized Tracks and Dispersal in Biogeography

The logical and theoretical basis of historical biogeography has received considerable attention in recent years as various authors have sought for a scientific theory of biogeography (Nelson, 1973, 1974; Rosen, 1974a, b, 1975; Cracraft, 1975; Ball, 1975). Nelson (1973) and Rosen (1974b) have drawn attention to Leon Croizat's contribution to biogeography (Croizat, 1952, 1958, 1964) and have joined Croizat (Croizat et al., 1974) in a discussion of the concepts and methods they consider essential to historical biogeography. While the *approach* espoused by these authors can make an important contribution to biogeography, there are flaws in its broad and general *application* in the manner these authors propose; in addition, there are assumptions in the approach that are neither logical nor justified.

Ball (1975) followed Munroe (1963) in suggesting that "biogeography is essentially the study of the distribution of living organisms in space and time and of the principles, processes, and parameters influencing this distribution." It seems to me that biogeography is an attempt to reconstruct what has taken place in the past on the basis of what can be observed in the present of the distributions of organisms; i.e., having observed the space dimension of distributions in the present (sometimes augmented by fossil data on the space dimension in the past), the time dimension becomes involved in the search to determine how spatial patterns have varied in the past, and how they have led to existing spatial patterns.

If biogeographical hypotheses of any sort are to be rigorously formulated they must be established upon hypotheses of phylogenetic relationships of the taxa under study. Croizat (1958, 1964) failed to recognize the significance of phylogenetic relationship to biogeographic analysis—in fact he wrote of "ruling taxonomic considerations out of biogeography in principle" (Croizat, 1964:6). This is a fundamental flaw in his work which is, for this reason alone, seriously suspect. Nelson (1974:557) and Ball (1975:421) have drawn attention to the need for phylogenetic analysis to precede biogeographical studies; Rosen (1975:432) has also affirmed this need, but, in general, his analysis of Caribbean biogeography examined the distributions of broad taxa regardless of the patterns of their internal phylogenetic relationships.

Just where phylogenetic relationships fit into biogeography is not wholly agreed upon. On the one hand Rosen (1975:431) stated that "The vicariance model is also shown to predict and therefore be tested by, phylogenies . . ."; on the other Ball (1975:421) stated that "Generalized tracks become meaningful only when strict phylogenetic principles have been applied." Thus while Rosen believes that generalized tracks can be used to predict phylogenetic relationships, Ball used phylogenetic relationships to establish and validate the generalized tracks. I believe Ball to be correct, and that only when phylogenetic patterns are understood (and these are *hypotheses* only) can vicariance events be identified. Pointers to past distributions can be obtained from hypotheses about phylogenetic relationships of recent species, based on the interpretation of morphological data.

GENERALIZED TRACKS

The method of biogeographic analysis developed by Croizat (1952, 1958, 1964)