

But if organisms and species do not have essences then their names have no role to play in biological theory.

REFERENCES

HULL, D. L. 1976. Are species really individuals? *Syst. Zool.*, 25:174-191.

HULL, D. L. 1984. Can Kripke alone save essentialism? A reply to Kitts. *Syst. Zool.*, 33:110-112.

KITTS, D. B. 1983. Can baptism alone save a species? *Syst. Zool.*, 32:27-33.

KITTS, D. B., AND D. J. KITTS. 1979. Biological species as natural kinds. *Philos. Sci.*, 46:613-622.

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The Terminology of Allopatric Speciation

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Different modes of speciation have traditionally been named with reference to geographic criteria. Thus, terms such as allopatric, parapatric, and sympatric are standard within the literature of systematic and evolutionary biology. Even though such terms are applied both to presently observed distribution patterns and to the processes thought to have produced those patterns, there is usually relatively little confusion over which is actually meant in any particular case.

In discussing these terms from the standpoint of observed distribution patterns, Smith (1965:57; see also 1955) proposed that two allopatric situations be distinguished: *parapatric*, in which ranges are abutting, and *dichopatric*, in which ranges are entirely separated. Although the term parapatric has entered the collective consciousness of biology, dichopatric has not. The reason, I suggest, is that the former has been associated with a specific mode of speciation, whereas the latter was simply subsumed within the concept of allopatric speciation itself.

Systematists have long recognized two modes of allopatric speciation. The first describes the segregation of a widespread population into two or more isolates by the initiation of a geological or ecological isolating barrier. This mode is sometimes

called the "dumbbell" pattern of allopatric speciation (e.g., White, 1978:16; Mayr, 1982a:1122, 1982b:3). Bush (1975:341) referred to this mode as "Type Ia: speciation by subdivision."

The second mode of allopatric speciation concerns the isolation, by a founder effect (dispersal) across a pre-existing barrier, of a small population (usually said to be only a few individuals) that subsequently differentiates into a new taxon. Bush (1975:346) called this "Type Ib: speciation by the founder effect." Mayr (1982a, b) has recently termed this mode *peripatric speciation*.

I support Mayr's new terminology because it creates a descriptive name for a clearly delineated mode of speciation that is considered to be of frequent occurrence by many systematic biologists. This leaves, however, the other mode of speciation, Type Ia or "dumbbell," without a corresponding term. Thus, I propose that this be called *dichopatric speciation* in reference to the division (vicariance) of a widespread ancestral population into two or more descendant populations.

Both peripatric and dichopatric are useful terms in that they call attention to a major question within evolutionary biology: Does taxonomic differentiation take place *primarily* through dispersal across

pre-existing barriers or through vicariance of populations via the origin of new barriers? Expressed somewhat differently, is the process of geographic isolation usually the result of intrinsic biological characteristics of individuals (dispersal capability) or of changes in earth history? No one questions that both can and do occur, yet in searching for general patterns in nature, the question of relative frequency is of paramount importance. Thus, does one mode predominate within certain taxa of organisms, or in continental as compared to archipelagic situations?

Bush (1975) and Mayr (1982a, b), for example, suggested that peripatric speciation is much more common than dichopatric, yet little direct evidence based on the analysis of phylogenetic pattern has been presented. That peripatric is the common mode of allopatric speciation seems to be an assumption derived from the analysis of island biotas where dispersal is taken to be important in geographic isolation (e.g., Mayr, 1942). The argument over relative frequency may be answerable once systematists determine whether patterns of differentiation exhibit congruence from group to group. If most taxa are not components of one or more common phylogenetic-biogeographic patterns, then peripatric speciation will be suspected; if, on the other hand, congruence in such patterns is ubiquitous, then dichopatric speciation (vicariance) will be implicated (for discussions of methods, see Platnick and Nelson, 1978; Rosen, 1978; Wiley, 1981; Cracraft, 1982, 1983a, b).

The terminology proposed here has one slight drawback. Parapatric distributions can arise via parapatric or dichopatric modes of speciation (by definition, peripatric speciation applies only to those cases in which a peripheral population is isolated from a larger population by a geographic or ecological barrier and, thus, would not be expected to produce parapatric distributions). Inasmuch as biologists are generally aware that parapatric distributions might arise from allopatric processes as well as a parapatric mode of

speciation, potential confusion should be minimal.

In a recent discussion of systematic terminology, Mayr (1978:83) noted that "the coining of new terms has often been instrumental in resolving long-standing confusions or controversies." Both peripatric and dichopatric refer to significantly different biological phenomena having important empirical and methodological consequences. The introduction of this new terminology emphasizes that distinction and should facilitate their study.

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REFERENCES

- BUSH, G. L. 1975. Modes of animal speciation. *Annu. Rev. Ecol. Syst.*, 6:339-364.
- CRACRAFT, J. 1982. Geographic differentiation, cladistics, and vicariance biogeography: Reconstructing the tempo and mode of evolution. *Am. Zool.*, 22:411-424.
- CRACRAFT, J. 1983a. Cladistic analysis and vicariance biogeography. *Am. Sci.*, 71:273-281.
- CRACRAFT, J. 1983b. Species concepts and speciation analysis. *Curr. Ornithol.*, 1:159-187.
- MAYR, E. 1942. *Systematics and the origin of species*. Columbia Univ. Press, New York.
- MAYR, E. 1978. Origin and history of some terms in systematic and evolutionary biology. *Syst. Zool.*, 27:83-88.
- MAYR, E. 1982a. Speciation and macroevolution. *Evolution*, 36:1119-1132.
- MAYR, E. 1982b. Processes of speciation in animals. Pages 1-19 in *Mechanisms of speciation*. A. R. Liss, New York.
- PLATNICK, N. I., AND G. NELSON. 1978. A method of analysis for historical biogeography. *Syst. Zool.*, 27:1-16.
- ROSEN, D. E. 1978. Vicariant patterns and historical explanation in biogeography. *Syst. Zool.*, 27:159-188.
- SMITH, H. M. 1955. The perspective of species. *Turtax News*, 33:74-77.
- SMITH, H. M. 1965. More evolutionary terms. *Syst. Zool.*, 14:57-58.
- WHITE, M. J. D. 1978. *Modes of speciation*. W. H. Freeman, San Francisco.
- WILEY, E. O. 1981. *Phylogenetics: The theory and practice of phylogenetic systematics*. John Wiley and Sons, New York.

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