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A Reinterpretation of the Concepts "Sympatric" and "Allopatric" with Proposal of the Additional Terms "Syntopic" and "Allotopic"¹

LUIS RENE RIVAS

In discussing their geographic relationships, Mayr (1942:148) indicated that there are two ways of delimiting species: "(1) *against other species that coexist at the same locality, and (2) against species with mutually exclusive geographic ranges.*" He then accepted the term "*sympatric*"² for species that ". . . occur together, that is if their areas of distribution overlap or coincide." The term "*allopatric*" was proposed by Mayr (loc. cit.) for species which ". . . do not occur together, that is if they exclude each other geographically."³ Cain (1953) has commented on Mayr's definitions and extensively discussed the meaning of "geographical" and "ecological," and the terms "sympatry" and "allopatry." Subsequently Mayr (1963:23) discussed the ranking of populations of closely related species and stated that "the criterion of species status, 'sympatric coexistence without interbreeding,' raises practical problems also where two populations occur in contiguous geographic areas but in very different habitats." He then goes on to say (after Cain, 1953) that "the terms 'sym-

patric' or 'coexistence' in species definitions must be conceived broadly, to include populations the individuals of which are within cruising range of each other during the breeding season, even though the habitats in which they occur do not overlap in space." Hanson (1962) defines the term "allopatric" as referring ". . . to organisms originating in or occupying different geographic areas" and the term "sympatric" as referring ". . . to the origin or area of occupation of two or more closely related species in the same geographical area." These terms were proposed and intended for a specialized use in systematic biology, i.e., in relation to closely related species or other populations. It was evidently not intended that, for example, a species of whale and a species of elephant be termed allopatric, although they obviously fit the definition of the term.

In spite of Mayr's, Cain's, and Hanson's comments, statements, and definitions it is still not clear whether the term "sympatric" refers to geographic distribution, ecologic distribution, or both. Two closely related species may have the same overall geographic distribution but not coexist at the same locality. The word locality is here understood as an area where the individuals of two or more closely related species are in close proximity and may or may not have the opportunity to interbreed ("coexistence" of Cain, 1953:78). In other words, they occupy the same "macrohabitat." There are many examples of this in species of fishes. Admittedly, the

¹ Contribution No. 50 from the Ichthyological Laboratory and Museum, Department of Zoology, University of Miami.

² Previously coined by Poulton (1903).

³ The following terms have been used for allopatric, related species: "geminat" (Jordan, 1908; Ekman, 1935:48), "parallel," "representative," "analogue," and "vicarious" (Ekman, 1935:48-49). The term "vicarious" was used in the same sense by Dunn (1934:170) and by Hanson (1962:366).

term "locality" is necessarily arbitrary since it is virtually impossible to define precisely, or establish the absolute limits of a given "macrohabitat." Cain (1953:79) defines "locality" as ". . . any continuous area of the earth's surface (land or sea)," and states that "there is no need to prescribe its size, since whatever locality is taken as a starting-point, extension from it will allow coverage of the geographical area of the species." In ichthyology, two or more species of fishes are usually said to "occur together in the same locality" when they are collected with the same sweep of a seine, or enter the same trap.

The term "sympatric" has become increasingly popular (at least in the ichthyological literature) in reference to closely related species "collected together in the same locality," without regard to their overall geographic distribution. In this case the ecologic connotation is obvious. But how are we going to refer to two or more closely related species that occupy the same, and sometimes very extensive range but different localities? That is to say, species which are never collected together in the same locality but which have the same, or broadly overlapping geographic distributions. The term "allopatric" certainly was not intended for, and is not used in this situation.

Regardless of original intent or present usage, and for the sake of clarity and precision, it would seem that the terms "sympatric" and "allopatric" should be reinterpreted and redefined. This necessitates the proposal of two additional terms as discussed below. These four terms may be defined as follows.

1. *Sympatric*. To be used in reference to two or more related species which have the same or overlapping geographic distributions, regardless of whether or not they occupy the same macrohabitat (whether or not these species occur together in the same locality). (Substantive form: sympatry.)

2. *Allopatric*. To be used in reference to two or more related species which have

separate geographic distributions. (Substantive form: allopatry.)

3. *Syntopic*. To be used in reference to two or more related species which occupy the same macrohabitat. These species occur together in the same locality, are observably in close proximity, and could possibly interbreed. (Substantive form: syntopy.)

4. *Allotopic*. To be used in reference to two or more related species which do not occupy the same macrohabitat. These species are presumably not in close proximity, cannot interbreed, and do not occur together in the same locality although they may have the same geographic distribution (sympatric). (Substantive form: allotopy.)

The terms "sympatric" and "syntopic," as herein defined, have been previously used by the present author (Rivas, 1960: 134; 1962:148, 153).

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