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PHYLOGENETIC BIOGEOGRAPHY

PHYLOGENETIC BIOGEOGRAPHY (Hennig, 1950, 1966; Brundin, 1966, 1981) was the first approach to consider an explicit phylogenetic hypothesis (a cladogram) of a given group of organisms as the basis for inferring its biogeographic history. This approach can be defined as the study of the history of monophyletic groups in time and space. Hennig (1966) stated that there is a close relationship between a species and the space it occupies. According to Hennig, each group of organisms has unique dispersal patterns and an independent history. The first applications of Hennig's ideas to real taxonomic groups may be found in Brundin (1966, 1972, 1981) and Ross (1974).

RULES AND METHODOLOGY

Phylogenetic biogeography applies two basic rules, the progression rule and the deviation rule. The progression rule states that primitive members of a taxon are found closer to its center of origin than more apomorphic ones, which are found on the periphery. Hennig (1966) conceived that speciation was allopatric, involving peripheral isolates, and

causally connected to dispersal. Within a continuous range of different species of a monophyletic group, the transformation series of characters run parallel with their progression in space, such that the youngest members would be on the geographic periphery of the group. The progression rule is based on the peripheral isolation allopatric mode of speciation, so it cannot be applied when other modes of speciation are considered, because it is rejectable a priori.

The deviation rule states that in any speciation event, an unequal cleavage of the original population is produced, in which the species that originates near the margin is apomorphic in relation to its conservative sister species, which are more plesiomorphic. In each event of speciation, the peripheral sister species develops more evolutionary novelties, whereas the other remains closer to the ancestor.

The methodology of phylogenetic biogeography can be summarized as follows:

1. A cladogram is constructed of the group under study;
2. the areas inhabited by the group are optimized onto the cladogram;
3. the center of origin of the group is inferred through the application of progression and/or deviation rules, and the dispersal direction is determined;
4. a hypothesis of the biogeographic history of the group is formulated; and
5. this hypothesis is confirmed by matching it against the geology of the area.

Although phylogenetic and dispersal biogeography may be lumped into the same approach, because both emphasize centers of origin and dispersal, some authors (Wiley, 1981; Humphries & Parenti, 1986) regard phylogenetic biogeography as an advance over dispersalism because of the explicit use of phylogenetic hypotheses instead of descriptive enumerations and scenarios. Phylogenetic biogeography provides a more rigorous methodology because it optimizes areas onto the phylogeny of a

group, and infers the fewest possible areas of dispersal for each group. Critiques of this method, however, note that it requires ad hoc assumptions about the center of origin, and that species migrate from the center of origin to other areas. Furthermore, according to Forey and colleagues (1992) and Humphries and Parenti (1999), interpreting individual cladograms as having individual histories leads to certain conceptual difficulties. One of these difficulties is the repetition of distribution patterns. For instance, if there are many distantly related taxonomic groups repeating a pattern of distribution among continents, for example, South America, Australia, and New Zealand, it is improbable that each taxon has a unique dispersal history from one continent to the other. The most logical and simplest conclusion would be that at one time, the continents were in contact and that the present-day pattern is caused by the breakup of a formerly continuous austral biota.

It is interesting to note that phylogenetic biogeography has, in part, continuity in a modern approach such as ancestral areas (see chapter 4). The idea of a center of origin located in the most plesiomorphic branches of a cladogram, one of the basic postulates of phylogenetic biogeography, is evoked by one of the criteria to determine the ancestral area (in this case ancestral area is the same concept as center of origin, though it goes by a different name).

CASE STUDY: THE CARABID BEETLES OF AUSTRALASIA

Some authors, such as Darlington (1970) in one of his studies on carabid beetles (Insecta: Coleoptera) of New Guinea, postulated that a number of these insects had dispersed (one way or another) between Asia and Australia. Brundin performed a theoretical analysis of this idea (Brundin, 1972) on the basis of phylogenetic biogeography. On the map of Australasia in Figure 3.1a each black dot marks the occurrence of a hypothetical endemic species of carabid. The species are supposed to be members of a group A + B + C + D + E that is strictly monophyletic. According to the phylogenetic biogeographic approach, this distribution picture
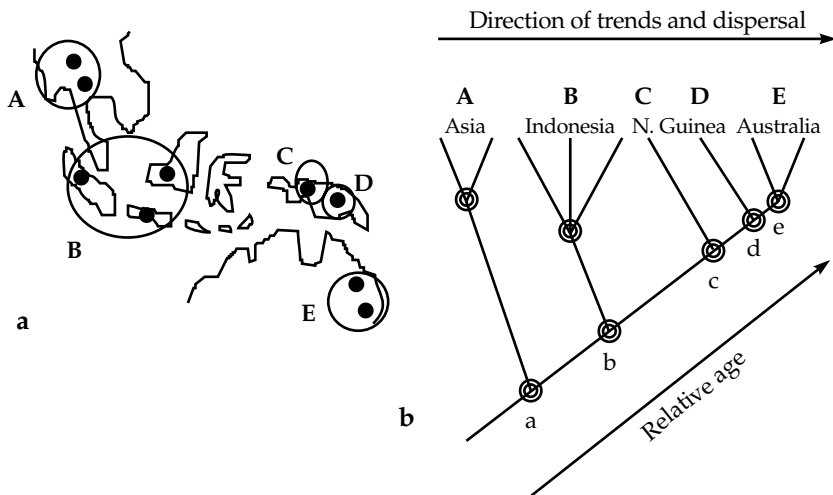
FIGURE 3.1.   Phylogenetic biogeography. *(a)* Map of Australasia showing the distribution of hypothetical species A, B, C, D, and E; *(b)* phylogenetic relation of species A–E, showing step by step dispersal from southeast Asia via Indonesia and New Guinea to Australia.

is the result of step-by-step dispersal from southeastern Asia via Indonesia and New Guinea to Australia. Consequently, the phylogenetic diagram of this group shown in Figure 3.1b is in accordance with the supposed dispersal event. If so, the Australian group E would be the most apomorphic group, because it is peripheral and a member of the youngest sister group, pair D + E, in a hierarchic sequence of successively subordinate groups. The nodes a, b, c, d, and e signify a sequence of decreasing age and increasing apomorphy. According to Brundin, this example has to be considered as an expression of the ever-present parallelism between morphological and chorological progression. Dispersal, seen in the time perspective, is a multiple process including progression in space, evolutionary change, and speciation. This is in turn a consequence of the norm that speciation by cleavage of a stem species is a product of time, progression in space, and isolation of peripheral populations.

Brundin applied the phylogenetic biogeographic approach to real data. His studies (Brundin, 1966, 1972, 1981) on Podonominae chironomid midges inhabiting the southern temperate areas of South America, southern Africa, Tasmania, southeast Australia, and New Zealand are widely known. Brundin first produced a cladogram of the evolutionary relationships of the chironomid species, and in place of the name of each species in the cladogram he inserted the name of the continent in which it is found. As a result, he hypothesized that the African genera diverged first, and that the divergence of the New Zealand species preceded the divergence between the South American and the Australian species.

RESEARCH USING PHYLOGENETIC BIOGEOGRAPHY

Recent examples of this approach consist mainly of papers that explicitly or implicitly apply this method or that employ its assumptions in part. Among them, we can cite that of Knox and Palmer (1998) on Lobeliaceae from eastern Africa.