



Homology, biogeography and areas of endemism

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Abstract. Hypotheses of biogeographic homology constitute the basis of historical biogeography. Primary biogeographic homology refers to a conjecture on a common biogeographic history, and secondary biogeographic homology refers to the cladistic test of the formerly recognized homology. Panbiogeography deals with the former, through the recognition of generalized

tracks and areas of endemism, whereas cladistic biogeography deals with the latter, through the generation of general area cladograms. A historical biogeographic analysis may include both approaches, in a two-stage analysis.

Key words. Biogeography, comparative biology, homology, evolution.

INTRODUCTION

Historical biogeography has undergone notable changes during the second part of the past century. Mainly based on Léon Croizat's (1958, 1964) insightful contributions, the search for common patterns among different taxa, instead of the particular stories of the dispersalist approach, has emerged as a distinct and powerful paradigm (Croizat *et al.*, 1974; Nelson & Platnick, 1981; Craw *et al.*, 1999; Humphries & Parenti, 1999). Within this 'vicariance paradigm', two alternative approaches have been developed: panbiogeography (Croizat, 1958, 1964; Craw *et al.*, 1999) and cladistic biogeography (Nelson & Platnick, 1981; Humphries & Parenti, 1999), which are portrayed by their supporters as alternative methodologies (Croizat, 1982; Craw & Weston, 1984; Seberg, 1986; Page, 1987, 1989; Platnick & Nelson, 1988; Humphries & Seberg, 1989; Craw *et al.*, 1999; Humphries & Parenti, 1999; Craw, 1982, 1983, 1988). Morrone & Crisci (1995) proposed that it was better to consider panbiogeography and cladistic biogeography as complementary methodologies, which may be applied in different steps of a biogeographic analysis.

In spite of its key role in systematics (see Patterson, 1982, 1988; Rieppel, 1988; de Pinna, 1991; Nelson, 1994; among others), the concept of homology has been rarely discussed in the context of biogeography. Craw (1983, 1984, 1988) pointed out the need for a biogeographic equivalent of homology, which he considered inherent to the panbiogeographic approach, but 'fatally absent from cladistic biogeography' (Nelson, 1994). Grehan (1988) considered that biogeographic homology — the criterion that should be employed to recognize common spatiotemporal elements of a shared evolutionary history — was a relevant part of a panbiogeographic analysis. Platnick & Nelson (1988) suggested that in cladistic biogeography, homology means 'congruent taxonomic distributions'. Nelson & Ladiges (1991, 2001), Page (1993), and Ebach (1999) referred to biogeographic distribution patterns that are equivalent of paralogy in molecular systematics. Humphries & Parenti (1999), although supporting cladistic biogeography, recognized Croizat's efforts to develop 'a general method of identifying biogeographic homologies'.

My objective here is to discuss the concept of biogeographic homology and its relationship to the available biogeographic methodologies.

BIOGEOGRAPHIC HOMOLOGY

In its more general form, homology means equivalence of parts, serving as a sorting procedure that is used to establish valid and meaningful comparisons within a hierarchic system (de Pinna, 1991). Homology is essentially a comparative concept, where an individual homology statement interacts with each other. If the analogy between systematics and biogeography is accepted (but see Cracraft, 1988 for a contrasting view), we may consider that the distributions of individual taxa are the statements about biogeographic homology that are compared.

Several authors have already recognized two stages in the proposition of homologies in systematics (see Nelson 1994 for a review), that have been named 'primary' and 'secondary' homology by de Pinna (1991). Primary homology refers to the stage of generation, whereas secondary homology refers to the stage of legitimation. A primary homology statement is conjectural, reflecting an expectation of correspondence between parts of different organisms (in morphological characteristics, topological correspondence is the basic criterion of primary homology). A secondary homology statement represents a test of such expectation, by congruence with similar statements in a cladogram.

Primary biogeographic homology refers to a conjecture on a common biogeographic history, which means that different plant and animal taxa are spatiotemporally integrated in a biota. For example, postulating a Caribbean subregion (Morrone, 2001) means that most of the taxa inhabiting Mesoamerica, the Western Indies and north-western South America share a common geobiological history. A panbiogeographic analysis allows comparison of individual tracks in order to detect generalized tracks (Craw *et al.*, 1999). In addition to sorting distributions of the taxa analysed into large generalized tracks or main biotic components, smaller areas of endemism can be detected within them. In fact, it can be reasonably argued that areas of endemism are equivalent to smaller generalized tracks (Morrone, 2001; Harold & Mooi, 1994). Although the ontological status of the areas of endemism is a rarely discussed issue, with some authors implying that they represent operational units, I tend to agree with Harold & Mooi (1994, p. 262) that

'areas of endemism are fundamentally historical entities, not distributional ones, and their definition should take history into account'. Thus, a panbiogeographic analysis can help identify areas of endemism or test the naturalness of the previously recognized ones. When cladograms are available for the taxa analysed, we can then proceed to the second stage.

Secondary biogeographic homology refers to the cladistic test of the previously hypothesized homology. A cladistic biogeographic analysis allows one to compare area cladograms — obtained by replacing terminal taxa in taxon-area cladograms by the areas of endemism they inhabit — in order to obtain a general area cladogram (Morrone & Carpenter, 1994; Morrone & Crisci, 1995; Humphries & Parenti, 1999). A key consideration in cladistic biogeography is the reduction and/or elimination of paralogy (Ebach, 1999; Nelson & Ladiges, 2001). Paralogous areas, namely those areas that conflict with duplications of themselves, are dealt by assumptions 1 and 2 of Nelson & Platnick (1981) and paralogy free subtrees (Nelson & Ladiges, 1996).

In view of the above considerations, I claim that the dispute between panbiogeography and cladistic biogeography stems from a false assumption: that these methodologies have the same objective. In fact, panbiogeography deals with primary biogeographic homology, whereas cladistic biogeography deals with secondary biogeographic homology. Thus, a historical biogeographic analysis may include both approaches, in a two-stage analysis.

It would be unnecessary to highlight the conceptual relevance of homology in comparative biology. During the last years, however, an uncritical revival of the dispersalist approach is taking place, through the 'ancestral area methodologies' (e.g. Bremer, 1992; Ronquist, 1994; Hausdorf, 1998). The logical problems associated with this approach, which ignores homology and uses paralogy to weight areas and locate centres of origin, has been demonstrated eloquently by Ebach (1999). As I have endeavoured to show, it may be wiser to combine the panbiogeographic and cladistic biogeographic methodologies, under the common denominator of biogeographic homology, rather than apply paralogy-based methods. The congruence among distribution data from different taxa coupled with the natural

hierarchy of the biogeographical system (e.g. regions, subregions, provinces and districts) implies the notion of historical association by descent, in the Darwinian/Hennigian sense. Unless a better framework for explaining evolution in space–form–time is devised, this may be reason enough to prefer this approach.

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