

The biogeographical patterns of disjunct distribution with special emphasis on the Mediterranean and southern African model

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SUMMARY

The authors introduce and shortly discuss the intriguing issue of biogeographical disjunctions, with special emphasis on the Mediterranean-southern African disjunctions, analyzed considering both dispersal and vicariance models. Combined data sets based on both morphological and molecular cues from a relatively large series of different animal and vegetal taxa (some of them extensively discussed in the present volume) indicate true and significant phylogenetic relationships between Mediterranean and southern African biota. Where molecular data are available, the estimated times of divergence frequently supports evidence of an "Arid Corridor", or of a "Central or Eastern High Africa Corridor", which connected a number of times in the last 20-25 MYs the European-Mediterranean and eastern/southern African areas, and facilitated species migration northwards and southwards. These corridors allowed the dispersal southwards of several taxa of European-Mediterranean origin, frequently reaching at least the main mountain systems and the coasts of Eastern and SE Africa. On the other hand, several taxa of eastern and southern African origin migrated northwards, colonizing the Mediterranean and southern Palaearctic areas. Finally, secondary radiations at specific level frequently occurred in the last MYs both in Mediterranean and African areas, involving taxa of African and Mediterranean origins, respectively.

INTRODUCTION

Among the most relevant topics in biogeography, a fundamental role is played by the analysis of the origin and the evolutionary timing of disjunct

distribution patterns among animals and plants (Brown & Lomolino, 1998). These patterns, already observed since Darwin (1859), are becoming increasingly known for both terrestrial (Croizat, 1958; Fryxell, 1967; Nelson & Platnick, 1981) and marine fauna (Briggs, 1974).

As far as terrestrial fauna, we can mention: the “Holarctic distribution pattern”, incorporating records from both the Palaearctic and Nearctic regions (Darlington, 1957; Wen, 1999; Sanmartín et al, 2001; Von Dohlen et al., 2002); the disjunct distributions including both the Nearctic and the Neotropical regions (Darlington, 1957; Croizat, 1958); the so-called “Transpacific distribution” (see McCarthy, 2003); and finally the well known disjunct Palaeotropical distributions, largely emphasized for plants (Croizat, 1968; de Winter, 1971; Bramwell, 1976; Axelrod & Raven, 1978; White, 1983; Coetzee, 1993; Ihlenfeldt, 1994; Jürgens, 1997) but also frequently tested in many animal groups. Among vertebrates, we can remember: bony fishes such as Cichlidae (Murray, 2001; Sparks, 2004; Sparks & Smith, 2004), Aplocheilidae (Murphy & Collier, 1997) and Anabantidae (Berra, 2001); amphibians such as Caeciliidae Caeciliinae (Wilkinson et al., 2002), Nasikabatrachidae and Sooglossidae (Biju e Bossuyt, 2003), Racophoridae (Pough et al., 1998; Wilkinson et al., 2002), Ranidae (Kosuch et al., 2001) and Microhylidae Melanobatrachinae (Loader et al., 2004), and the Plethodontidae salamanders; reptiles such as Boidae of the genus *Python* (McDiarmid et al., 1999); birds such as Bucerotidae and Nectariniidae (Sibley & Ahlquist, 1990); and, finally, mammals such as Lorisidae (3 Afrotropical and 2 Indo-Malayan genera) and Manidae (Wilson & Reeder, 2005); while for invertebrates, we can mention: earthworms (Oligochaeta) such as Megascolecidae and Acanthodrilidae (Omodeo, 1963, 2000; Sims, 1980); velvet worms (Onychophora) of the families Peripatidae and Peripatopsidae (Monge-Najera, 1995), crabs (Crustacea Decapoda) such as Gecarcinucidae (Cumberlidge, 1996; Tan & Peter, 1997); millipedes (Diplopoda) such as Harpagophoridae (Demange, 1961; Hoffman & Burkhalter 1978); the Holarctic Archostemata beetles of the families Cupedidae and Crowsoniellidae, ground beetles (Coleoptera Carabidae; Jeannel, 1942), blister beetles (Coleoptera Meloidae) (Bologna, 1991; Bologna & Pinto, 2002), scarab beetles (Coleoptera Scarabaeoidea) (Carpaneto et al., 1993) and flea beetles (Coleoptera Chrysomelidae Alticinae) (Biondi, 2001). Again about beetles Jeannel (1942), in one of his classic and pioneer contributions to Biogeography, cited and illustrated some of these cases (among others, beetles of the family Carabidae, tribe Trechini, of the so called Homaloderina group). A molecular approach to an example of disjunct distributions in carabids was recently presented by Prüser and Mossakowski (1998), concerning the so-called supertribe Carabitae, which occurs with two groups in the northern

hemisphere (Carabini and Cychrini), another one with world wide distribution (Calosomini), and two isolated taxa (Ceroglossini and Pamborini) living in the southern hemisphere, in Chile and Australia respectively.

As regards marine fauna, great emphasis has been given to the analysis of the Trans-equatorial (Vermeij, 1992) and Bipolar distributions (Crame, 1993; Pierce & Turner, 1993; van Oppen et al., 1993; Darling et al., 2000).

Disjunctions can be evidenced at different taxonomical levels. At a specific level, typical and numerous examples of disjunct ranges are those of mountain species, with isolated populations over the summits of mountain chains, or those of insular populations of the same species. This model of distribution rarely regards a bicentric or polycentric range of the same species, with greatly distanced sub-ranges, as that of the small African Dik dik, *Madoqua kirkii* (Günther, 1880). Anyway, disjunct distributions generally pertain to taxa at a taxonomic level higher than the species rank. More commonly it concerns, in fact, the distribution of supraspecific taxa at the genus or family rank.

The interpretation of the disjunct distributions requires different theoretical and methodological approaches, generally inspired to the two basic conceptual models of vicariance and dispersal. The dispersal tenet interprets disjunct distributions in two different ways: (a) long jumping dispersal, with several examples among Phanerogamae (Raven, 1973) or among crustacean taxa (Amat et al., 1995), probably linked to dispersion events by means of propagules transported over long distance by wind or birds; (b) dispersal from a centre of origin, followed by subsequent extinction in intermediate areas (see Darlington, 1957, for a synthesis).

This theoretical framework, based on dispersal, was widely adopted by European and North-American biogeographers, but subsequently it was partly replaced by the vicariance model, which instead interprets disjunct distributions as the result of the appearance of geographic barriers, which fragmented the ancestral continuous distribution range of a species. On this model, the Croizat's Panbiogeography (Croizat, 1958, 1962) was developed along with the introduction of the "generalised tracks" concept, which refers to disjunct distributions shared by taxa belonging to different phylogenetic lineages. On the same line, many modern methodological approaches, based on vicariance and cladistic biogeography, were proposed and developed in the last years (Nelson & Platnick, 1981; Humphries & Parenti, 1999; Crisci et al., 2003).

In order to explain disjunct distributions, contrasting hypotheses might be formulated:

a) taxa showing disjunctions are actually not closely related to each other and morphological similarity is a product of adaptive convergence (Jablonski & Sepkoski, 1996), i.e., the combined effect of intervening phenomena of com-

munity-scale convergent evolution under the pressure of shared macroclimatic parameters. These phenomena may lead to misinterpret the true significance of a given disjunct distribution, and increase the difficulty of interpreting extant animal assemblages in a historical perspective. It is therefore very important, to avoid this “trap”, that first analytical step is to determine whether the observed patterns are real (true disjunction) or an artifact of incorrect taxonomy (false disjunction).

b) Sampling bias in some areas may obscure real continuous distributions of taxa, for which information is not available for interposed areas; in these cases, a low sampling effort in the intermediate areas may led to false disjunct distributions due to artifact of data missing.

c) Taxa showing a disjunct distribution are closely related from a phylogenetic point of view and consequently their current distribution is the result of the fragmentation of the ancestor’s range, followed by speciation. Of course, when the same disjunct distribution is shared by more taxa belonging to different phylogenetic groups, a generalized track could be recognizable, giving ground for a common vicariant mechanism explaining such “recurrent” patterns (Fryxell, 1967; Jablonski & Sepkoski, 1996; Ribera & Blasco-Zumeta, 1998).

In the last twenty years, our attention was focused on the existence of recurrent disjunct distributions between terrestrial and freshwater fauna of the Mediterranean Basin and the southern Africa, that we name “The Mediterranean-southern African disjunct distribution model”. Patterns of distribution referable to this model are already known from literature especially for plants (e.g. Croizat, 1968; de Winter, 1971; Bramwell, 1976; Axelrod & Raven, 1978; White, 1983; Coetzee, 1993; Ihlenfeldt, 1994; Böhle et al., 1996; Jürgens, 1997; McGuire & Kron, 2005), but also for animals (e.g. La Greca, 1970, 1990 for a synthesis). Consequently they represent a generalized biogeographical phenomenon, which usually concern sister-taxa, usually genera or groups of species, widespread in the Mediterranean Basin and in southern Africa, and including related species in both areas.

The accumulation of examples of a particular pattern in different taxa has statistical relevance, and claims for a common explanation (Fryxell, 1967; Jablonski & Sepkoski, 1996; Ribera & Blasco-Zumeta, 1998). As concerns particularly insects, the main experimental group of our research, this particular model of disjunct distribution was evidenced by several specialists: Chopard (1938), Peyerimhoff (1938), Uvarov (1938), Jeannel (1957), Basilewsky (1963), La Greca (1970, 1990), Oberprieler (1988), Bousquet & Smetana (1986), Colonnelli (1984, 1986), Alonso Zarazaga (1990), Bologna (1991), Audisio (1993), Louw (1993), Kirejtshuk & Audisio (1995), Osella et al. (1998), Mateu (2002), Biondi & D’Alessandro (2006, 2008a, 2008b), Bologna et al. (2008). E.g., in one of his monographs, Jeannel (1957) stressed the markedly disjunct

distribution of the small, endogean Carabidae Scaritinae of the subtribe Reicheina, currently known from a few extant representatives in South and Central Africa, and many genera and species distributed in the Euro-Mediterranean area, from the Iberian peninsula and Maghreb to the Caucasus. More recently, another remarkable example has been the object of both morphological and molecular studies: the Tribe Promecognathini. Known until a few years ago from North-Western America and South Africa, it was recently discovered in the Mediterranean area with an exceptional, troglobitic species (*Dalyath mirabilis* Mateu, 2002) in a “Sierra” of the Southern Iberian Peninsula (Mateu and Bellés, 2003; Ribera et al., 2005). In the present volume additional examples were discussed among several groups of animals, particularly insects.

AIMS, MATERIALS AND METHODS

To tackle the specific problem of Mediterranean-southern African disjunct distributions, since 1993 some zoologists of the Roma Tre, Roma Sapienza, L'Aquila and Sassari Universities performed several field expeditions in southern Africa (Mozambique, South Africa, Namibia) focused on some beetles families, centipedes and lizards, and aimed to recognize possible cases of this disjunct distribution model. In addition, a Research Project supported by grants from the Ministry of University was performed between 2004 and 2006 by researchers of these four Universities. This project (“Zoogeography of Mediterranean-southern African disjunct distributions by a multimethod approach”), coordinated by one of us (MAB), involved four Research Units, 22 University Researchers, 15 Ph.D. students or Post Doc, 4 associate researchers. In this scenario, the involved specialists studied thousands of specimens in several European and African museological institutions.

The animal groups studied as models for the project were: Porifera Spongillidae; Crustacea Harpacticoidea; Chilopoda Geophilomorpha; Diptera Tachinidae; Coleoptera Carabidae, Nitidulidae, Meloidae, Oedemeridae, Scarabaeoidea, Chrysomelidae, Curculionoidea; Reptilia Lacertidae; Mammalia Macroscelididae.

Aims of the research programme was to:

(i) Point out the existence of a generalized distribution pattern represented by Mediterranean-southern African ranges, scarcely discussed for animals. Test and evaluate similar distribution patterns in both terrestrial and freshwater animals to assess their biogeographical significance as results of one or more vicariance events. Distinguish these from analogous distribution patterns due to adaptive convergence in xeric and Mediterranean biomes.

The congruence of areas relationships, coming from cladistic biogeographical analysis, developed on different sets of morphological and molecular char-

acters (Hershkovitz and Zimmer, 2000), will permit to clarify the origin of these disjunct distributions.

(ii) Define phylogenetic affinities within the selected taxa by cladistic analyses on morphological and molecular characters data sets (mtDNA, nDNA). The recent advances in the application of molecular techniques greatly increased both in systematics (e.g. Page, 1994; Caterino et al., 2000; Felsenstein, 2004) and in cladistic biogeography applied to the resolution of disjunct distributions (e.g. Humphries et al., 1988; Oosterbroek and Arntzen, 1992; Morrone and Crisci, 1995; Ronquist, 1998; Morrone, 2002; Page, 2003; Sanmartin, 2003). This approach, in particular, allowed to exclude that some genera of Carabidae Pterostichini of the Southern Hemisphere (South Africa and Madagascar included) are related to Euro-Mediterranean genera of “Molopina”, as previously hypothesised (Casale and Ribera, 2008).

(iii) Assess the biogeographical affinities between area systems through a biogeographical cladistic analysis. To interpret relict endemic taxa in Eastern Africa, related with Mediterranean and southern African ones, as the evidence of ancient dispersion routes, followed by vicariance events.

(iv) Calibrate molecular clocks, in order to date the vicariance events suggested by disjunct distribution patterns, with the support of paleogeographic and paleoecological evidences.

Further target of the project is the inter-taxa calibration of a molecular clock and accurate phylogenies. This calibration will be based on estimates of genetic distances among taxa of the Mediterranean Basin, where paleogeographical information are available (Caccone et al., 1994; 1997; Ronquist, 1997; Oliverio et al., 2000). This calibrated molecular clock will be afterwards used among southern African relatives within each of the studied cases (e.g., Audisio et al., 2008).

RESULTS AND CONCLUSIONS

The present volume, including this introductory paper, represents part of the results of the Italian Biogeographical project, and includes most of the contributions presented in the Workshop organized by us in Rome on September 2007, under the patronage of the Società Italiana di Biogeografia (Italian Society of Biogeography).

According to the results, particularly to dating by molecular clocks, and comparing them with the previous literature, we propose the following hypothesis. The “Mediterranean-southern African disjunct distribution model” is not an homogenous model referable to a single biogeographical event. We pointed out the existence of two distinct sub-models of distribution: (i) Complete disjunction; (ii) Disjunction with intermediate relicts in Sahara and East Africa.

Each sub-model represents similar distributional typologies, which derive from distinct events of both dispersal and vicariance, occurred in different periods, but probably determined by the same type of ecological events. These included drying up phenomena, such as the desertification or the formation of xeric savannahs, which produced the interruption or the extended fragmentation of the forest ecosystems in East Africa, allowing bilateral dispersal events, followed by vicariance events, due to the forest re-expansion.

The origin of previous continuous ranges can rise from Tertiary dispersal events from southern Africa, along the Eastern Africa to Mediterranean Basin, or from Quaternary dispersal events along the opposite direction. Massive extinctions in the interposed tropical and subtropical African areas, or alternatively open and closed geographical and ecological routes and corridors throughout the Eastern in the Pliocene and Pleistocene ages (Hedberg, 1965; Axelrod and Raven, 1978), alternatively due to the expansion of tropical forests or deserts, were hypothesized to explain such present-day distributions (Weidner, 1941; Moreau, 1952, 1963; Livingstone, 1975; Ozenda, 1983; Williamson, 1985; Louw, 1986; La Greca, 1990).

Another issue of this phenomenon is to define if the Mediterranean-southern African links occurred only one or several times since late Tertiary. There are some evidences of a middle and late Tertiary dispersal of southern African karoid elements before the Quaternary (e.g. Osella et al., 1998; Bellstedt et al. 2007) which could represent vicariant relicts of an ancient continuous biome extending throughout Africa when the ecological conditions of Sahara were very different than the present, and more or less continuous vegetation of savannah and sclerophyll thorn scrub existed in most of the Saharan region until the late Pliocene. As discussed by several authors (McGuire and Kron, 2005, and citations herein), the most reliable opportunity for large-scale range expansions into or from Africa most recently occurred during the mid-Miocene (about 17 MYA), when a land connection formed between Europe and Africa after the closure of the Tethys Sea. This phenomenon allowed later several of the involved taxa to radiate in their secondary distribution areas (in both southern Africa and Mediterranean) during the last few MYs (McGuire and Kron, 2005; Audisio et al., 2008). On the other hand, the dispersal of Mediterranean elements from North to South is supported by the evidence, both floristic and faunistic, that Saharo-Mediterranean vegetation existed along the coasts of eastern and southern Africa during the dry periods of late Tertiary and Quaternary, as demonstrated by fossil pollens and relict taxa (e.g. de Winter, 1971; Axelrod and Raven, 1978; van Zinderen Bakker, 1978; Ozenda, 1983; Werger, 1983; White, 1983; Bologna, 1990; Quezel and Barbero, 1993; Coetzee, 1993; Jürgens, 1997; McGuire and Kron, 2005). Audisio et al. (2008) e.g., suggested the occurrence of several heterochronic phenomena of large-scale range expansion in African

groups of Meligethinae (pollen beetles of the family Nitidulidae) towards the Mediterranean and southern Palaearctic areas during the last 20-25 MYs, associated with larval host shifts and with large-scale northwards and southwards range expansion of their herbaceous host-plants (Böhle et al., 1996)

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