MACARONESIA - A BIOGEOGRAPHICAL PUZZLE

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ABSTRACT. Biogeographical relationships differ within the Macaronesian archipelagos; several taxa of the islands' fauna and flora are widespread in the Mediterranean or the Saharosindian province. Some taxonomical groups are highly relictual with disjunct distribution regarding their next relatives whereas neoendemic units (*e.g.*, *Aeonium*) show adaptive radiation to different ecological nishes of the islands and were used to perform a biogeographical homogeneity of a "Greater Macaronesia". Incidental access to the individual islands of the archipelagos may have played a major role to compose each's flora and fauna. The biogeographical validity of the "Macaronesian exclaves" on the adjacent continents is discussed anew.

THE IDEA OF MACARONESIA

The term Macaronesia has often raised discussions on its meanings (SUNDING 1970, 1979; BRAMWELL 1976; KUNKEL 1980; LOBIN 1982). LOBIN (1982) strongly pointed to the fact that on the Capeverdean Islands non-macaronesian plant species do exist and he proposed not to use the terms "Macaronesia" and "Macaronesian" any longer or only after all problems around them are solved. Following this view, there are two floristic components the areas of which are separated from each other: 1. *Saharo-Sindian* which combine the Cape Verdes and the lowlands of the Canaries and Madeira with Africa, and 2. Macaronesian which combine the Capeverdeans with the rest of Macaronesia. BEYHL & *al.* (1990) concluded therefore that the Capeverdean Islands form a transition zone between the "Macaronesian" and "Saharo-Sindian" floral provinces. Similarly the Azores form a transition zone between the "Macaronesian", Mediterranean, and Eurosiberan provinces (EVERS & *al.* 1973; BORGES 1992). Does "Macaronesia" mean a true biogeographic entity, or does it only denote a traditional topographic nomenclature without any biogeographic meaning, i.e. only an abbreviation for the complicated expression "Azores plus Madeira plus Selvagens plus Canaries plus Capeverdeans" resp. for the expressions "East Atlantic Islands", "Middle

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Atlantic Islands", "Ilhas do Atlântico Norte", "Iles Atlantides", "Archipels de l'Océan Atlantique", "Mittelatlantische Inseln", and "Ostatlantische Inseln" which are all similarly insufficient?

The most Macaronesian botanists, e.g. SUNDING (1970, 1979), KUNKEL (1980), and GONZALEZ HENRIQUEZ & *al.* (1986) believe the first of the two possibilities to be true and use the termini "Macaronesia" and "Macaronesian" not only as topographic names but particularly as biogeographic items. Two important plant formations on these islands bear the attribute "Macaronesian" in their names: 1. the so-called "Macaronesian Succulent Shrub", 2. the so-called "Macaronesian Laurel Forest". These two plant formations got their common attribute because they are found on the so-called "Macaronesian Islands". The mythological designation "Macaronesian Islands" first meant the Canaries, later on, all East Atlantic Islands.

Thereupon, one concluded from that common attribute that both plant formations must be related to each other. This argument is supported by the fact that members of some genera occur in both formations such as those of *Aeonium s.l.* (LEMS 1960). Also *Euphorbia mellifera* of the Madeiran and Canarian laurel forest and *E.stygiana* from the Azores are similar to the various dendroid *Euphorbia* species occurring in the so-called "Macaronesian Succulent Shrub" (LÖSCH & *al.* 1990) and thus seem to connect the two plant formations.

This article points to the following facts:

1 - The two formations, the so-called "Macaronesian Succulent Shrub" and the so-called "Macaronesian Laurel Forest" are not related to each other in the sense that they descend from a common "Macaronesian" ancestor.

2 - The two formations themselves are heterogeneous in their biogeographical origins.

3 - The so-called "Macaronesian Exclaves" belong to the same context and are the key to the solution of the "Macaronesia" problem.

4 - Additionally, the existence of the so-called "Canarian pine forest" poses an even greater problem as to its origin and biogeographical relationship.

THE MACARONESIAN LAUREL FOREST

The so-called Macaronesian Laurel Forest is believed to be a unique phenomenon but one must be award that elsewhere there are similar laurel forests which at least bear physiognomical similarity. It is striking that nearly all woody plants of the so-called Macaronesian Laurel Forest have berries or berry-like fruits. Their seeds must have been brought to these islands by birds in their feces. Many of these plant species have relatives in the Mediterranean-North Ar. tolian-Caucasian-Iranian-Himalayan belt and seem to originate therefrom, such as *Prunus lu. tar.ica*, *Laurus azorica* and *Pistacia atlantica*. Other species like *Myrica faya* and *Canarina c. ariensis* (the last species a herbaceous climber, also with a berry) have relatives in ast African mountains.

There are some sp cies which themselves or whose relatives live at disjunct places

on earth such as *Maytenus*, *Notelaea*, *Clethra*, *Heberdenia* and *Myrsine* (SUNDING 1970, 1979). Birds had to travel far in order to bring seeds of these plants to the East Atlantic Islands. They may have been accidental migrants to these islands.

Other sclerophyllous trees such as members of the genus *Quercus* occur together with such laurisilvan components elsewhere, e.g. in the Mediterranean Basin and in the Himalayas (MEUSEL & SCHUBERT 1971), but obviously they could not reach these islands because of their relatively heavy fruits and their differing biology of propagation. *Erica arborea*, present in East African mountains, has small, volatile seeds and might have reached the islands either from the Mediterranean or via a southern route through or south of the Sahara. Also ferns, musci, and lichens as well as orchids and many asteraceans develop diaspores which are propagated easily by wind. It is not clear however, by which way some other plants like *Ranunculus cortusaefolius* and Apiaceans could have reached the so-called Macaronesian Laurel forest. As a whole, structure and taxonomic composition of the so-called Macaronesian Laurel forest is indeed unique, as a consequence of incidental immigration phenomena.

THE MACARONESIAN SUCCULENT SHRUB

The name of this plant formation is also a historical convention which should be replaced by a more suitable designation.

There are several growth types which must not necessarily constitute a homogenous formation: 1. so-called "Federbusch" shrubs (*Euphorbia obtusifolia & al.*, *Echium spec.*, *Dracaena draco.*) (LÖSCH *& al.* 1990), 2. a subgroup with more or less globular appearance (*Euphorbia balsamifera*), 3. rosette formers (*Sonchus spec.*, *Aeonium spec.*), 4. true succulents (*Aeonium spec.*, *Euphorbia canariensis*, *E. handiensis*, *E.aphylla*, *Ceropegia spec.*, *Caralluma*, *Kleinia*). The relationships of these plants are African-Arabian ones: *Caralluma, Euphorbia balsamifera*, *E. canariensis, E. handiensis*, *Dracaena* (SUNDING 1970; MIES & ZIMMER 1993), and *Kleinia* all have their nearest relatives in Africa and Arabia. Some have also North West African-Mediterranean relatives like *Euphorbia obtusifolia & al.*, *Aeonium*, *Caralluma*, *Kleinia*, *Lavandula spec.* Among these plants, there are different ways of propagation, namely by birds (*Phoenix canariensis*, *Dracaena*), by flying seeds (*Kleinia*, Asclepiadaceans, perhaps *Aeonium*) and by catapultation mechanisms (*Euphorbia spec.*). As with the *Euphorbia* species, catapultation mechanisms can propagate seed only over relatively short distances and do not explain how these species could migrate from one island to the other or how they could reach the East Atlantic Islands at all.

THE CANARIAN PINE FOREST

Pinus canariensis is so similar to the Himalayan *P.roxburghii* (MEUSEL & SCHUBERT

1971) that some authors put them together into one species, *P.longifolia* (MIROV 1967). The occurrence on some of the Canarian Islands of *Pinus canariensis* therefore should rather be regarded as an exclave of the Himalayan areal. The disjunct areal of this tree rises a couple of questions. Why did this pine reach only some of the Canaries but not Madeira? How did it reach the Canaries? Volatile seeds and swimming cones are no sufficient explanation. Intermediate stations are unknown at the moment. So this problem is unsolved at present.

GENERAL ASPECTS

Colonization of new areas is always incidental. There are certain probabilities whether a migrating species reaches this area. It is a question of probability, *i.e.*, of the waiting time, if and when all species of an original area can be found in the colonized area. Probability is high when origin and target areas are close together but it is low when they are remote. Therefore remote areas may have incomplete species composition compared to neighbouring areas (*e.g.*, Azores *versus* Canaries).

Species may colonize a target area repeatedly giving rise to speciation events. Different target areas to be colonized from the same original area may have different uncomplete species composition but this is only the case for a transit period: If one waits long enough one will (probably) find all species of the original area in the colonized areas. By incident, even species from very far remote areas can be driven on such an area to be colonized. Therefore a newly formed biocenosis may be heterogeneous in itself. One must take into account succession, geographic condicions, geographic changes, and climatic change to consider colonization events (BEYHL 1988). Climatic changes always induce migrations of biocenoses giving way both for extinction of species and for the immigration of new species or the reimmigration of formerly extinct species.

It appears urgent to do pollen-analytical profiling in the lakes and bogs of the Azores and in the sediments of the former lake of La Laguna (Island of Tenerife) which will give elucidation of climate and plant history on the East Atlantic Islands.

THE QUESTION OF THE MACARONESIAN EXCLAVES

An exclave is an area which is separated from the main area, which is smaller than the main area, and which has the same or similar faunistic and/or floristic composition. The name is derived from geopolitics and has found entrance into biogeography.

Based on other authors, KUNKEL (1980) developped a concept of "Greater Macaronesia" which included also the so-called "Macaronesian exclaves". These are places in Northwest Africa and on the Iberan peninsula which conventionally bear this name. In both cases, the attribute "Macaronesian" means something different. The Iberan "Macaronesian Exclave" contains elements of the so-called Macaronesian laurel forest such

as *Prunus lusitanica* and *Culcita macrocarpa*. Its real existence, as an entity different from Mediterranean, North Anatolian, Caucasian, and Iranian biocenoses, still appears to be questionable. It may be just a more humid version of the ordinary Mediterranean flora. So it can be neglected.

In the following, we only speak about the so-called "Macaronesian exclave" in Northwest Africa. It means places in the area of North West Africa off the Canaries where indeed elements of the so-called "Macaronesian succulent bush" and/or their vicariants exist, *e.g.*, *Euphorbia obtusifolia* and *E.balsamifera*, besides that *E.beaumieriana* and *Kleinia anteuphorbium*. PEYERIMHOFF (1946) stresses its near relationship to African biocenoses and takes it even as a proof that the corresponding "Macaronesian" elements are positively descendants from the African continent. This "Macaronesian Exclave" appears on the maps of PEYERIMHOFF (1946), SUNDING (1979), KUNKEL (1980), GONZALEZ HENRIQUEZ & *al.* (1986), and KÖNIG & BLEY (1988), with different extensions, on each one. In the map of KÖNIG & BLEY (1988), it is named "succulent-rich vegetation".

If one compares the area of this "exclave" with that of the "Macaronesian Mainland" as depicted in the maps of all these authors, one instantly sees that the exclave is at least as large as the mainland or even larger. Obviously none of the authors communicating on "Macaronesian exclaves" ever realized that striking fact. It is simply not allowed to assume that the area of an exclave is larger than that of the corresponding mainland: This conflicts with the definition of an exclave!

Therefore we cannot longer agree that the parts of North West Africa which bear this kind of succulent shrub are only a small exclave of the Macaronesian "main land". We feel obliged to think just in the opposite direction. So we propose to regard those parts of Madeira, the Canaries and the Capeverdeans which bear the so-called "Macaronesian succulent shrub" to be an exclave of the Northwest African succulent zone. Our opinion is supported by the studies of ZAKI & SCHMIDT (1973) who, on the reason of their vegetational analysis of Lanzarote and Fuerteventura, consider these two islands to belong to the North West African vegetational area, in congruence with the opinion of DIETZ & SPROLL (1970) that they are a kind of microcontinent drifting away from Africa. The authors did not extend this assignment to the North West African flora, of Lanzarote and Fuerteventura, to those parts of the rest of the Canaries, of Madeira and the Capeverdeans what would have been the logical consequence of their findings.

A biogeographically homogenous "Macaronesia" does not exist, and the use of this word connected to this meaning must be neglected in biogeography. However, in order to save the widely venerated termini "Macaronesia" and "Macaronesian", we herewith suggest to restrict them only to the laurel forest and no longer to the succulent formations.

The East Atlantic Islands, similar to the situation of Palestine and the Sahara, contain several floristic provinces which have their origins from different biogeographic areas, belong to different floral regions, enclose each other in an insular-like manner, and are interconnected

with each other secondarily by adaptively radiating plants. The laurel forest belongs to the Holarctis (in spite of some incidental tropical elements). The North West African succulent region, together with its exclaves in the East Atlantic Islands, belongs to the Paleotropis or forms the transition to that. Not only the Capeverdeans (BEYHL *& al.* 1990) but all East Atlantic islands form a biogeographical transition zone. The common view that the East Atlantic Islands represent a biogeographically homogenous entity "Macaronesia" is misleading.

REFERENCES

BEYHL, F. E.:
1988. Zur Besiedlung der Mittelatlantischen Inseln. I. Allgemeine Überlegungen. *Cour. Forsch.-Inst. Senckenberg*, **105**: 19 - 25.

BEYHL, F. E., R. LÖSCH, B. MIES, & B. SCHWEIHOFEN:
1990. Bilden die Kapverden ein einheitliches Florengebiet? *Cour. Forsch.-Inst. Senckenberg*, **129**: 47 - 53.

BORGES, P. A. V.:
1992. Biogeography of the Azorean Coleoptera. *Bol. Mus. Mun. Funchal*, **44** (237): 5 - 76.

BRAMWELL, D.:
1976. The endemic flora of the Canary Islands; distribution, relationships and phytogeography. In G.Kunkel (ed.) *Biogeography and Ecology in the Canary Islands*. pp. 207 - 240. W. Junk. The Hague.

DIETZ, R. S. & W. P. SPROLL:
1970. East Canary Islands as a microcontinent within Africa-North America continental drift. *Nature*, **226**: 1043 - 1070.

EVERS, A. M. J., P. OHM & R. REMANE:
1973. Allgemeine Gesichtspunkte zur Biogeographie der Azoren. *Bol. Mus. Mun. Funchal*, **27**: 5 - 17.

GONZALEZ HENRIQUEZ, M. N., J. D. RODRIGO PEREZ, & C. SUAREZ RODRIGUEZ:
1986. *Flora y Vegetación del Archipiélago Canario*. - 355 *pp*. Cedirca s. L. edición regional canaria. Las Palmas de G.C.

KÖNIG, P. & K. A. BLEY:
1988. Von Marokko zur Elfenbeinküste - zur Pflanzenwelt des westlichen Afrika. *Natur u. Mus.*, **118**: 1 - 22.

KUNKEL, G.:
1980. *Die Kanarischen Inseln und ihre Pflanzenwelt.* - 185 pp. Gustav Fischer Verlag. Stuttgart New York.

LEMS, K.:
1960. Botanical notes on the Canary Islands. II. The evolution of plant forms in the islands: Aeonium. *Ecology*, **41**: 1 - 17.

LOBIN, W.:
1982. Untersuchung über Flora, Vegetation und biogeographische Beziehungen der Kapverdischen Inseln. *Cour. Forsch.-Inst.Senckenberg*, **53**: 1 - 112.

LÖSCH, R., F. E. BEYHL, B. MIES & B. SCHWEIHOFEN:
1990. Relative Standortkonstanz der Federbuschvegetation auf den Mittelatlantischen Inseln und das Fehlen klimatisch-orographischer Voraussetzungen für eine Waldklimax auf den Kapverden. *Cour. Forsch.-Inst. Senckenberg*, **129**: 75 - 82.

MEUSEL, H. & R. SCHUBERT:
1971. Beiträge zur Pflanzengeographie des Westhimalayas. *Flora*, **160**: 137 - 194, 373 - 432; Jena.

MIES, B. & H. ZIMMER:
1993. Die Vegetation der Insel Sokotra im Indischen Ozean. *Natur u.Mus.*, **123**: 253 - 264.

MIROV, N. T.:
1967. *The Genus PINUS.* - 602 *pp.* The Ronald Press Company. New York.

PEYERIMHOFF, P. DE:
1946. Les Coléoptères des Atlantides et l'élément Atlantique. *Mém. Soc. Biogéographie*, **8**: 153 - 197.

SUNDING, P.:
1970. Elementer i Kanarioyernes flora, og teorier til forklaring av floraens upprinnelse. *Blyttia*, **28**: 229 - 259.
1979. Origins of the Macaronesian Flora. In D.Bramwell (ed.) *Plants and Islands*, pp.13 - 40. Academic Press. London.

ZAKI, M. A. & V. M. SCHMIDT:
1973. On the systematical structure of flora of south mediterranean countries. III. Comparison of the structure of flora of separate regions. *Vestn. Leningrad Univ., No.3, Ser.Biol.*, **21**: 44 - 53.