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Origin and speciation of the Cupressaceae in Sub-Saharan Africa

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SUMMARY

The author discusses the past and present distributions for the *Juniperus excelsa* complex and of *Widdringtonia* spp. in Africa. Possible migration routes are presented. The synonymy of *Juniperus excelsa* is given.

RÉSUMÉ

L'auteur présente la répartition géographique actuelle de *Juniperus excelsa* coll. et celle des espèces de *Widdringtonia* en Afrique, en discutant de leur distribution dans le passé ainsi que des diverses voies de migration possibles. La synonymie de *Juniperus excelsa* est établie.

The principal aim of this paper is to record and explain the past and present distribution of the *Cupressaceae* in Africa south of the Sahara, and to clarify the taxonomic relationships of its component species.

The family *Cupressaceae* has an interesting and unusual global distribution with a wide but frequently discontinuous range seemingly indicative of an ancient origin, and many taxa are more or less endemic. Nevertheless, it is clear that there are certain characteristics common to the two genera which are the sole representatives of this family south of the Sahara. There is also a remarkable degree of homogeneity and affinity in synecological relationships. Within the broad categories of climate, soil (topographic) and chorology therefore, a study of *Juniperus* and *Widdringtonia* and the communities with which they are associated, has revealed some semblance of unity in a family and more particularly sections of taxa, hitherto considered somewhat anomalous.

Geological background

It is unnecessary to survey the general development of the earth's surface from the first appearance of the conifers as a recognizable group, i.e. during the late Palaeozoic era some 250 000 000 years ago. Inevitably, in view of this long evolutionary history and the contemporary configuration of land and sea south of the Tethyan region, the influence of adjacent land masses on the migration of specific taxa is highly significant. In fact, distribution of many taxa in the *Coniferales* has frequently been cited as further proof of Continental Drift and the former existence of a southern continent Gondwanaland (Sneath, 1967; Wardle, 1968).

The plotted distributions of contemporary conifers seem to confirm both the position of the southern continents during the late Palaeozoic era, and the concept of Gondwanaland. They may also be indicative of ancient climates rather than ancient land connections, depending on how long northern and southern genera have been divided, and the degree of influence imparted by the Tethyan Sahara (cf. Adams & Ager, 1967; Melville, 1966).

Despite the incomplete and erratic fossil record, it is clear that the *Cupressaceae* has a more pronounced bi-hemispherical distribution than any other family of the *Coniferales* (Godley, 1967; Kerfoot, 1970). *Juniperus* and *Widdringtonia* can be considered typical representatives of the two major phytogeographical dominions: one markedly polytypic, the other narrowly oligotypic.

No general agreement has yet been reached on many aspects of Continental Drift, but migration routes of many plants were undoubtedly determined by Tethyan movement (cf. Godley, op. cit.). Before and during the Palaeocene, land masses on both sides of the geosyncline were populated, first by a mesic tropical flora and later by a xeric "savanna-type" flora. Some of the former still survive in local enclaves bordering the Persian Gulf.

Palaeomagnetic and other evidence indicate that Africa finally separated from the remainder of Gondwanaland during the early Cretaceous period, while the Red Sea became permanently established during the Pliocene. The evolution of important mountain systems which accompanied the reduction of the Tethyan Sea provided niches for species migrating from Asia Minor to the inner Himalaya and southwards via peninsular Arabia to Africa (Zohary, 1963; Creer, 1965; Runcorne, 1965).

Climatic background

A steady decline in temperature was a feature of Quaternary development providing a reasonable explanation for the retreat of tropical floral elements. Some evidence is available which seems to confirm an erratic sequence of climatic oscillations during the Pleistocene period, but there is no proof of a similar sequence of events during the preceding Pliocene period. There is no doubt that Pleistocene fluctuations influenced the distribution of the *Coniferales*, and many other taxa of African origin colonized Asia at this time (Zohary, op. cit.; Li, 1953).

Chorological background

The eastern Mediterranean region acted as a refuge for the genus *Juniperus* when conditions over its former range in Europe deteriorated with the onset of the Pliocene period and were maintained to as late as the last interglacial period of the Pleistocene (cf. Fig. 1).

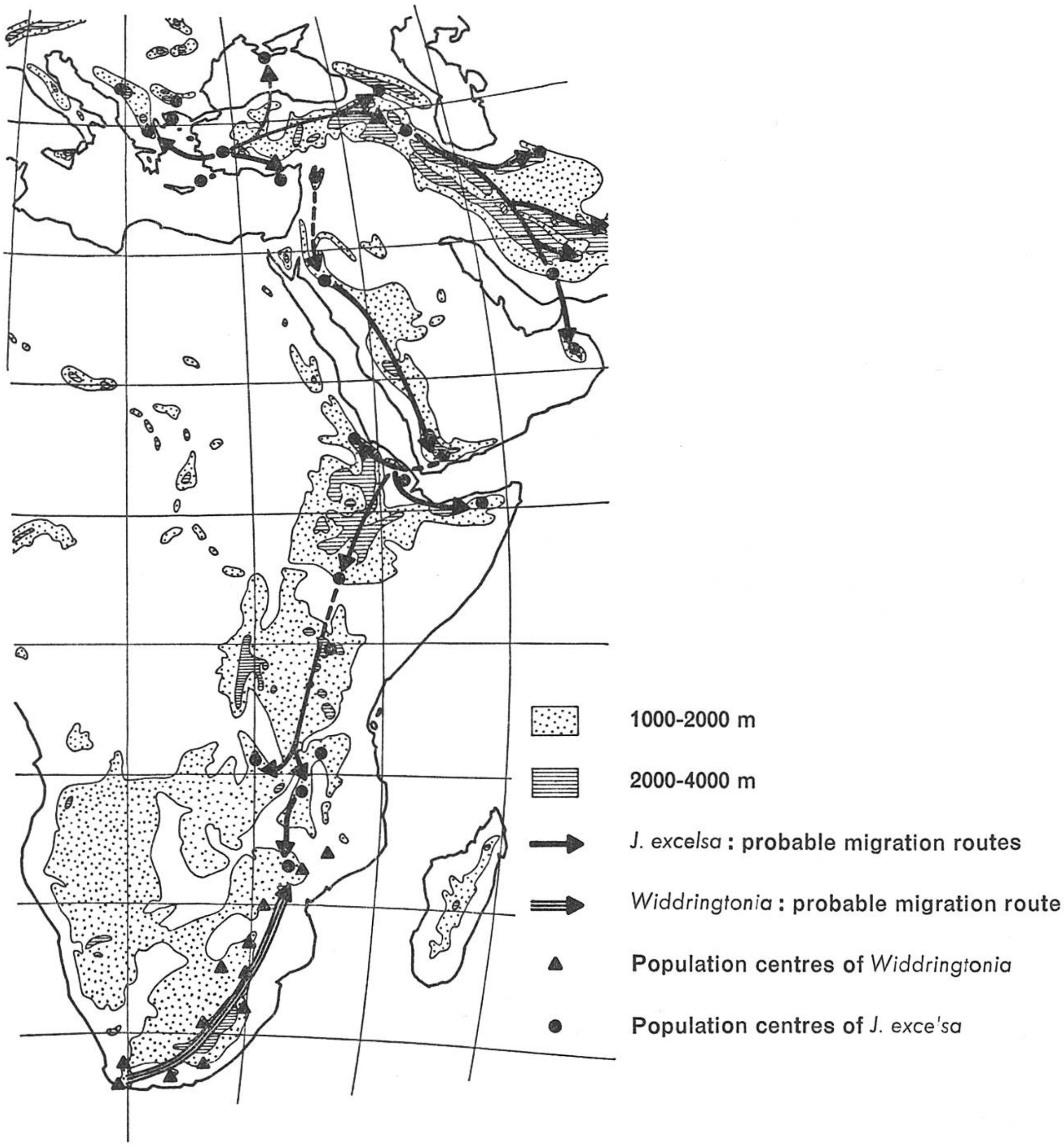

Fig. 1. — Distribution and probable migration routes of *Juniperus excelsa* and *Widdringtonia* spp.

Recent studies of the section *Sabina* indicate that species populations south of the Sahara are closely linked to floras of Arabia and Sinai and phytogeographical regions of Turkey and south-western Arabia. It is now beyond doubt that *Juniperus* migrated from Asia Minor in Mio-Pliocene times when continental uplift reunited adjacent land masses.

One cannot yet be precise about its centre of origin. The oldest authentic fossil material is of early Tertiary age, and by the end of the Pliocene, it was widely distributed in the Northern Hemisphere. It is, in fact, the only living member of the *Cupressaceae* to occur in *both* hemispheres and its extension in Africa to the southern limit of the tropical zone is unique amongst the *Coniferales* (Fig. 1).

Widdringtonia on the other hand, has a restricted range as a result, we believe, of northerly shifts of tropical to sub-tropical conditions during the late Miocene period.

There are three species of evergreen trees or shrubs, whose contemporary range extends from the Cedarberg mountains in the Cape Province eastwards and northwards to Malawi.[1] Its former chorological limits are practically unknown now. The earliest authentic fossil material is of Tertiary age but from within its present area of distribution. *Widdringtonia*, like all genera of the *Cupressaceae* from the southern hemisphere, must be considered regionally endemic.

Both genera are essentially montane and xeric: *Juniperus* occurs in a variety of situations from about 800 m to 3000 m above sea level, while *Widdringtonia* has a wider range of altitude, at least at the lower end of the scale, occurring from near sea level in the extreme south to 2500 m on the Mlanje Range, Malawi.

Phyto-taxonomic relationships

Juniperus has a light resinous seed enclosed in a fleshy, edible dispersal unit, 1 cm or so in length. *Widdringtonia* has heavier, winged seeds which, when released from the resinous woody cone, are easily dispersed by the wind. It is impossible to understand the relationships between these taxa if such fundamental differences in disseminules are not taken into account.

It is often stated that conifer distributions are largely dictated by climate, and particularly the restrictive limits of temperature. Thus, whenever a northern species moves away from its (presumed) centre of origin to lower latitudes, the inevitable increase in its altitudinal amplitude is merely a reflection of temperature adjustments. Provided that the general climate does not change, it may be anticipated that temperature limits operative at these new altitudinal levels will be more or less coincident with those characteristic of the centre of origin of the taxa concerned.

The rather prominent irregularities in the vertical and latitudinal distribution of both *Juniperus* and *Widdringtonia* introduce a number of environmental limitations other than that of temperature, however. Many authors have tried to explain these contradictions by postulating a "diminished vitality and distributional area" for these and other disjunct taxa. A more likely alternative, in view of evidence from such sites as the Marungu Plateau (Zaire), Kalambo Falls (Zambia) and the Cedarberg (South Africa), is that the extensive formations known to have existed in the past must have developed during optimal climatic conditions. Today, these conditions are replicated only in smaller and more isolated habitats.

Most members of the *Sabina* section of the genus *Juniperus* are associated with dry or semi-arid habitats at medium to high altitudes, represented south of the Sahara, by a single species, *J. procera* Endl. The present writer has already described (Kerfoot, 1970) the Arabian extension of this taxon, and the close relationships between it and other species of the *Sabina* group, namely *J. polycarpos* Koch (= *J. macropoda* Boiss.), *J. excelsa* Bieb., *J. turcomanica* Fedtsch. and *J. seravschanica* Kom.

As a result of taxonomic studies *(in litt.)*, the present author has concluded that we are dealing with a complex generic group with its epicentre in Asia Minor and that all the "species" cited above are one variable taxon *Juniperus excelsa* Bieb.

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[1] Dr. R. Polhill has kindly drawn attention to the existence of a herbarium specimen from Tanzania (*Geilinger* 2215) N of Lake Malawi, but lacking confirmatory evidence, the writer is inclined to believe the material was derived from a cultivated plant.

The range of this species is immense: from Yugoslavia to western Tien-Shan, and from Arabia to Rhodesia (Fig. 1). But it confirms what we know—or have suspected—concerning the past floral record of those regions and reinforces current phytogeographical concepts (cf. Godley, 1967).

It is predominantly a species of the Irano-Turanian territory, but also occurs in Mediterranean environments as far afield as the Himalayas and southern Arabia. The existence of mountain barriers has not prevented many Mediterranean elements, particularly montane woody species, penetrating deep into Asia, just as Turanian elements have become established in mountainous terrain of Mediterranean lands (cf. Eig, 1931-1932). *Quercus* spp., *Crataegus azarolus* and *Cercis siliquastrum* are examples of the former, while *Pistacia* spp. have reached Egypt and East Africa. African elements in Asia include *Helianthemum sessiliflorum* and *Gymnarrhena micrantha.*

Probably the basic formation is "steppe" although more mesic variants of Eu-Siberian affinity occur in suitable localities and there is much ecological and floristic diversity. Much of this "steppe" forest in which *Juniperus* occurs belongs to the Tethyan belt (Adams & Ager, 1967). An egregious component is the genus *Pistacia,* species of which have survived in fragments of forest from western Tien-Shan to the Canary Islands and one, *Pistacia lentiscus,* extends into East Africa in association with *Juniperus.*

It is probable that a number of species have migrated across what is now the south-eastern tip of Arabia, but in view of the dispersal features of both *Juniperus* and *Pistacia,* the major discontinuity between Oman and the South Yemen of approximately 1800 km would seem to be wholly incompatible with their doing so. Furthermore, there is not a vestige of evidence for a climatic change having occurred since the Pleistocene, great enough to have created even a temporary corridor of migration for these taxa.

On the other hand, a depauperate African flora, which includes species of *Rosa, Lavandula, Trichodesma* and *Ochradenus,* occurs in the Yemen, and Saharo-Sindian elements have penetrated to the Jordanian border. Many Mediterranean and Irano-Turanian species have strong East African montane connections which have probably been maintained until fairly recently.

It is also true, of course, that some characteristic associates of *Juniperus* have failed to penetrate beyond the plateaux and Rift Valley system of Central Ethiopia. It is very likely that Pleistocene orogenic activity was responsible for the formation of extensive troughs which act as barriers to migration. The forests of the Dai and Adonta plateaux in Somalia are intermediate in character between those of the Yemen and what remains of the Saharan forests on Tibesti and Hoggar.

Widdringtonia is less well documented but all available evidence points to derivation from a cool-climate ancestor which already existed in the Tertiary period and not, as has been suggested, from warm-climate ancestors similar to the modern genus *Callitris.* A post-Tertiary development can no longer be considered because of:

a) the known fossil record;

b) taxonomic isolation and geographical distribution.

Wardle (1968) has come to a somewhat similar conclusion with regard to ancestral forms of elements established in New Zealand. They have their equivalents in South America and Australia as well. Most are oligotypic or monotypic genera restricted to cool, wet, infertile sites, and many belong to the so-called "Antarctic Element" (Darlington, 1965).

Unfortunately, no fossil evidence for the existence of *Widdringtonia* in what is now known as Antarctica ("that much-trodden road between America and Australia—New Zealand", Skottsberg, 1956), is yet available, but the genus is undoubtedly one representative of an ancient Austral flora which also included *Fitzroya cupressoides* in South America, several groups of the genus *Podocarpus* in Australia, South America and New Caledonia; and *Phyllocladus* in New Zealand, Tasmania and Malaysia. It almost certainly existed in Africa before Gondwanaland fragmented and its Australasian relatives, *Callitris, Actinostrobus* and so on, share a common ancestry. *Fitzroya* and its allies in South America, *Austrocedrus* and *Pilgerodendron* have a similar relationship.

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