

The historical phytogeography of the Disinae (Orchidaceae)

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ABSTRACT

The Disinae (Orchidaceae) are widespread in tropical montane Africa and the Cape temperate region, therefore showing a distribution range typical of a temperate herb in Africa. Centres of endemism and high species richness are recognized in the southern and western Cape Province, the Natal-Transvaal escarpment mountains, the watershed between the Rivers Zaire and Zambesi and the southern highlands of Tanzania, the East African highlands and Madagascar. The number of species and their degree of endemism decrease from south to north. Several regions, e.g. Zimbabwe and West Africa, are outliers of other regions, or overlap zones between regions.

An attempt is made to determine the history of the group by vicariance biogeographical analysis, but the resultant area cladogram is uninformative. This may be due to the vagility of the taxa.

Areas of endemism of supra-specific taxa are determined. These areas appear on recent palaeoenvironmental data to be possible refugia (Cape fold mountains, the South African Drakensberg and the East African Rift Valley mountains), from where the taxa spread when the climate ameliorated after the last glacial. This model is corroborated by recent studies on Cupressaceae, Pooidae and Compositae.

RÉSUMÉ

LA PHYTOGÉOGRAPHIE HISTORIQUE DES DISINÉES (ORCHIDACEAE)

Les Disinées (Orchidaceae) sont largement répandues en Afrique tropicale montagnarde et dans la région tempérée du Cap, montrant donc une aire de distribution typique d'une herbe tempérée d'Afrique. Des centres d'endémisme et une richesse élevée en espèces sont reconnus dans la Province du Cap australe et occidentale, les montagnes de l'escarpement Natal-Transvaal, la ligne de crête entre le Zaire et le Zambèze, ainsi que les hauts plateaux méridionaux de Tanzanie, les hauts plateaux de l'Est Africain et Madagascar. Le nombre des espèces et leur degré d'endémisme décroît du Sud au Nord. Plusieurs régions, comme le Zimbabwe et l'Afrique de l'Ouest, sont des massifs détachés d'autres régions ou des zones de chevauchement entre régions.

Une tentative est faite pour déterminer l'histoire du groupe par une analyse bio-géographique de la vicariance, mais le cladogramme qui en résulte ne fournit pas d'information. Ceci peut être dû à la mobilité des taxa.

Des régions d'endémisme de taxa supra-spécifiques sont déterminées. Ces régions, suivant des données paléontologiques récentes, semblent être des refuges possibles (les montagnes plissées du Cap, le Drakensberg sud-africain et les montagnes du Graben de l'Est africain), d'où les taxa se sont disséminés quand le climat s'est amélioré après le dernier épisode glaciaire. Cette interprétation est corroborée par de récentes études sur les cupressacées, les pooidées et les composées.

INTRODUCTION

Over the last 80 years, certain patterns in the distribution of species of the Cape flora and the Afro-montane flora have been documented (Weimarck, 1933, 1936, 1940, 1941; Levyns, 1952, 1955; Wild, 1968, 1975, 1964; Hilliard, 1978; Morton, 1972; Ayodele Cole, 1974; Chapman & White, 1970; White, 1978; Nordenstam, 1969). These have resulted in the recognition of a very distinct Cape flora (Good, 1953; Takhtajan, 1969), whereas the Afro-montane flora has only recently been distinguished as occupying numerous small areas in tropical Africa (White, 1978).

How did the distribution patterns of the species constituting the Afro-montane and Cape floras develop, and what controls them? The answer to this problem can only be found in the evolutionary and phytogeographical histories of the taxa constituting these floras. However, very few taxa have been studied to elucidate their histories (Kerfoot, 1975). The Disinae (Orchidaceae) form an excellent group to study as an example. The subtribe has recently been revised (Linder, 1981a, b, c, d, e, f). It is ubiquitous in the Afro-montane and Cape regions (Fig. 1), and the distribution and biology of the species is relatively well known.

BIOLOGY OF THE DISINAE

The biology of the taxa has to be taken into account, as it may strongly influence the present distribution, the rates of migration, under what conditions speciation may be expected, and how the species would respond to changing environments.

The Disinae are low terrestrial herbs that cannot successfully compete with tall perennial vegetation. Consequently, the majority of the species are restricted to Cape fynbos, Afro-montane grassland or edaphic grasslands, all pyrophytic vegetation types (Knapp, 1973; Vesey-Fitzgerald, 1963; Chapman & White, 1970; Kruger, 1979; Killick, 1978; White, 1978). The distribution is almost limited to temperate climates: a mediterranean climate in the southern and south-western Cape Province (Weather Bureau, 1972) and a cool summer-rainfall climate in the Afro-montane region (Chapman & White, 1970; Ayodele Cole, 1974; Jackson, 1961). Generally, the rainfall regime is between 700 and 2 000 mm p.a. The seeds are very easily dispersed. Each flower produces in excess of 8 000 minute dust-like seeds that are readily dispersed by wind.

Speciation in the Disinae does not appear to be predominantly allopatric, as has been suggested for some other taxa in the Cape flora (Levyns, 1955; Rourke, 1972; Bremer, 1976; Strid, 1972; Goldblatt, 1978, 1981). Although there is some evidence for allopatric speciation, the majority of species in

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FIG. 1.—Total distribution of the Disinae (outline) in relation to the Afro-montane regions (according to White, 1978) indicated in black.



FIG. 2.—Distribution of centres recognized in Africa: 1, Cape centre; 2, Natal-Transvaal centre; 3, Zimbabwe overlap region; 4, South-Central African centre; 5, Madagascan centre; 6, East African centre; 7, West African outlier. The Reunion centre is not indicated.

species groups are more readily analysed along ecological gradients, suggesting that differential selection may be more important than isolation. Various ecological factors appear to be of importance: moisture gradients, altitudinal gradients, substrate types, climate, fog-regimes, annual rainfall, etc.

DISTRIBUTION PATTERNS

To analyse the distribution patterns, 11 more or less geographically isolated areas were delimited. Centres of endemism, overlap regions and outliers were synthesized out of these 11 areas by comparing the species lists of the areas. Centres are defined as having more than 30% endemism, outliers are areas with less than 30% endemism, and with the majority of the non-endemic species held in common with a nearby centre, whereas in overlap regions endemism is less than 30%, and the non-endemic species are held in common with two other centres. The centres recognized are shown in Fig. 2, and the patterns of species richness and supraspecific richness for the centres, as well as the similarities among the centres, is shown in Table 1.

The patterns of decreasing species richness, supra-specific richness and endemism as one proceeds from the Cape northwards are relatively well documented (Baker & Oliver, 1967; Beard, 1963; Rourke, 1980; Weimarck, 1940, 1934; Goldblatt, 1977, 1978; Brenan, 1978). The high degree of endemism in the Cape is also quite typical (Taylor, 1980; Goldblatt, 1978).

TABLE 1.—Species richness, supraspecific richness, levels of endemism and patterns of affinities among the centres

	Cape	Natal-Transvaal	Zimbabwe	South-Central Africa	East Africa	West Africa	Madagascar	Reunion
Cape	99	11	3	0	0	0	1	0
Natal-Transvaal	52	15	9	3	3	3	0	0
Zimbabwe		23	15	4	5	2	0	0
South-Central Africa			39	9	7	2	0	0
East Africa				12	6	1	0	0
West Africa					8	0	0	0
Madagascar							7	0
Reunion								1
Number of endemics	89	29	1	17	4	1	3	1
% endemics	90	56	4	45	31	13	43	100
Number of sections	11	10	7	7	4	3	3	1
Number of subgenera	5	5	4	4	3	3	3	1
Number of genera	4	4	4	3	2	2	3	1

Within the Cape Centre, Weimarck (1941) recognized several centres. However, only two centres can be recognized in the Disinae: a western centre and a southern centre with an overlap region on the Cape Peninsula and in the mountains of the Caledon Division. A similar pattern has been recognized for *Leucodendron* (Proteaceae) (Williams, 1972). Typical Cape flora species that extend

outside the Cape Floral Region (Goldblatt, 1978) are restricted to Table Mountain Sandstone in the Transkei and southern Natal.

The lack of endemism in Zimbabwe is rather peculiar, as the area is geographically isolated. Wild (1964) recorded a relatively high percentage of endemism for the Chimanimani mountains, and Goldblatt (1977) regarded it as a centre for *Moraea* (Iridaceae). On the whole, the data for Zimbabwe are confusing. As about half of the non-endemic species in Zimbabwe also occur in South Africa, and the other half in South-Central Africa, Zimbabwe is regarded as an overlap region.

The Eastern Cape Province in South Africa totally lacks endemic species. It appears as if this lack of endemism might be common in the Cape floral element in the area.

South-Central Africa is remarkably rich (see also Goldblatt, 1977). The majority of the endemic taxa are quite widespread, reaching from Angola to the Southern Highlands of Tanzania. Six taxa are restricted to the high mountains around the northern edge of Lake Malawi. The area is generally rich in endemic species (Hedberg *et al.*, 1980) and has a remarkably rich orchid flora (Williamson, 1979).

Although several studies have indicated that the montane grassland of the West African mountains is most closely related to that of the East African highlands (Morton, 1972; Hamilton, 1974; Ayodele Cole, 1974; Hall & Medler, 1975), the Disinae are, with one exception, common to the South-Central African centre. The area is therefore regarded as an outlier of the South-Central African centre. Species richness decreases rather rapidly from east to west in West Africa.

The East African centre has four (31%) endemic species. There is an interesting distribution pattern, connecting the Kenyan uplands to the Ethiopian highlands via Mt Elgon, Mt Kadam, Mt Moroto and the Imatong mountains.

Wild (1975) showed that Madagascar shared many more species with southern Africa than with eastern Africa, a pattern which is corroborated by the distributional data of the Disinae. There is a single endemic species on Reunion. Levyns (1937) recorded a similar situation for the Composite genus *Stoebe*.

Clearly, the phytogeographical patterns in the Disinae agree in the main with the general patterns found in the Cape and Afro-montane floras.

BIOLOGY AND ENVIRONMENT AS A PREDICTOR OF DISTRIBUTION

The hypothesis that the distribution patterns in the Disinae are correlated to, and probably caused by, the combination of the biology of the species and the present environment predicts some of the observed patterns, but not others. The total distribution range in Subsaharan Africa is clearly related to the present environment. The intervals in Africa are also related to the environment: a change in substrate in the Cape-Natal interval, change in the monthly distribution of precipitation in the

Western-Southern Cape interval, and regions of inhospitable vegetation in most of the tropical intervals. However, this hypothesis cannot account for the absence of the subtribe from the Mediterranean basin, where the habitat appears to be eminently suitable, or for the patterns of diversity and endemism observed among the various centres.

Consequently, it is necessary to investigate the history of the subtribe (i.e. migrations and past distributions determined by palaeoclimates) to provide an alternative hypothesis on the evolution and diversification of the subtribe.

HISTORY

The most rigorous method for reconstructing the history of a group in the absence of fossil evidence is by vicariance biogeography (Platnick & Nelson, 1978; Rosen, 1978; Humphries, 1981). In this method, the phylogenetic classification of the group is superposed over the geographical regions, to form an area cladogram (Fig. 4). This is based on the cladogram in Fig. 3. (from Linder, 1982). The area cladogram is clearly uninformative as to history of the group. This could be due to the invalidity of the assumption in vicariance biogeographical analyses of the absence of long-distance dispersal.

A less rigorous approach is to analyse the distributions of supra-specific taxa, and to study the occurrence of patterns of vicariant taxa. Supra-specific groups, especially at sectional level, show striking patterns: (a) Only one section contains species in the Cape Centre as well as the tropical centres, and in this section the Cape species belong to different series from the tropical species; (b) With one exception, all the sections found in tropical

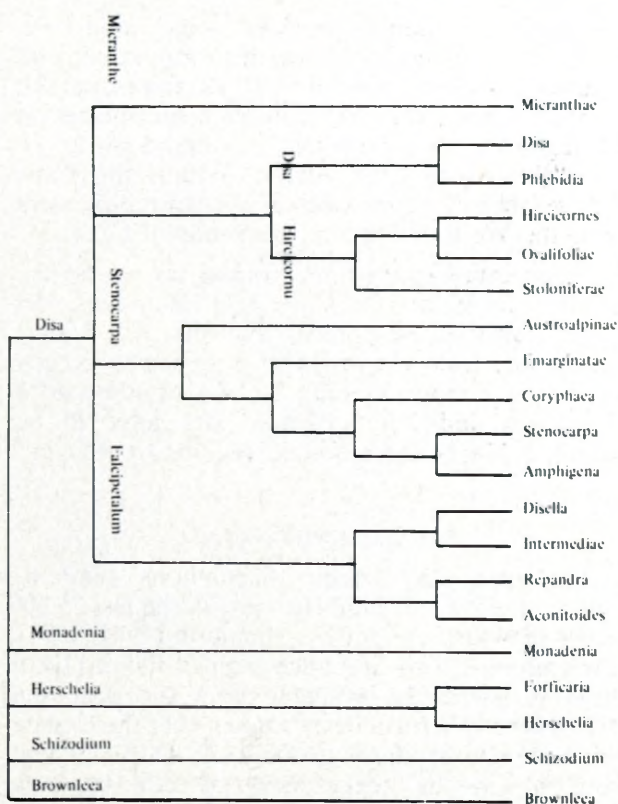


FIG. 3.—Cladogram of the Disinae, according to Linder (1982).

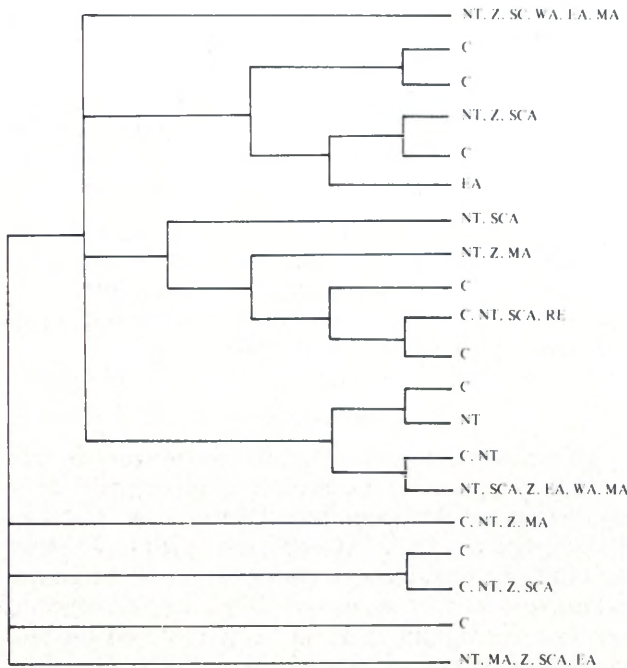


FIG. 4.—Area cladogram of the Disinae, based on Fig. 3. C = Cape centre; NT = Natal-Transvaal centre; SCA = South-Central African centre; EA = East African centre; WA = West African outlier; MA = Madagascar; RE = Reunion.

Africa are represented in the Natal-Transvaal centre. However, in some of the sections there is differentiation at the series level between the Natal-Transvaal centre and the South-Central African Centre; (c) There is one section endemic to the high mountains along the western Rift Valley; (d) There are no sections or series endemic to Madagascar or to West Africa.

Specific vicariance provides some interesting information. *Disa borbonica*, the only species on Reunion, is closely related to *D. vaginata* from the Western Cape, while the only endemic species on Madagascar, *Disa incarnata*, is very near to *D. scutellifera* from East Africa. Within the Cape Centre, there are nine cases of species replacement from the Western Cape to the Southern Cape.

These data indicate three 'source' regions for the Disinae in Africa (the Cape fold mountains, the Natal-Transvaal escarpment and the Rift Valley mountains) from where the taxa spread to occupy their present range. Possibly the watershed between the Zaire and Zambezi may also have to be included. Maybe these 'source' regions are refugia.

PALAEOENVIRONMENTS

The data on climatic fluctuations (and by inference environmental changes) in the last 25 000 years in Africa are patchy. Hamilton (1974, 1976), Livingstone (1975) and Nicholson & Flohn (1980) have reviewed the available data for East and North-central Africa. They suggest that the climate was cold and dry from 10 000 to 25 000 years ago, resulting in the replacement of Afro-montane vegetation (the habitat of the Disinae) by dry savanna grassland. Between 10 000 and 1 000 years

ago the present Afro-montane regions were occupied by Afro-montane forest, possibly with patches of Afro-montane grassland. The present large expanses of Afro-montane grassland possibly only date from the advent of iron-smelting, leading to the rapid decimation of the forests (Chapman & White, 1970; Hall & Medler, 1975; Hall 1971). This could mean that the mountains of West Africa did not have suitable habitats for Disinae until either 10 000 years B.P. or 1 000 years B.P., whereas the higher and more extensive mountains of East Africa are more likely to have maintained at least some suitable habitats. The data for South-Central Africa are lacking. Scott in this symposium showed that for the Transvaal between 30 000 and 10 000 years B.P. sclerophyllous vegetation, possibly Drakensberg macchia, was more widespread. This could mean that the habitat for the Disinae was more widespread during this period, as several species are at present associated with macchia. For the Cape Region, Martin (1968) and Schalke (1973) suggested that prior to 30 000 years B.P. the Knysna forests were widespread. Evidence from archaeological work indicates that during the last glacial (10 000 to 25 000 years ago) conditions were colder and drier, leading to the replacement of the forests by grasslands (Klein, 1972; Parkington, 1978), which were replaced by scrubby vegetation after the glacial. It appears unlikely that these fluctuations could have led to the loss of the characteristic Cape flora from the Cape fold mountains, or to the disappearance of the Afro-montane vegetation from the Drakensberg, whereas this could well have been the case on the lower mountains, such as the mountains of the Eastern Cape Province.

These data and interpretations corroborate the historical scenario suggested in the previous section, as it appears to be unlikely that the Disinae lost their habitats in the Cape fold mountains and the South African Drakensberg during the Pleistocene, whereas most of the available, if not all, habitat was lost in West Africa and East Africa, probably with the exception of the high Rift Valley mountains.

CONCLUSIONS

The overall distribution of the Disinae in Africa is determined by their biology. On this basis, they may be described as a temperate African element.

It is not possible to determine where the Disinae originated. This appears to have been obscured by the vagility of the taxa. However, three, and possibly four, refugia can be determined. These are the Cape fold mountains, the South African Drakensberg and the East African Rift Valley mountains, with a fourth possible refugium on the watershed between the Rivers Zaire and Zambezi. These areas are characterized by high levels of endemism at the specific level, and endemism at the sectional level. Present palaeoenvironmental interpretations indicate that it is unlikely that the temperate habitat was entirely lost from these regions during the last glacial, while the less mountainous areas appear to have been quite arid. When the climate ameliorated about 10 000 years ago, these refugia acted as source areas, from where

the Disinae spread into West Africa, Zimbabwe, Madagascar, Reunion and possibly South-Central Africa (Fig. 5).

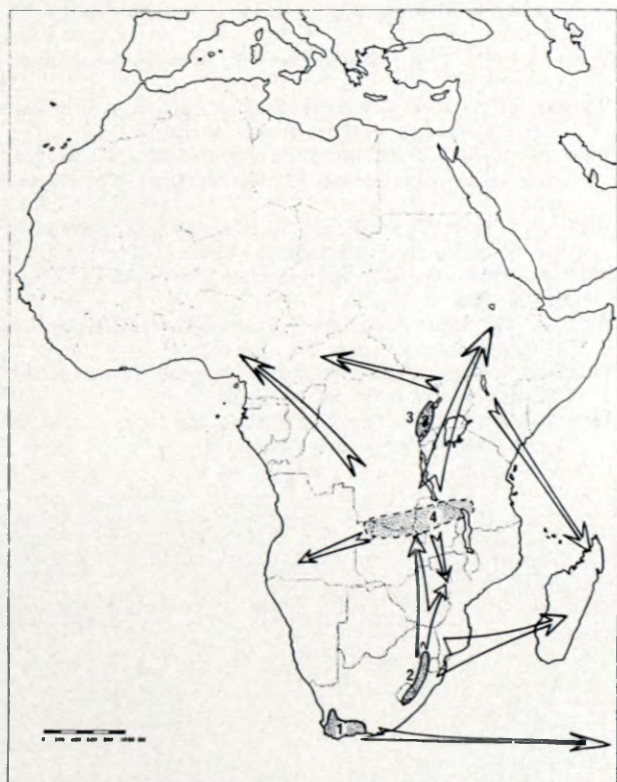


FIG. 5.—Suggested Pleistocene 'refugia': 1 = Cape fold mountains; 2 = South African Drakensberg; 3 = East African Rift mountains; 4 = possible refugium on the watershed between the rivers Zaire and Zambesi. The arrows indicate the probable directions of post-glacial migration.

This may well be a general pattern for African temperate plants, and analyses done on the Pooidae (Clayton, 1976), the Compositae of Natal (South Africa) (Hilliard, 1978) and the Cupressaceae (Kerfoot, 1975) corroborate this hypothesis.

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