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Aspects of the phytogeography of African Pteridophyta

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ABSTRACT

A diversity of distribution patterns exhibited by African pteridophytes on intercontinental and continental scales are presented. Occasional random dispersal among the Pteridophyta over long distances is accepted. The ecological importance of the gametophyte phase is inferred. Future progress in the elucidation of African fern phytogeography will require a broader alpha-taxonomic pan-African base and the plotting of many more distribution maps.

RÉSUMÉ

ASPECTS DE LA PHYTOGÉOGRAPHIE DES PTÉRIDOPHYTES AFRICAINS

Une diversité de modes de distribution montrée par les ptéridophytes africains sur des échelles intercontinentales et continentales est présentée. Une dispersion occasionnelle due au hasard parmi les Ptéridophytes sur de longues distances est acceptée. L'importance écologique de la phase gamétophyte est présumée. Les progrès à réaliser dans la connaissance de la phytogéographie des fougères africaines nécessiteront une base pan-africaine alpha-taxonomique plus vaste ainsi que l'établissement de beaucoup plus de cartes de distribution.

INTRODUCTION

Although the spores of pteridophytes are small in comparison to the seeds of most angiosperms and could be liable to widespread dispersal by wind, many African pteridophytes exhibit distribution patterns similar to those of some African angiosperms. As in angiosperms there are endemic species in various habitats and in various regions. At the other extreme there are pantropic fern species as well as those occurring in two continents.

Phytogeographic concepts are immediately suspect unless there are sound taxonomic data bases. There are few critical world wide revisions of pteridophyte genera; consequently the data presented and used in this paper has been investigated and evaluated by the author.

DISTRIBUTION PATTERNS OF SOME WORLD-WIDE SPECIES COMPLEXES

Dryopteris wallichiana is a large and conspicuous fern confined to mountain habitats in many parts of the world. It has a distribution ranging through the Himalayas and high mountains of Sri Lanka, south east Asia, the Hawaiian islands and the mountains of central America and along the Andes. In the African region, it is only known from Inyangani Mountain in Zimbabwe in the shade of *Widdringtonia* sp. and the highest mountain in Madagascar; it is absent from the high mountains of east tropical Africa.

A different distribution pattern is exhibited by the predominantly temperate *Asplenium trichomanes* complex. It is widely distributed in temperate south America, Europe, eastern Asia, South Africa and temperate Australia; it is apparently absent from temperate South America and the east tropical African mountains. Yet another pattern is shown by the *Hymenophyllum tunbridgense* complex, which is apparently absent from North America and Asia.

One even more puzzling distribution pattern is that exhibited by the *Polypodium vulgare* complex which is widely distributed in the northern hemisphere but which is only represented in the southern hemisphere in South Africa and on Kerguelen Island in the Indian Ocean. Other species, such as *Doryopteris concolor*, are virtually confined to the southern hemisphere.

SOME OTHER INTERCONTINENTAL DISTRIBUTION PATTERNS

The *Polypodium polypodioides* complex is widespread in the Americas and is represented in south and east Africa by *P. polypodioides* subsp. *ecklonii*. *Asplenium platyneuron* exhibits a similar but more restricted range in eastern North America and South Africa. *Woodsia montevidensis* which is widespread in South America is confined in Africa to the Natal Drakensberg. Conversely, *Cyathea capensis*, which is widespread in southern Africa, is restricted in South America to a small area in south eastern Brazil. Among the strictly tropical species common to the Americas and Africa, it is interesting to note comparable wide variation in frond dissection in the South American and west African populations of *Ctenitis protensa*.

A number of African fern species also occur in Asia. Some, such as *Nephrolepis acutifolia* and *Lindsaea odorata*, are widespread in south east Asia but are only known from a few localities in tropical Africa and the Mascarene Islands. Others can be regarded as African species with outliers in Asia; an example is *Pellaea angulosa* from East Africa and the Mascarenes which also occurs in Sri Lanka and the southern tip of India.

Among the more temperate South African ferns, *Todea barbara* is represented by a possibly distinct subspecies in south eastern Australia and New Zealand. At even more southerly latitudes, the cold temperate, south circumpolar *Grammitis poeppigiana* only occurs on the African continent on two high mountain summits near its south western extremity.

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The world-wide distribution of many of the species still needs to be plotted, after critical taxonomic evaluation, before clear trends in patterns can be expected to emerge. However, it is apparent from the available evidence that there is more diversity in distribution patterns among the pteridophytes than one would initially expect in a group with presumably wind-dispersed spores.

DISTRIBUTION PATTERNS OF FERNS IN AFRICA

Many montane pteridophytes in Africa exhibit a basic distribution pattern through the east tropical African mountains with outliers to the west (Cameroon Mountain, Fernando Po) southwards to the Natal Drakensberg in South Africa, frequently also in the mountains of Madagascar, and often in the Comoro and Mascarene Islands. Such a pattern is exhibited by *Elaphoglossum hybridum* (Schelpe, 1968). A similar pattern is exhibited by the more subalpine *Xiphopteris flabelliformis* (Schelpe, 1968) of which only depauperate plants occur at the southernmost extremity of its range in the high Drakensberg. The large forest fern *Didymochlaena truncatula* has interesting outliers in northern Angola and Zaire.

Among the species from drier habitats, many ferns such as *Pellaea pectiniformis* (syn. *P. goudotii)* (Schelpe, 1968) have a predominantly south east African distribution with outliers in the Huilla Plateau of Angola or in the mountains of South West Africa/Namibia. Comparable outliers are exhibited by the marsh fern, *Thelypteris confluens* (Schelpe, 1968). Discontinuities among the African ferns vary considerably in distance and in direction. An intriguing pattern of discontinuities is that shown by *Adiantum reniforme* with isolated populations in the Canary Islands, northern Kenya and Malawi and with a subspecies in Madagascar.

Although long-distance wind dispersal in many directions cannot be discounted, it appears that many of the disjunctions are more likely to have resulted from climatic change.

ENDEMIC SPECIES

Christensen (1932), in the absence of a then up to date enumeration of African Pteridophyta, considered that two thirds were 'known in this part of the world only' and that 'with some few exceptions these endemic species are closely related either to American or Asiatic ones or belong to groups richly represented throughout the Tropics'. Despite the publication of a number of regional monographs on the African pteridophytes, only a few families have been revised on a continental scale for Africa south of the Sahara (Holttum, 1974; Launert, 1968; Schelpe, 1969). An up to date checklist is still not available.

In the same publication, Christensen (*l.c.*) estimated that about 46% of the pteridophytes of Madagascar are endemic. Regional endemicity in continental Africa is much lower. For example, in the Flora Zambesiaca area (Schelpe, 1970) only 3,7% of the pteridophyte species are endemic. In the Flora of Southern African area the percentage endemicity of the pteridophyte flora is about 19%. However, it is interesting to note that many of the distinct Southern African endemic species occur not only in the semi-arid areas (Schelpe, 1956) but also in fynbos, woodland and coastal forest. Also noteworthy, is that the nearest relatives of the localized southern Karoo endemic species, *Pellaea rufa* occur along the western sides of North and South America (Tryon, 1957).

DISCUSSION

It is accepted that long distance wind dispersal of pteridophyte spores can occur. No other reasonable explanation can be postulated for the occurrence (Tryon, 1970) of the South American fern *Eriosorus cheilanthoides* on Tristan da Cunha and Gough Islands in the South Atlantic Ocean, some 3 200 km from its nearest known American locality. Concurrently, one must ask why no other fern species from that locality in South America reached these oceanic islands and became established there.

More recently, it has become apparent that a *random* sample of six species of southern South African ferns has become established on Amsterdam Island (S. Indian Ocean, 38°S latitude) which is less than a million years old. In contrast, only two species of ferns known from southern South Africa have become established on the geologically much older Indian Ocean island of Kerguelen (47°S latitude). *Lycopodium cernuum,* widespread in South Africa, occurs around hot springs (46°C) on St Paul Island (39°S latitude) in the Indian Ocean.

Although these examples indicate the likelihood of random long-distance wind dispersal of spores at the northern limit of prevailing westerly winds, it raises the whole complex issue of the establishment of a foreign pteridophyte on new soil. Not only must the spore be transported over long distances, it must land on a substrate suitable for the germination into a gametophyte, and after fertilization to form a sporophyte. To perpetuate in its new location, conditions have to be suitable for both the gametophytic and sporophytic phases of the life history, even if apogamy is involved. However, should climatic conditions change adversely for the gametophytic stage, the sporophytic stage may well continue to exist and even multiply vegetatively. It is thought that this may well apply to populations of *Ophioglossum polyphyllum* in the Namib Desert.

A comparable case is the behaviour of fern sporophytes introduced and cultivated outdoors in a different climatic regime. For example, in the National Botanic Gardens at Kirstenbosch, which experience a winter rainfall regime, there are vigorous sporophytic plants of South African summer rainfall area ferns which never, or very rarely, produce young sporophytes. In fact, the absence of young sporophytes in a fern population would indicate that a species in a particular locality is veering towards extinction in that locality. However, a difficulty arises since few collectors attempt to gather a range of juvenile sporophytes.

The spread of ferns introduced by human activities to new continents can provide a measure of what could result from a chance long distance dispersal to a far off congenial habitat. An historical study of records of the conspicuous 'silver backed' South American fern *Pityrogramma calomelanos* (Schelpe, 1975) showed how rapidly a fern species could spread from foci of introduction and even become weeds.

The evidence available at present concerning the phytogeography of the pteridophytes in general, and the African representatives in particular, is meagre and often confusing, but indicates probabilities and possibilities. Pteridophyte taxonomists are a rare breed and relatively few of them have the opportunity or show an inclination to devote their research potential to revision, let alone monographs, of major groups on world wide or even continental scale. Progress in alpha-taxonomic evaluations on a broad scale and the plotting of distribution maps based on the data emerging from such studies form a prerequisite for future phytogeographical interpretation.

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