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Cladistic Biogeography of Afromontane Spiders

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Abstract

The application of cladistic data is seen as crucial to answering questions regarding the definition, mode of origin and age of historical biogeographic patterns. From the cladograms and distributional data for four groups of afromontane spiders [*Microstigmata* (Microstigmatidae), the *Moggridgea quercina* group (Migidae), and the subfamilies Vidoleini and Phyxelidini (Amaurobiidae)] a set of nine disjunct areas of endemism is defined for African and Malagasy forests. Taxon/area cladograms are combined through a parsimony method to produce a general area cladogram. General conclusions are: (1) Madagascar is related to eastern Africa and/or eastern South Africa rather than being the sister area to all of Africa; (2) eastern South Africa shows affinities with tropical Africa rather than with the nearby Cape region; (3) the Cape region of South Africa is highly distinctive; and (4) the area cladogram is hard to reconcile with historical scenarios involving primarily dispersal or Pleistocene vicariance events, and a Mesozoic origin for parts of the biogeographic pattern for afromontane spiders is possible.

Introduction

The forest biota of Africa is known for its heterogeneity. The existence of several biotic patterns has been suggested, including centres of endemism and gradients in species richness within unbroken blocks of forest, and the presence of distinct, disjunct montane and alpine forest islands surrounded by a sea of lowland forest. Since patterns of species richness and endemism in African forests were first recognised (Lönnberg 1929), their origin has frequently been attributed to the general effects of climatic changes on the distribution of forests. Acceptance of the reality of such patterns has not been unanimous, and the historical biogeography of African forests continues to be the focus of a lively debate. I perceive that three foci of controversy repeatedly emerge in biogeographic analyses of the African forest biota: (1) the reality of biogeographic patterns and definition of areas of richness and endemism; (2) the mode of origin of recognised patterns; and (3) the age of recognised patterns. Virtually all previous analyses relevant to these questions have been conducted under what I term the 'phenetic paradigm' in historical biogeography. This paper briefly summarises and critiques the phenetic paradigm and discusses why it is inadequate to address historical questions. It outlines the alternative 'cladistic paradigm' that offers greater hope of recognising and defining patterns and elucidating historical processes. Finally, as an example of the cladistic approach, it focuses on framing and answering these three questions with regard to the remarkable cool-temperate or 'afromontane' forest biota using cladistic data from several groups of spiders.

Paradigms in Historical Biogeography

Phenetic Paradigm

The majority of attempts to understand the historical biogeography of the forest biota of Africa have been undertaken under what I call the phenetic paradigm utilising lengthy

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tabulations of numbers of widespread species in common between the area of interest and other areas (e.g. Keay 1954; Gillet 1955; Morton 1972; Cole 1974; Hall and Medler 1975; Wild 1975; Diamond and Hamilton 1980; Struhsaker 1981; Stuart 1981; Rodgers *et al.* 1982). I refer to this approach as phenetic through analogy with phenetics in taxonomy because of the primacy given to estimates of overall similarity among the objects (taxa, areas) to be classified. Under this paradigm, data to assess the relationships among areas are the presence or absence of taxa, with widespread species considered informative and absence treated in the same way as presence. Cladistic interrelationships among taxa are usually not specified because they are not recognised as relevant. Historical relationships among areas are estimated by assuming that recency of common connection is directly proportional to the number of taxa in common.

While very useful in the description and comparison of biotas, the varied ages, ecological requirements and dispersal capacities of the individual species making up these biotas make phenetic assessments of the relationships among biotas difficult to interpret historically. Estimates of overall similarity do not accurately reflect historical relationships (Farris 1981), but are highly sensitive to the effects of local extinction or differentiation which may be unrelated to the common history of areas. The widespread taxa which provide the basic comparative data in phenetic biogeography may simply represent a failure to respond to historical events, and therefore not represent the common histories of areas. In this respect they are analogous to plesiomorphic characters in taxonomy (Nelson and Platnick 1978). The very data that may be most relevant to the common history of areas, the allopatric distributions of related lineages, are usually excluded from comparison. In short, the basic datum of phenetic biogeography, the species list, seems inadequate as a tool for historically meaningful comparisons of two or more areas.

Cladistic Paradigm

In the cladistic method (Nelson and Platnick 1981; Humphries and Parenti 1986), sister-group relationships among taxa endemic to different areas form the primary source of information about the relationships among areas. It assumes that (*a*) differentiation results primarily from the fragmentation of formerly continuous biotas through the action of barriers; (*b*) the increasing age of former connections among areas may be estimated by relationships of greater inclusivity on a cladogram of taxa endemic to those areas; and (*c*) by combining cladograms of taxa endemic to a set of areas a general cladogram for those areas may be proposed. The cladistic method has a number of advantages: (1) the independent assessment of the cladistic relationships of the taxa providing the raw data insures that we are dealing with natural groups; (2) it provides an unambiguous statement about the sequential, historical relationships among areas and, because of this, the dating of any part(s) allows relative dating of other parts; and (3) the 'signal' is less subject to being obscured by 'noise' (widespread taxa, absence of data).

Cladistics is just beginning to be applied to studies of African biogeography (e.g. Griswold 1985, 1990; Smiles 1985; Anderberg 1986; Louw 1986; Willassen and Cranston 1986; Endrödy-Younga 1988). Each of these studies deals with a single taxon, and the set of area relationships specified by each taxon has not yet been tested for generality. It is only when a set of area relationships is shown to be general (i.e. common to two or more taxa) that parsimony favours the hypothesis of common cause over unique, chance explanations, and historical biogeography becomes a predictive as well as descriptive science. As a model for the use of the cladistic paradigm in historical biogeography, I would like to focus on the remarkable 'afromontane' biota, and apply this method toward answering the three crucial questions regarding the definition, mode of origin, and age of this pattern.

Cladistic Biogeography and the Afromontane Biota

The Afromontane Biota

The existence of a distinct, homogeneous, and strikingly disjunct montane forest biota has been apparent to many workers. Among the earliest to document such as pattern were Carcasson (1964) in a study of African butterflies, and Moreau (1966) in his comprehensive study of the bird faunas of Africa. It was White (1978) who, in a study of forest trees, first used the term 'afromontane'. According to White (1983*b*) the afromontane region is an 'archipelago-like centre of endemism' occurring primarily above 2000 m altitude in the tropics but occurring at lower elevations where oceanic conditions ameliorate the climate (as in the West Usambara Mountains in Tanzania) and extending nearly to sea level in the temperate latitudes of South Africa. The afromontane archipelago is scattered from the mountains of Sierra Leone in the north-west to Somalia in the north-east, and from Sudan in the north to the Cape Province of South Africa in the South (White 1983*b*: fig. 14). Typical of the afromontane region are tree ferns (*Cyathea*), the plant family Oliniaceae, and the plant genera *Podocarpus* (Podocarpaceae), *Curtisia* (Cornaceae) and *Xymalos* (Trimeniaceae).

Defining the Afromontane Biota

Although many workers have recognised a distinct upland forest biota (Carcasson 1964; Moreau 1966; White 1978, 1983*b*; Stuart 1981; Feijen 1983; Dowsett 1986), others have suggested that there is no clear altitudinal boundary between lowland and montane biotas (Bigalke 1968; Diamond and Hamilton 1980; Stuart *et al.* 1987; Scharff 1991). Scharff (1990) investigated the vertical distribution of linyphiid spider species along an altitudinal gradient from 300 to 1850 m in the Uzungwa Mountains in south-western Tanzania. He found that whereas there were no true forest species in common between the highest (1700–1800 m) and lowest (300–500 m) parts of the forest, species from lower and higher altitudes met in a broad zone of intermixture such that it was not possible to draw any well defined borderline between a highland and lowland biota. Stuart *et al.* (1987) also found a very wide altitudinal zone of overlap between lowland and montane bird species. Delimitation of distinct biotas based upon the altitudinal distribution of single species has been unsuccessful. Perhaps the definition of an afromontane biota based on the phylogenetic relationships among its component taxa will be more successful than one based on their ecology. The question is not whether a species occurs above or below a certain altitude, but whether there is a pattern of sister-group disjunctions among isolated mountains.

Mode of Origin of the Afromontane Pattern

There is much debate regarding the relative contributions of general (i.e. vicariance) and unique (i.e. dispersal) historical factors to the creation of present-day patterns in the African forest biota. A profound influence has been attributed to the general effects of climatic changes which led to the dissection of forest into restricted patches during times of aridity and their subsequent coalescence during humid periods. Such a cyclical, climate-driven 'refugium' scenario is widely believed to have led to the complex biotic patterns currently observed within otherwise homogeneous forest (Carcasson 1964; Bigalke 1968; Grubb 1978, 1982; Diamond and Hamilton 1980; Struhsaker 1981; Stuart 1981; Rodgers *et al.* 1982; Mayr and O'Hara 1986). Whereas the refugium scenario as applied to Africa deals specifically with the origin during the Pleistocene of centres of endemism and gradients in species richness within lowland forest, conceptually it is equally applicable to the cyclical establishment and severance of contact between afromontane forest blocks. Acceptance of this model is not unanimous. Livingstone (1982) judged the palaeoecological evidence insufficient to support the concept of large forest blocks under conditions of Pleistocene aridity in East Africa, and both he and Hamilton (1976) suggested that dispersal played an important role in establishing the distributions of modern forest animals and plants.

A fresh approach that focuses on the phylogeny and distribution of component groups may illuminate this problem. Any causal explanation for biotic patterns invoking the primacy of unique events (i.e. dispersal) would not be expected to produce replicated sets of sister-group relationships among the areas making up the pattern. On the other hand, a vicariance scenario which involves sequential fission and coalescence of areas implies a specific set of hierarchic relationships among those areas which should be general. This could be tested through an area cladogram inferred from taxon cladograms. Indeed, the different phylogenetic patterns (or lack thereof) implied by different historical scenarios may be an effective and telling way to test their validity.

Age of the Patterns Within the Afromontane Biota

The presence of temperate montane forest in Africa can be documented well back into the Tertiary. Typically afromontane Monimiaceae are known from the late Cretaceous of South Africa (Mädel 1960), and fossil floras containing many taxa currently typical of afromontane forest are known from the South African Eocene (Phillips 1927; Adamson 1931). The palaeobotanical record from tropical Africa is not as complete, but Ethiopian Miocene *Podocarpus* fossils suggest widespread distribution of afromontane forest type in Africa at least by the mid-tertiary (Lemoigne and Beauchamp 1972). Forest containing many taxa which are today components of afromontane formations would seem to have been established in Africa at least at the beginning of the Tertiary (Axelrod and Raven 1978).

At least two bouts of aridification separated by several million years have been suggested, and both could have caused forest dissection leading to patterns within the forest biota. Past cycles of Pleistocene humidity and aridity (Van Zinderen Bakker and Coetzee 1988) in moist forest regions are well documented for southern, central and eastern Africa (Coetzee 1964; Morrison 1968; Kendall 1969; Van Zinderen Bakker and Coetzee 1972; Livingstone 1975; Van Zinderen Bakker 1976; Hamilton 1982; Scott 1982, 1984; Butzer 1984; Deacon *et al.* 1984; Thomas and Goudie 1984). Acceptance of the pre-eminent influence of these late Pleistocene climatic changes in shaping modern patterns in forest biota has been nearly unanimous (e.g. birds: Moreau 1966; Diamond and Hamilton 1980; Stuart 1981; Jensen and Stuart 1986; mammals: Booth 1958; Bigalke 1968; Grubb 1978, 1982; Struhsaker 1981; Rodgers *et al.* 1982; butterflies: Carcasson 1964), though some workers caution that late Quaternary events may not suffice to account for the complexity of patterns (Carcasson 1964, White 1983*a*; Griswold 1990; Scharff 1991).

Pleistocene climatic changes were not the first to affect Africa, and the possible effects of earlier events upon biotic distribution must be considered. Evidence of vegetational change during the Tertiary is sketchy, but studies from South Africa (Coetzee and Rogers 1982; Coetzee and Muller 1984) and tropical East Africa (Andrews and Van Couvering 1975; Bonnefille 1985; Retallack *et al.* 1990) suggest persistence of general forest cover into the mid-Tertiary that was then fragmented due to increasing aridity during the Miocene, presumably with profound evolutionary and biogeographical consequences (Laporte and Zihlman 1983), with the possibility of similar episodes occurring at intervals since the Cretaceous (Brain 1984).

Similar sets of evolutionary pressures (e.g. dissection of forest into isolated patches during periods of aridity) acting upon biotas under different geographic configurations would be expected to lead to different sets of biogeographic patterns. The Pleistocene desiccation took place in an Africa with modern topography, whereas the Miocene–Pliocene desiccation took place prior to or coincident with significant changes in African topography [e.g. uplift along the Natal Monocline in South Africa (King 1982); marine incursion during the Pliocene in the Uitenhage basin effectively isolating the eastern and western parts of the Cape Province of South Africa (King 1972); volcanism in East Africa which produced major lakes, e.g. Lake Victoria (Kendall 1969), and mountains, e.g. Kenya, Kilimanjaro and Meru (Grove 1983)]. Consideration of the age and mode of origin of biogeographic patterns must encompass the whole history of a biota, recognising at least the possibility of a palimpsest of ancient patterns interwoven among more recent. The application of phylogenetics to African forest biogeography will help to unravel the effects of general causes of differing ages and isolate and identify those patterns which could be attributable to stochastic (e.g. dispersal) causes.

Cladistic Biogeographic Analysis of Afromontane Spiders

Taxon Cladograms

Within this theoretical framework for the use of cladistics in historical biogeographic analysis, cladistic data from several groups of spiders can be used to define and investigate the age and mode of origin of the afromontane biota. The particular spider taxa were chosen for revision because each was largely or wholly restricted to afromontane forest and each was made up of many narrowly distributed, monophyletic groups. The spider taxa revised exhibit a variety of lifestyles, and include cursorial hunters (Microstigmatidae), fossorial ambushers (Migidae), and terrestrial and aerial web-builders (Amaurobiidae).

The family Microstigmatidae includes small to minute mygalomorphs occurring in leaf litter, beneath stones and logs, and within wet, rotting logs in moist forests. The African genus *Microstigmata* is currently known only from the eastern part of South Africa, where endemic, montane forest species in the Zuurberg Mountains, Amatola Mountains, Transkei-Natal Midlands, and Natal Drakensberg suggest origin through vicariance events in the late Miocene to early Pliocene (Griswold 1985). These area relationships are untested by phylogenies for other taxa. Based upon the occurrence of the sister-genus *Ministigmata* in South America (Raven and Platnick 1981), I suggested Cretaceous age for the genus and predicted the occurrence of this family in tropical Africa (Griswold 1985).

The Migidae are often referred to as 'tree trapdoor spiders' because many species build remarkably well camouflaged trapdoor nests on the trunks and buttresses of trees. Biogeographic data come from the revision of *Moggridgea* (Griswold 1987). The 31 *Moggridgea* species are known only from Africa and some surrounding islands, where they occur in virtually all habitats. Of interest to afromontane biogeography are six endemic, forest-dwelling species of the *quercina* group comprising *Moggridgea teresae* Griswold, *M. quercina* Simon, *M. intermedia* Hewitt, *M. microps* Hewitt, *M. verruculata* Griswold and *M. anactenidia* Griswold.

The amaurobiid subfamily Phyxelidinae includes taxa from south-east Asia, the eastern Mediterranean, Africa and Madagascar. The majority of species occur in moist forest, although some species may be found in drier habitats, including deserts. The cladogram (Griswold 1990) reveals two clades relevant to afromontane biogeography: the tribe Vidoleini, which occurs in southern and eastern Africa, and the *Lamaika* plus *Phyxelida* groups of the Phyxelidini, which occur in southern and eastern Africa and in Madagascar. It is justifiable to treat these clades as independent with regard to the information provided on the interrelationships among afromontane areas of endemism because these clades are separated on the subfamilial cladogram (Griswold 1990: fig. 13) by the genus *Namaguarachne* which occurs primarily in arid regions and is thus not relevant to analysing afromontane patterns.

Areas of Endemism

In defining areas of endemism in African and Malagasy forests the principal criteria were the smallest coincident ranges of two species and the geographic extent of forest islands. Each species was apparently restricted to forest habitats and there was detailed sister-group information relevant to the species. Distributions of all species of the four taxa were mapped. In some cases these were a point (i.e. a species might be known only from the type locality), or they might include several to many points. A species' range was considered to encompass at least all space between the points. Coincidence in ranges was tabulated. If the ranges of two species (not sister taxa) overlapped they were considered coincident, even if one was only a point. The smallest coincident ranges were taken to define an area of endemism. The areas of forest considered here are island-like, surrounded by areas of grassland or bushveld. If a species' range encompassed only part of a forest island, the whole island was defined as an area of endemism. The distributional ranges of monophyletic taxa took precedence over topographic boundaries. If a species' range encompassed more than one forest island, the area of endemism was defined to include all forest islands within the species' range. A species was considered widespread if its range included two or more of the areas defined by the smallest coincident ranges of two other species. The areas of endemism, as circumscribed on the map (Fig. 1), may contain both forest and non-forest vegetation types. As forest typically occurs as small, discrete patches, depiction of only these patches on a map covering most of Africa would be impossible. The biogeographic discussion here is relevant only to the forest habitats within the circumscribed areas of endemism.

Following are the nine areas of endemism, along with taxa that define and characterise them.

(1) Table Mountain: this includes the forests on the slopes of Table Mountain near Cape Town. While small in area, it is noted for a high rate of endemism. Defining taxa are *Moggridgea teresae* Griswold and *Malaika longipes* (Purcell).

(2) Knysna Forest: includes large areas of forest stretching from the South African coast between Mossel Bay and Cape Saint Francis onto the southern slopes of the Outeniqua and Tsitsikamma Mountains. Defining taxa are *Moggridgea intermedia* Hewitt, *Lamaika distincta* Griswold and *Matundua silvatica* (Purcell).

Areas 1 and 2 are in the 'Cape Fold Mountains' of South Africa. The oldest of these mountains were in existence in the Permian (Truswell 1977; Halbich *et al.* 1983), and are perhaps the oldest mountains in Africa. To the east of the Knysna Forest (area 2) is the region of the Algoa Bay and the Uitenhage Basin on the southern coast of South Africa. This is a region of aridity that is thought to be a barrier to the spread of forest organisms. Its significance as an interval in the distributional patterns of forest arthropods has been discussed by Griswold (1985) and Stuckenberg (1962). To the east and north of the Uitenhage Basin the topography of eastern South Africa consists of a series of step-like, north-east to south-west trending escarpments (King 1982). Moist winds move onshore from the Indian Ocean and drop their moisture as rain or mist at the bases of these escarpments, encouraging the development of forests. Three separate escarpment forest formations may be recognised at different elevations, each isolated from other forests at lower or higher elevations by intervening grassland or bushveld.

(3) Natal–Zululand Coast: comprises coastal forests stretching up the coast from the vicinity of Port St Johns in Transkei to Zululand, and extending into the interior of Zululand (montane forest at Nkandla) as well. The northern boundary of this area is not well defined for spiders

due to the scarcity of collections from Mozambique. Defining taxa are *Microstigmata zuluense* (Lawrence) and *Moggridgea microps* Hewitt. *Themacrys irrorata* Simon, *Vidole lyra* Griswold and *Xevioso amica* Griswold also characterise this area.

(4) Transkei–Natal Midlands: comprises the area of mid-elevation forests that typically occur along misty escarpments at around 800 m elevation in the midlands of the Transkei and Natal from at least Umtata in the south to at least Kranskop on the Tugela River in the north. Defining taxa are *Microstigmata lawrencei* Griswold and *Themacrys cavernicola* (Lawrence). *Vidole helicigyna* Griswold also characterises this area.

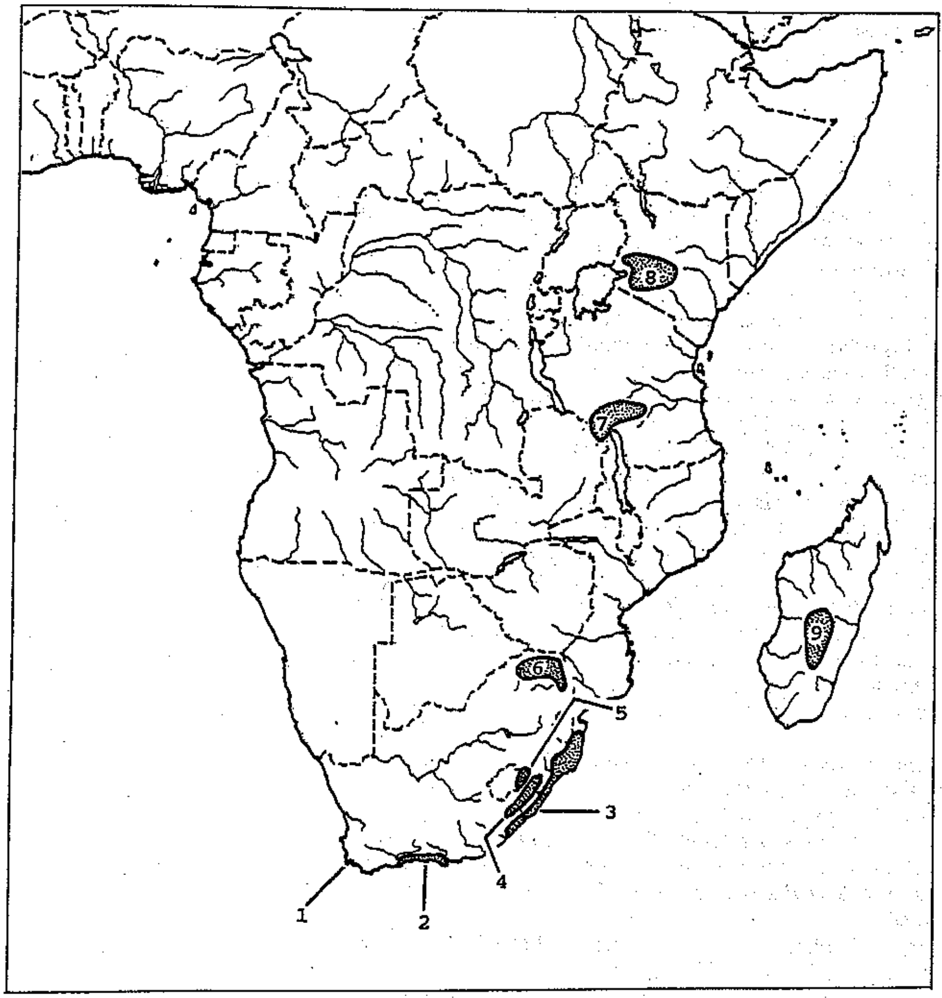

Fig. 1. Afromontane areas of endemism defined by distribution of monophyletic spider taxa: *1*, Table Mountain; *2*, Knysna Forest; *3*, Natal–Zululand Coast; *4*, Transkei-Natal Midlands; *5*, Natal Drakensberg; *6*, Transvaal Drakensberg; *7*, Eastern Arc Mountains; *8*, East African Volcanoes; *9*, Central Madagascar.

(5) Natal Drakensberg: comprises forests along the northern portion of the Drakensberg escarpment in Natal at elevations of 1000–2000 m. Defining taxa are *Microstigmata ukhahlamba* Griswold and *Themacrys ukhahlamba* Griswold.

(6) Transvaal Drakensberg: the escarpment of the Drakensberg mountains reappears in the Transvaal, where cool temperate forests occur at about 1500 m elevation along the moist eastern side. The Soutpansberg mountains in the northern Transvaal, which contain patches of montane forest, are also included in this area. The defining taxon is *Xevioso kulufa* Griswold. *Phyxelida makapanensis* Simon also characterises this area.

North of areas 1–6 lies the basin of the Limpopo River. This is another zone of aridity, comprising an ancient trough bordered on the south by Jurassic and Cretaceous faults. It has been considered a barrier to the dispersal of forest organisms that may have operated well back into the Tertiary (Stuckenberg 1962).

Two areas are defined in tropical East Africa.

(7) Eastern Arc Mountains: a series of crystalline mountains extends from south-eastern Kenya to northern Malawi. These mountains are formed along mesozoic faults (Sowerbutts 1972) and are frequently cited as being of mesozoic age. They may be the oldest mountains in East Africa. The 'eastern arc' mountains are noted for high rates of endemism and extraordinary richness (Schiotz 1981; Rodgers and Homewood 1982; Lovett 1988). Scharff (1991) found the proportion of endemism for linyphiid spiders to be much greater in the eastern arc mountains than in the volcanic mountains of Kenya and Tanzania. These mountains are thus of great biogeographic interest. For this reason I have allowed topography and geologic history to take precedence in this case over the distributions of spider taxa in defining an area of endemism. I define area 7 to include at least the uplands of the Nyika Plateau west of Lake Malawi (locality of *Phyxelida eurygyna* Griswold) and the Uzungwa Mountains north-east of Lake Malawi (locality of *Phyxelida kipia* Griswold). No taxon range defines this area. My use of the term 'eastern arc' differs from that of Lovett (1988) in that it includes Nyika in Malawi as well as areas in Tanzania.

(8) East African Volcanoes: the volcanic mountains of East Africa are far younger than the nearby eastern arc mountains, dating from the early Miocene to late Pliocene (Grove 1983). I define this area by the range of *Phyxelida pingoana* Griswold that occurs on Mount Elgon and Mount Kenya. *Phyxelida crassibursa* Griswold also characterises this area.

(9) Central Madagascar: comprises the highlands of Fianarantsoa and Tananarive Districts in the central part of Madagascar. The defining taxon is *Ambohima sublima* Griswold, and *Phyxelida fanivelona* Griswold and *P. malagasyana* Griswold also characterise this area.

Analysis

Taxon cladograms were converted to area cladograms by replacing the terminal taxon with the number for the area of endemism in which it occurred. These taxon/area cladograms were then combined using a modification of Kluge's (1988) implementation of a parsimony method for comparing area cladograms. The application of parsimony to historical biogeography treats areas as analogous to taxa and taxon cladograms as analogous to characters. The method searches for the most parsimonious hypothesis of ancestral distributions on a single cladogram for the areas of endemism assuming that the ranges of descendent sister-groups, when added together, provide the best estimate of the range of their hypothetical common ancestor. These hypothetical ancestral ranges form the characters ('syntaxa' of Kluge 1988), and are coded in an additive binary manner from the most distal to the most basal nodes on each taxon cladogram. The analysis is rooted by including a hypothetical 'outgroup' area with 0 values for all characters. This is analogous to assigning 0 values to the outgroup node in the phylogenetic analysis of taxa, and in a biogeographic analysis signifies the assumption that the set of areas are monophyletic with regard to the taxon data. The length of the resulting cladogram is measured in steps, and steps may be interpreted as vicariance events, failure to differentiate, dispersal, or extinctions.

Kluge's implementation of parsimony for historical biogeographic analysis recognises the ambiguity of area information provided by widespread taxa and deletes this potentially noisy information from consideration. Taxon cladograms were converted to reduced taxon/area cladograms by eliminating all widespread taxa and all taxa with redundant distributions if these taxa simply duplicated the hypothetical ancestral distribution specified by relatively more distal taxa. The reduced taxon/area cladograms for *Microstigmata*, the *Moggridgea quercina* group and the Phyxelidinae are depicted in Fig. 2, and syntaxa are coded in Fig. 3. Syntaxa were extracted from particular taxon cladograms: a syntaxon value of '1' was assigned for an area if that area was represented for a taxon distal to that syntaxon node, '0' was assigned if that area was represented somewhere on a given taxon cladogram but not distal to that syntaxon node, and '?' was assigned if that area was not represented on the taxon cladogram from which that syntaxon was extracted.

Results

Analysis for the nine replicated, unambiguously interrelated areas plus the hypothetical outgroup area by 17 syntaxa was done with Hennig86 (Farris 1988) using the 'ie*' routine to

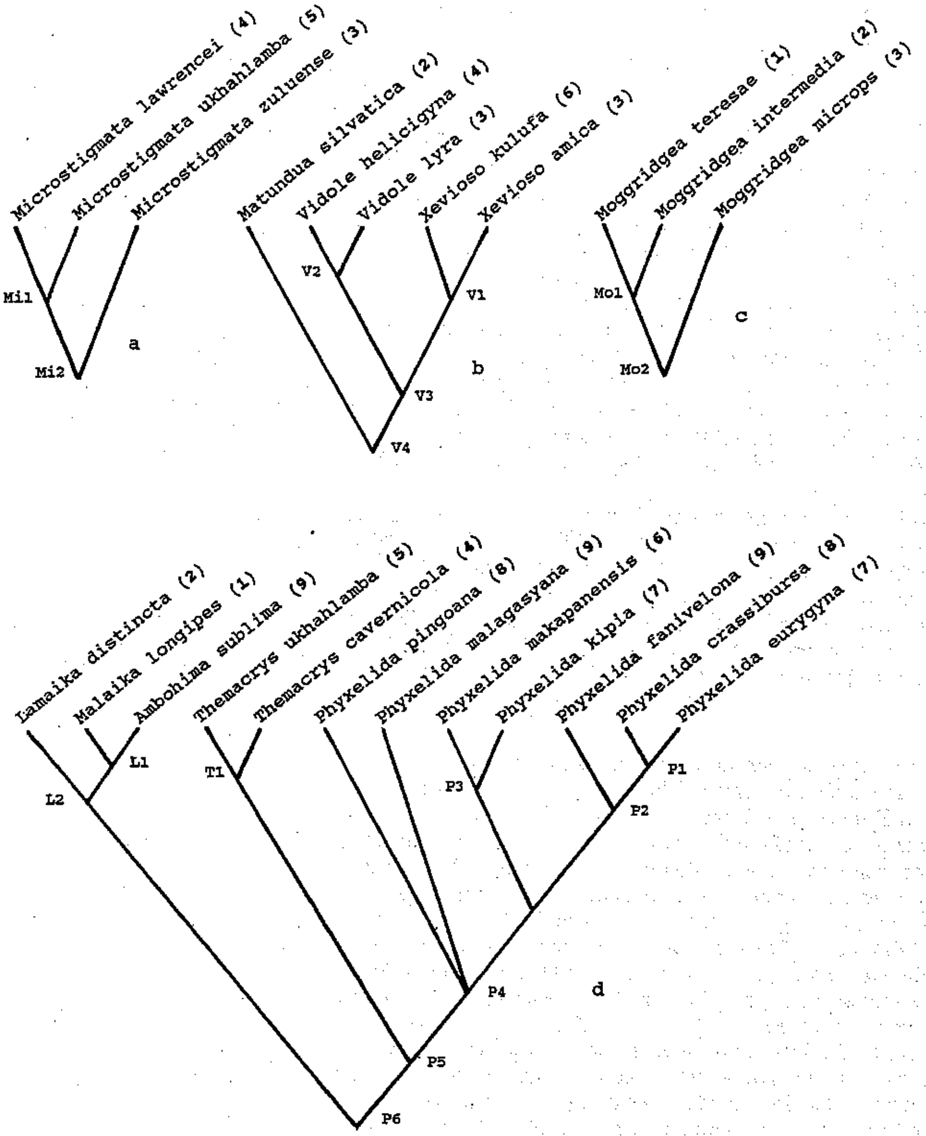

Fig. 2. Reduced taxon/area cladograms for (*a*) *Microstigmata*, (*b*), the Vidoleini, (*c*) the *Moggridgea quercina* group, and (*d*) the Phyxelidini. Numbers following terminal taxa represent areas of endemism; syntaxa are designated at nodes.

	Mo1	Mo2	Mi1	Mi2	V1	V2	V3	V4	L1	L2	T1	P1	P2	P3	P4	P5	P6
1 Table Mountain	1	1	?	?	?	?	?	?	1	1	0	0	0	0	0	0	1
2 Knysna Forest	1	1	?	?	0	0	0	1	0	1	0	0	0	0	0	0	1
3 Natal-Zululand Coast	0	1	0	1	1	1	1	1	?	?	?	?	?	?	?	?	?
4 Mid Transkei-Natal	?	?	1	1	0	1	1	1	0	0	1	0	0	0	0	1	1
5 Natal Drakensberg	?	?	1	1	?	?	?	?	0	0	1	0	0	0	0	1	1
6 Transvaal Drakensberg	?	?	?	?	1	0	1	1	0	0	0	0	0	1	1	1	1
7 Eastern Arc Mountains	?	?	?	?	?	?	?	?	0	0	0	1	1	1	1	1	1
8 East African Volcanoes	?	?	?	?	?	?	?	?	0	0	0	1	1	0	1	1	1
9 Central Madagascar	?	?	?	?	?	?	?	?	1	1	0	0	1	0	1	1	1

Fig. 3. Area by Syntaxon matrix for afromontane spiders.

give eight equally parsimonious trees of 21 steps with a consistency index of 0.80 and a retention index of 0.77. These eight trees are identical except for the placement of area 3 (Natal–Zululand Coast), which could be placed with equal parsimony at any of eight positions (Fig. 4). For graphical simplicity I present a consensus of these trees with area 3 (Natal–Zululand Coast) placed at its lowest unambiguous node (Fig. 5). Syntaxa were optimised on this tree, requiring 22 steps with a consistency index of 0.77 and a retention index of 0.72. Ambiguous optimisations were resolved to favour delayed transformations. Although this consensus tree is inferior to each of the eight trees upon which it is based, I do not believe that the precision gained by presenting all eight 21-step trees with syntaxon optimisations would be worth the space and effort. All syntaxon optimisations shown on the consensus tree (Fig. 5) were found on at least one of the 21-step trees, and the optimisations shown for 11 syntaxa (Mo1, Mo2, Mi1, V3, V4, L1, L2, T1, P3, P5, P6) were found on all eight trees.

This area cladogram (Fig. 5) has several features of interest. The basal node of the area cladogram is between the Cape region of South Africa [areas 1 (Table Mountain) and 2 (Knysna Forest)] and the remainder of Africa and Madagascar (areas 3–9). The distinctness of the Cape biota is strongly emphasised. A region south of the arid Limpopo River Basin in northern South Africa [area 6 (Transvaal Drakensberg)] shows affinities with tropical Africa [area 7 (Eastern Arc Mountains) plus area 8 (East African Volcanoes)] and Madagascar (area 9). Eastern South Africa [areas 3 (Natal–Zululand Coast), 4 (Transkei–Natal Midlands) and 5 (Natal Drakensberg)] shows affinities with tropical Africa and Madagascar rather than with the nearby Cape region. Two upland escarpment areas 4 (Transkei–Natal Midlands) and 5 (Natal Drakensberg) in eastern South Africa are sister-areas. Perhaps the most striking aspect of this area cladogram is that Central Madagascar (area 9) is related to eastern Africa [area 7 (Eastern Arc Mountains) plus area 8 (East African Volcanoes)] rather than being the sister-area to all of Africa.

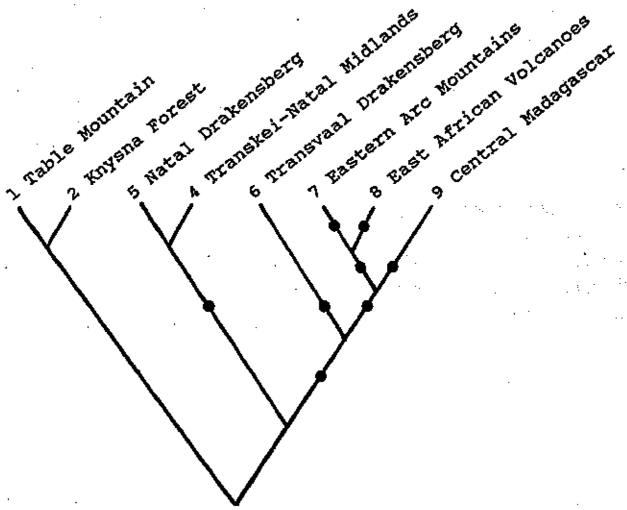

Fig. 4. Area cladogram calculated by Hennig86 showing possible positions of area 3 (Natal–Zululand Coast).

The afromontane regions of Africa do not represent a distinct biogeographic region, but rather some parts of the afromontane regions of Africa are more closely related to areas in another continent (Madagascar) than to other afromontane regions of Africa. A close relationship between East Africa and Madagascar is not confined to spiders, as a similar pattern has been suggested for several groups of plants on the basis of taxa in common (Pocs 1975; Wild 1975; Leroy 1978; Lovett 1988), and a few studies (Smiles 1985; Puff 1988) suggest explicit sister-group relationships between East African and Madagascan taxa.

The fit of the hypothetical ancestral spider distributions to this area cladogram is not perfect, and homoplasy is required for 5 of the 17 syntaxa. Kluge (1988) suggests that homoplasious syntaxa may reflect several possibilities: the terminal taxon is not a historical entity, or its sister-taxon relationships may be erroneously construed; a defined area of endemism may be a composite of areas with two or more independent histories; the geographic range of the terminal taxon may be erroneously defined; there may be unsampled taxa (uncollected taxa, or taxa that have become extinct) that are/were distributed in those areas between the apparently homoplasious occurrences of the syntaxon on the area cladogram; or dispersal may have occurred. Two instances of parallelism in syntaxa involve area 3 (Natal–Zululand Coast), suggesting that area 3 may be misdefined and have a composite history. The homoplasy for P3 between areas 6 and 7 may indicate that it was incorrect to lump Uzungwa and Nyika as area 7; or, if the area cladogram is true, dispersals may be postulated.

Homoplasies in some syntaxa (Fig. 5) may represent dispersals between those areas for which homoplasies are required (areas 3 and 6 for V1, 3 and 4 for V2, and 6 and 7 for P3). Homoplasy in syntaxon L1 (hypothetical ancestor of *Malaika longipes* and *Ambohima sublima*) might also be interpreted as dispersal of the ancestor of either one of the terminal taxa between area 1 (Table Mountain) and area 9 (Central Madagascar), but this homoplasy may be misleading or artefactual due to the present dearth of knowledge regarding the distribution and phylogeny of the afromontane spiders of tropical East Africa. In the case of *Ambohima*, its sister-taxon (*Kulalania antigua* Griswold; see Griswold 1990: fig. 13) also occurs in East Africa (in the volcanic Kulal Mountains), but as these mountains fall outside the area of endemism [area 8 (East African Volcanoes)], this sister-group relationship is not included in the biogeographic data set. In fact, for all Madagascan members of the spider taxa used in this analysis, the sister-group occurs in the mountains of East Africa. The homoplasy in syntaxon L2 (hypothetical ancester of *Lamaika distincta* and *Malaika longipes* + *Ambohima sublima*) is more difficult to interpret. Either the ancestor of either one of the terminal taxa dispersed between the Cape and Madagascar, or there is a set of extinct or extant but as yet undiscovered relatives of *Lamaika distincta* in areas 1 and 3–8.

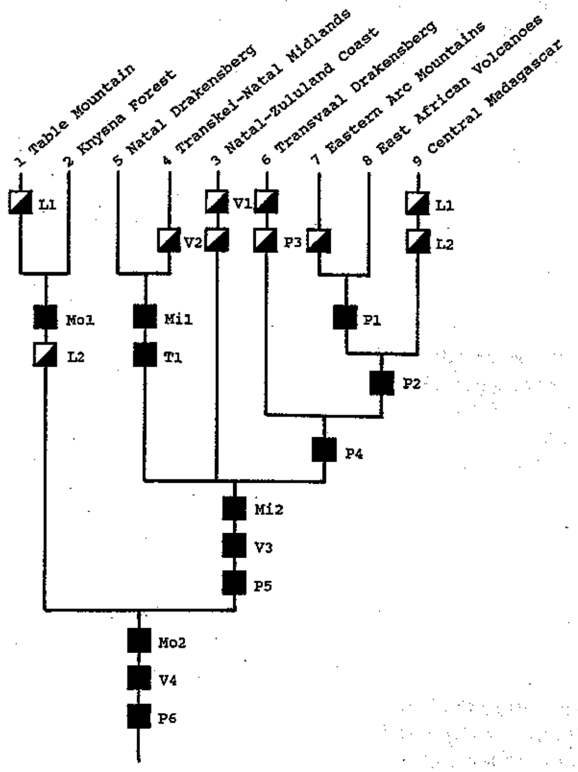

Fig. 5. Consensus area cladogram for afromontane spiders with syntaxa (hypothetical ancestral distributions) optimised. Black squares: apomorphies; half-shaded squares: homoplasies.

Discussion

History of Afromontane Spiders

The general area cladogram calculated from the cladistic and distributional data from the Phyxelidini, Vidoleini, *Moggridgea quercina* group and *Microstigmata*, provides answers to each of the three questions posed previously concerning the afromontane biota: its reality, mode of origin and age.

If we define an afromontane biota as comprising those taxa disjunct among forest patches in temperate South Africa and on mountains in tropical Africa, the four groups of spiders treated here clearly describe such a pattern. The nine areas of endemism (Fig. 1) defined by the distributions of spider taxa coincide with several of the afromontane areas depicted by White (1983*b*: fig. 14).

The set of area relationships specified by the spider distributions may be considered to be general, suggesting origin through events affecting many components of the biota simultaneously. Little homoplasy in hypothetical ancestral distributions is necessary for these data, and it is these exceptions that may be explained as dispersals.

Finally, some nodes on the area cladogram correspond with possible barriers of known age and allow suggestions of the ages of parts of the pattern. The area cladogram is hard to reconcile with a historical scenario involving primarily Pleistocene vicariance events. A Pleistocene vicariance scenario in which forest expanded and contracted in an essentially modern Africa suggests that geographic proximity of disjuncts should be a good predictor of sister-area relationship. Such is not the case as areas 1+2 (the Cape Region of South Africa), are not the sister-areas of 3, 4 and 5 (eastern South Africa), and all of Africa (areas 1–8) is not an area distinct from Madagascar. I have previously suggested (Griswold 1985) that a species characteristic of area 4 (*Microstigmata lawrencei*) may have originated at the Miocene–Pliocene boundary and, if this is true, the age of the disjunction between areas 4 and 5 should be as old or older than this. The disjunction between area 1 (Table Mountain) and area 2 (Knysna Forest) may date from forest dissection in response to Pleistocene climatic changes documented in the southern Cape (Schalke 1973). A vicariance interpretation of the sister-area relationship between Madagascar and East Africa implies great age for the taxa involved. Rabinowitz *et al.* (1983) suggested that the separation of Africa and Madagascar began during the Jurassic (approx. 165 my) and that Madagascar had reached its present position by the mid-Cretaceous (approx. 121 my). Whereas no evidence exists to challenge this estimate for the age of the Indian Ocean between Madagascar and East Africa it is not clear that this was the only route of biotic communication between these areas.

Briggs (1989) has recently suggested possible biotic connections between Africa and Madagascar via India and an emergent Seychelles Bank that may have continued through the Late Cretaceous. Great age does not necessarily rule out the possibility of vicariance for spiders, as spiders may be extremely ancient, with fossils of modern superfamilies and families known from the Lower Cretaceous (Selden 1989, 1990). Nor is this the only case in which spider distributions may be explained by mesozoic events. Platnick (1976) presented an example in which an apparent late Cretaceous vicariant event separated sister-groups within a genus of gnaphosid spiders.

Testing Hypothesis of Biogeographic History

An area cladogram conveys an implicit prediction regarding the place of occurrence and sister-group relationships of as yet undiscovered taxa. The known distributions of *Microstigmata* and the *Moggridgea quercina* group are mapped on the area cladogram (Fig. 6). The area cladogram predicts that species of *Microstigmata* should be discovered in East Africa and Madagascar. It also predicts that members of the *Moggridgea quercina* group should be discovered in East Africa and Madagascar and that, if the area cladogram is true, these should be more closely related to one another and to species from eastern South Africa than to species from the Cape.

This method also permits us to compare alternative hypotheses. We may ask how well the spider data fit a scenario for Pleistocene vicariance of afromontane forest. Although detailed interpretations may differ regarding the timing and geographic scope of events, the prevailing opinion among palaeoecologists and biogeographers is that climatic changes during the Pleistocene, particularly changes in temperature and rainfall related to glacial advance and retreat, affected the distribution of the afromontane forest biota. Altitudinal zonation of vegetation belts on mountains moved up and down, and forest patches expanded and contracted.

Furthermore, by some means, communication among what are today disjunct patches of forest was at times much easier, and large geographic areas may have supported common afromontane biotas. At the end of the Pleistocene, or shortly after, biotic exchange among patches became unlikely, leading to the present pattern of disjunct distributions. In this scenario geographic proximity of disjuncts should be a good predictor of sister-area relationship.

There has been no explicit statement of the set of area relationships predicted by this Pleistocene scenario, but I will venture to offer one. Based upon geographic proximity of areas of endemism and the distributions of zones of aridity that may have acted as barriers, I predict the following area cladogram (Fig. 7) containing five components. *A*: southern Cape Fold Mountains west of Algoa Bay and Uitenhage Basin, areas 1 and 2; *B*: eastern southern Africa east of Algoa Bay and Uitenhage Basin and south of the Limpopo, areas 3, 4, 5 and 6; *C*: Africa south of the Limpopo, areas 1–6; *D*: tropical East Africa, areas 7 and 8; and *E*: Africa, separated from Madagascar by the Indian Ocean, areas 1–8.

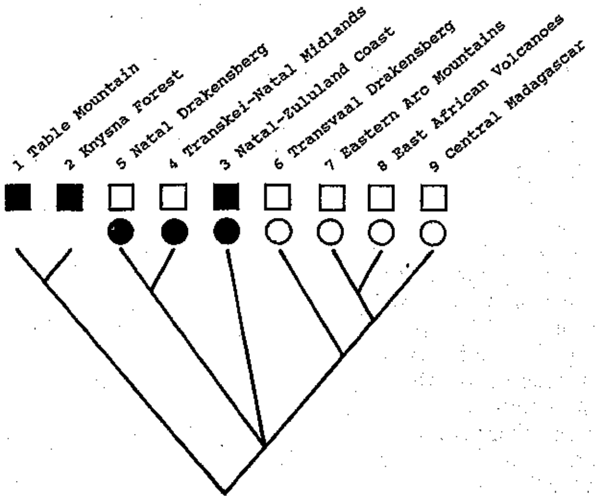

Fig. 6. Area cladogram for afromontane spiders with distributions of *Microstigmata* (circles) and the *Moggridgea quercina* group (squares) mapped on cladogram. Black symbols represent known distribution of taxon, open symbols represent predicted occurrence of taxon.

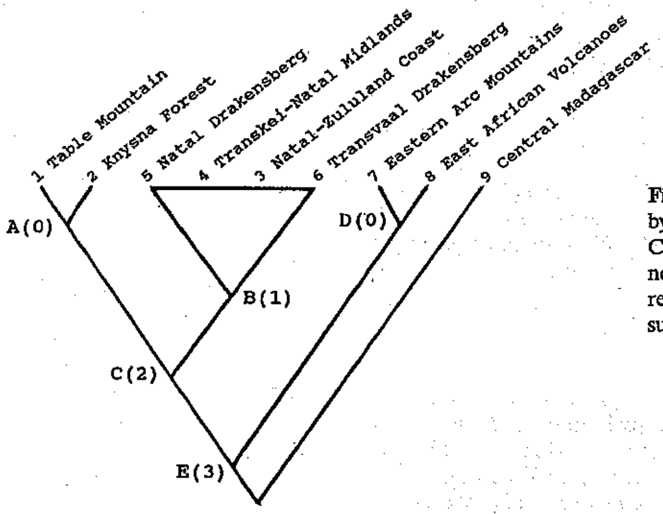

Fig. 7. Area cladogram predicted by Pleistocene vicariance scenario. Components noted by letters at nodes, along with additional steps required for spider data set to support monophyly of that node.

The parsimony of these two area cladograms can be compared quantitatively in explaining the spider distributions. I have no reason to hypothesise resolution among the areas within component B for the Pleistocene scenario, and, rather than perform tests on all 15 possible resolutions of these four areas, I have left them unresolved. This renders comparison of the two cladograms by simple calculation of their relative lengths unfair to the Pleistocene scenario, because, all other things being equal, an unresolved tree always requires more steps than a fully resolved tree. To avoid this bias, I asked what it would cost in parsimony to force a given component to come out as a monophyletic group on the area cladogram. To test this I added five dummy characters at the end of the data set, each supporting the monophyly of component A, B, C, D or E. I then tested each component individually by incrementally weighting its character through a series of analyses until monophyly of that component was achieved. Characters supporting the other components were deactivated during each analysis. I took the length of the tree for which the monophyly of a given component was achieved, and subtracted the weight of its character that was necessary to achieve that monophyly. The result was considered to be the tree length forced by the monophyly of that component. The minimum tree length for the unconstrained parsimony analysis (21 steps) was then subtracted from the minimum tree lengths required by the forced monophyly of each component. This was repeated for each hypothetical Pleistocene component and the additional steps necessary to support the monophyly of each were tabulated (Fig. 7). There is no cost in the monophyly of components A (Cape Region, areas 1 and 2) and D (East African highlands, areas 7 and 8). These components also appear on the most parsimonious area cladogram calculated from the spider data. Significant costs in parsimony are required to support B (eastern South Africa, areas 3, 4, 5 and 6) and C (South Africa, areas 1–6), and the greatest cost, 3 additional steps, is required for E (Africa, areas 1–8), i.e. to consider afromontane Africa a biogeographic region separate from Madagascar. Clearly, the Pleistocene scenario for the origin of the disjunctions in the afromontane biota is not the most parsimonious for the spider data, and the alternatives are to seek a more ancient explanation or allow the possibility of wholesale dispersal.

Conclusions

The pertinence of the cladistic paradigm in historical biogeography to defining the afromontane biota and investigating the age and mode of origin of its distributional pattern is clear. Among the points that emerge from this study is that areas that are clearly defined geographically (e.g. South Africa, Africa) were not found to be natural biogeographic regions, at least with respect to the afromontane biota. This underscores the importance of defining areas of endemism based on the distributions of monophyletic taxa rather than *a priori* based on geographic or political boundaries. The fit of the spider data to a single area cladogram is good, and it appears that a basic assumption of the parsimony approach to historical biogeography, that there is a single cladogram for the areas of interest, is not violated in this case. This may not necessarily hold for all cases (Cracraft 1988), and the danger exists that the data will be forced on to a model that is not appropriate. However, the application of cladistics to historical biogeography is still in its preliminary stages, and the notion of a single cladogram for areas of endemism if these areas are carefully defined on the basis of distributions of monophyletic groups may still serve as a reasonable null hypothesis. Dating a biogeographic pattern would seem filled with pitfalls, only one of which is the correctness of the area cladogram. Establishing the age of a taxon through fossils and of a barrier through geologic evidence are both open to wide margins of error, while establishing the concordance of a barrier with a node on an area cladogram is subjective. Geological hypotheses should not be considered more reliable than biological hypotheses. One need only consider the generations of biogeographers who felt compelled to interpret intercontinental disjunctions in the southern hemisphere in light of the hypothesis of continental stability. Still, I can think of no better way to suggest an age for a biogeographic pattern. The great ages suggested here for the spider distributions may not necessarily apply to similar disjunctions in other groups of plants and animals. Some groups that exhibit afromontane distributions may be too young to have been affected by mesozoic events. But until the phylogenetic relationships among other groups exhibiting afromontane disjunctions have been worked out and the degree to which they coincide with or contradict the area relationships specified by these spiders is understood, I believe that the potential of great age for these other groups can not be discounted out of hand. If a chance dispersal explanation is still to be preferred, it should at least be noted that it is less parsimonious than the vicariance explanation and that it presumes that a particular geological hypothesis is true. Finally, the use of parsimony to quantitatively compare alternative biogeographic hypotheses based upon how well each explains the distributions of monophyletic groups removes debates about biogeographic history from the realm of relative authority of proponents or plausibility of scenarios to a realm where alternative explanations can be objectively compared. This may be the greatest contribution of parsimony to historical biogeography.

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