

EVOLUTIONARY PATTERNS AND SPECIATION IN THE  
SOUTHWEST AUSTRALIAN FLORA

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## INTRODUCTION

The southwest of Australia has an extremely rich flora with at least 4 000 native species of which 75-80% are endemic to the region (Marchant, 1973; Hopper 1979; Beard, 1981; Keighery pers comm). This level of endemism is unusually high and comparable to oceanic islands whose floras have evolved in isolation such as Mauritius and the Hawaiian group and mainland regions of the world such as the Cape Peninsula South Africa, California, Turkey and Greece, which unlike the southwest have relatively high and extensive mountainous regions.

It would appear that the southwest has functioned as an island for a considerable period, isolated from the east of Australia by both physical and climatic barriers. Studies to date indicate that evolutionary patterns and modes of speciation are numerous and varied (James and Hopper, 1981; Paterson and James, 1973) even though the region is characterised by few major topographical features. As a consequence, a number of botanists have commented on the richness of the flora and at the same time expressed surprise at the lack of mountainous areas which characterise the other mainland regions of the world rich in endemic species.

## BIOGEOGRAPHICAL ASPECTS OF DIVERSITY AND SPECIATION

Although there is a noticeable lack of high mountain systems and other major geographic features which might be expected to play a major role in population isolation, adaptation and speciation there are still a number of factors both geo-historical and climatic which would appear to have contributed significantly to species richness and high endemism in the region (Hopper, 1979). Indeed the high rate of endemism is perhaps not unexpected given the differences in climate, geological features and soils between the south west and the southeast of the continent.

Biogeographical studies have indicated a significant role for climatic fluctuations and landscape change in facilitating population divergence and speciation in the region (Hopper, 1979). The relationship between the three major climatic zones in the southwest; permanently humid (800-1400 mm annual rainfall), permanently arid (300 mm annual rainfall), semi-arid transitional (300-800 mm rainfall) and species richness indicates that the coastal and inland shrublands (kwongan) of the semi-arid transitional climatic zone have the greatest species richness (Fig 1). In fact 70% of the species which occur in the southwest are found in kwongan (Lamont et al., 1982). In contrast the high rainfall forest and arid zone communities are relatively species poor. Evidence to date indicates that conditions favourable for prolific speciation were present in the semi-arid transitional climatic zone in the recent geological past while evolutionary stability was favoured in the permanently humid and permanently arid zones. This is supported by data which indicate that recently evolved species occur in greater numbers in the transitional climatic zone. (Table 1).

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In addition to climatic patterns, soil characteristics have been found to exert considerable influence on the local distribution patterns of vegetation. Areas of highest species richness are associated with highly leached nutrient poor sands and laterites with 99% of the kwongan communities occurring on sand plain (Lamont et al., 1982). Further, although climatic and edaphic factors have no doubt had a significant influence on diversity and speciation within the southwest flora landscape changes in the late Tertiary and Quaternary are also considered to have been important in the evolution of the flora in this region (Hopper, 1979).

In summary, species richness and high endemism in the southwest flora would appear to be associated with three major geo-historical phenomena; 1) the existence of marine, edaphic and climatic barriers since the Eocene, which have effectively isolated the southwest flora from related groups

in the east and contributed significantly to the high levels of endemism; 2) the formation of nutrient deficient sands and laterites favouring a shrubland flora which could readily adapt to the increasing aridity of the late Tertiary and Quaternary; 3) climatic and landscape instability in the transitional climatic zone which provided conditions promoting evolutionary change and speciation.

#### INTRASPECIFIC VARIATION AND POPULATION DIFFERENTIATION

Evidence from studies on a number of species in the southwest region indicate that patterns of polytypic intraspecific variation are numerous and due to a variety of factors. Intraspecific variation has been investigated by using markers such as morphological characters, allozymes and chromosomes. There are examples where such variation is associated with population divergence and the development of partial reproductive isolation. In many instances, this polytypic variation can be explained in terms of geographical, ecological and climatic factors.

Alternatively there are a number of examples where polytypic variation for chromosomes or allozymes occurs with no clear association with any ecological or environmental variables. In these cases intraspecific variation would appear to be the result of changes in the genetic system, such as the breeding system or meiotic chromosome behaviour, and or the genetic structuring of populations.

Extensive intraspecific morphological variation has been demonstrated in a number of species in Anigozanthos (Kangaroo Paws) (Hopper and Campbell, 1977; Hopper, 1978a) Conostylis (Hopper, 1978b) and Acacia (Hopper and Maslin, 1978). In the kangaroo paws interpopulation geographical variation is most pronounced in A. bicolor, A. viridis, A. manglesii and A. pulcherrimus with variation in A. humilis and A. flavidus being more subtle. All these species, with the exception of A. viridis, occur in the transitional climatic zone where factors promoting population



differentiation are likely to be more prevalent. A. manglesii is of particular interest in this case since it occurs in two morphologically distinct disjunct groups of populations forming northern and southern races. As indicated by Hopper (1978) the present allopatric distributions of these two northern and southern races can be readily attributed to barriers arising from reasonably well documented climatic and physiographic events during the quaternary. Although intraspecific morphological variation has not been studied extensively in either Acacia or Conostylis similar patterns involving species in the Transitional Climatic Zone have been described.

The use of chromosome and allozyme markers in detailed investigation of population differentiation within a species has proved invaluable in increasing our understanding of evolutionary processes within the southwest flora. The following case histories demonstrate the utility of these methods and indicate in particular the influence of the genetic system and population structuring on population differentiation.

Isotoma petraea is a mainly self-pollinating, herbaceous perennial endemic to granite outcrops and other rocky areas throughout the Eremaean province of Australia. Most populations are composed of structurally homozygous plants which form seven bivalents at meiosis. However in southwest Australia a number of populations are composed of complex hybrids, plants which are multiple interchange heterozygotes (Table 2) (James, 1970). The species exists in small isolated populations between which there is little migration. Complex hybridity apparently arose on Pigeon Rock, a large granite rock some 145 km north of Southern Cross under conditions of extreme inbreeding. Then, by a process involving migration and interpopulation hybridization, the genetic system spread in a south westerly direction so that the multiple interchange  $\odot 6$  at pigeon rock has enlarged, through a series of intermediate stages, to  $\odot 14$  in the extreme southwest population. From allozyme

studies the complex hybrids populations are some 12.5 times more heterozygous than the structural homozygotes (James et al., 1983). Associated with the evolution of complex hybridity in this species has been high levels of self-pollination, reduced flower size, increased gametic sterility following meiosis, the development of increasingly efficient balanced lethal systems and an increase in the number of ovules per ovary. At the same time, the evolution of complex hybridity has resulted in the development of post-zygotic isolation between populations since hybridization between populations of derived complex heterozygotes results in plants with reduced vigour. The evolution of such a system can be readily explained in terms of heterozyote advantage since selection for heterozygosity would appear to be the only suitable explanation for the displacement of apparently fully fertile structural homozygotes with 14 complex heterozygotes exhibiting 90% sterility.

Intraspecific population variation in the form of extensive chromosome variation has also been demonstrated in the triggerplant Stylidium crosssocephalum (Coates and James, 1979) a common and morphologically uniform species of the northern sandplains of the southwest region. Both polymorphic and polytypic chromosome variation occurs in this species, resulting in a mosaic of at least 16 different cytotypes or karyotypic forms in different regions of the species distribution (Fig. 2). Hybrids between plants from different localities with different karyotypes exhibit multiple chromosome associations at meiosis and are completely sterile. However pollen fertility in native plants, including those from transects between different cytotypes, is generally high ( 90%) and never below 40%, indicating there are no barriers to gene exchange between adjacent natural populations. While some of the cytotypes in this species have ranges bounded by recognisable eco-geographic barriers most do not. Seed set following self pollination results in substantial post-zygotic abortion and is much less than that following cross

pollination. As with most other Stylidium species in the southwest S. crossocephalum appears to be characterised by a recessive lethal system which results in the elimination of seed from selfing and thus promotes outcrossing. A hypothesis has been proposed which links the presence of a recessive lethal system with chromosome repatterning. It is postulated that the recessive lethal genes are chromosome segment deletions and that lethal systems are locally coadapted so that cross pollination within populations results in maximum seed production. Thus each population carries its own uniquely coadapted array of lethal factors (chromosome segment deletions). Coadaptation need not extend between populations and selection may have favoured karyotypic divergence as a means of conserving population coadaptation. The results of crossing within and between populations and between cytotypes provides support for this proposal. As will be discussed in the following section there is strong circumstantial evidence linking the evolution of a post zygotic lethal system and chromosome variation with speciation in the triggerplants in the southwest (James, 1979).

Recent studies using allozyme techniques have also provided valuable insight into patterns of population differentiation within species of this region. Eucalyptus caesia, a small mallee or tree species, is confined to the very specialised habitat of granite outcrops or rocks which are isolated from one another in the central wheatbelt (Moran and Hopper, 1983). The species consists of two morphological forms subsp. caesia and subsp. magna. The granite rocks on which this species occurs have been separated spatially for a long period of time and present populations may have been isolated for many thousands of years. This ancient isolation is reflected in the extensive population genetic differentiation of E. caesia (Fig. 3) and the significant correlation of geographic distance with genetic distance. Population differentiation in subsp. caesia is twice that in subsp. magna which indicates that subsp. caesia is more

likely the ancestral form from which subsp. magna later evolved in a restricted part of the species distribution.

Allozyme studies in another species Acacia anomala illustrate not only the genetic consequences of population isolation but also the dramatic effects of differing modes of reproduction (Coates in press). Acacia anomala is a naturally rare and extremely localised grasslike wattle occurring in two small disjunct population groups, some 30 km apart, on the edge of the Darling Scarp near Perth. The northern populations, near Chittering, reproduce sexually and are insect pollinated (native bees) although seed yields are rather low. In contrast the southern populations near Kalamunda, appear male sterile and reproduce primarily by vegetative means. The genetic data indicates little differentiation between the Chittering populations whereas the average genetic divergence between Kalamunda populations is three times higher (Fig. 4). This clearly reflects the clonal nature of the Kalamunda populations and the lack of sexual reproduction. In addition the genetic distance ( $D = 0.243$ ) between these two population groups is unusually high when inter population differentiation is considered in other plant species. This indicates that these population groups have been isolated for a prolonged period and that they are probably remnants of what was originally a much wider species distribution on the edge of the Darling Scarp.

The case histories presented in this section are by no means exhaustive and along with detailed studies on other species in the southwest such as Dampiera linearis (Bousefield and James 1976; James 1982) and Laxmannia sessiliflora (Keighery pers comm; James, 1982; Paterson and James, 1973) indicate the dramatic effects changes in the breeding system can have on chromosome organization and the population genetic structure of a species.

PATTERNS OF SPECIATION AND SPECIES RELATIONSHIPS

Although the number of biosystematic and evolutionary studies on the southwest flora are limited, they are sufficient to indicate that speciation has occurred in a variety of different ways even in closely related species groups. In some genera such as Anigozanthos, Conostylis, Acacia and Eremaea, geographic speciation would appear to be common although there are a number of cases within these groups where the evidence supports other modes. However in Stylidium although geographic speciation has no doubt taken place other factors associated with changes in the genetic system would also appear to have had a major influence on the development of reproductive isolation between populations and speciation.

In the genus Stylidium (triggerplants) 100 of the 143 currently recognised species are endemic to the southwest region indicating that this area is the major centre of triggerplant speciation (James, 1979). Species within this region, with the exception of the ephemeral annuals, are characterised by recessive lethal factors which eliminate most of the products of self pollination soon after fertilization while allowing the majority of cross pollination products to survive. Such a system promoting outcrossing does not apparently occur in species outside this region. The primitive chromosome number in the Stylidiaceae ( $n = 15$ ) is characteristic of all its species outside the southwest region. However within the southwest chromosome numbers are extremely variable with  $n = 5 - 15 - 16$  and polyploidy occurring on  $x = 13, 14$  and  $15$ . Many closely related species pairs differ in chromosome number. The presence of extensive chromosome repatterning in association with the development of a post zygotic lethal system for promoting outcrossing and the explosive speciation in this region has lead to the proposal that speciation within the genus is causally related to these factors rather than eco-geographic factors. That is, speciation in the genus has been primarily initiated by changes in the genetic system reflected in extensive chromosome repatterning with eco-geographic factors

generally being of secondary importance. Indications that divergence may occur in this manner comes from the studies on S. crossocephalum referred to previously. At the same time, however, it has been suggested by Carlquist (1969) that the mosaic of soil types found in the southwest may provide the necessary selective differentials for promoting speciation in Stylidium in this region. Biosystematic studies on the following species complexes, although not sufficient to provide a detailed mechanistic description of speciation in the genus as a whole do provide valuable insight into the relationships between chromosome change, eco-geographic variables and speciation in the genus.

The Stylidium crassifolium species complex consists of three species S. elongatum (n = 13, 26) S. crassifolium (n = 14, 28) and S. confluens (n = 14) with distinct tetraploid forms occurring within S. elongatum and S. crassifolium (Banyard and James, 1979) (Fig. 5). The close relationship between these three species was demonstrated in a previous study (Carlquist, 1969) where it was concluded that there is only one species, S. crassifolium, with the only other taxon then currently recognized S. elongatum, being considered a northerly subspecies. However, the discontinuities in distribution, chromosome number and morphological characters demonstrate there are clearly three distinct species and tetraploid forms which, although morphologically indistinguishable from their diploid progenitors, are reproductively isolated by substantial triploid infertility.

Stylidium elongatum is found in populations of several hundred plants in red loamy soils amongst open Acacia-Casuarina scrub inland from Geraldton. East of it in an area of yellow sandplain covered with proteaceous-myrtaceous heath scrub is found tetraploid elongatum. Thus the tetraploid form occurs in contiguous and non-overlapping areas which are ecologically quite different and it is clearly a distinct biological species. Further east of the sandplain and southwards in an area dominated by red earths and lateritic ridges S. confluens is



found in Acacia-Casuarina scrub. Finally both the diploid and tetraploid forms of S. crassifolium are confined to the extreme southwest and are geographically isolated from the other species in the complex. It appears that chromosome number differences between S. elongatum, its tetraploid form and S. confluens, which have parapatric distributions, associated with distinctive ecological preferences isolates these species in a similar fashion to the spatial isolation between S. confluens and S. crassifolium.

In the scale-leaved triggerplants, not only is chromosome number change associated with speciation but even species on the same number have markedly different chromosome complements (Coates, 1982). In addition distribution patterns and ecological data demonstrate that speciation in a number of instances is also associated with restriction to quite specific eco-geographic regions in the southwest. In all cases parapatric or sympatric species which are known on morphological criteria to be very closely related have either different chromosome numbers or karyotypes. For example the parapatric species S. albomontis and S. pilosum overlap in a small area around the base of East Mount Barren near Hopetoun. Both occupy ecologically distinct areas with S. albomontis occurring on clay type soils in association with quartzites characteristic of the Barren Ranges whereas S. pilosum occurs in deep coastal sands eastwards to Pt Culver. Both species have diverged to the extent that they now have different flowering times with only a slight overlap (1-2 weeks).

Of particular interest in the scale leaved triggerplants is the S. caricifolium species complex. Currently, five species are recognized (Fig. 6, Coates, 1981), although a previous study indicated that four of the five differed only at the subspecific level (Carlquist, 1969). Marked chromosome differences occur between all five species with chromosomally polymorphic populations occurring in S. affine, S. caricifolium and S.sp.2. When considering the origin of species within this complex it is apparent that a

number of factors including eco-geographic variables need to be taken into account. For instance *S.sp.1* differs from the rest of the species in this complex, not only chromosomally and morphologically, but because it lacks an efficient post zygotic lethal system with seed set following self pollination being nearly as high as that following crossing. It is the only species in the complex not found on lateritic soils and it would appear that this coastal species evolved from an inland affine like ancestor fairly recently in the Quaternary in conjunction with the sea level fluctuations and climatic changes which occurred during that period. At the same time adaptation to the coastal environment was clearly associated with or perhaps event initiated by a drastic change in the genetic system. The relationship between S. affine and S. caricifolium is also of interest since both species, although allopatric over most of their range, are linked by a series of populations of morphological and in some cases chromosomal intermediates in an ecological transition zone between the wheatbelt and Darling Scarp woodland systems. The origin of these transition zone populations is at present open to speculation. They may be the result of hybridization and introgression between the two species or they may represent an ancestral relic from which both S. affine and S. caricifolium have evolved. Although the precise role of chromosomal and ecological factors in speciation in Stylidium is open to debate there is no doubt that both have been crucial in the development of reproductive isolation and thus speciation, in this genus.

Another group in which evolutionary relationships and speciation have been extensively studied are the Kangaroo paws (Anigozanthos and Macropidia). These genera consist of twelve species of bird pollinated perennial rhizomatous herbs endemic to the southwest. They show a complete range of divergent population systems consistent with that expected under geographical and quantum models of speciation (Hopper; 1977, 1978, 1980). Patterns of geographical variation between populations within species have already

been described in the previous section with examples of allopatric geographical races in A. manglesii and continuous intergrading geographical races in A. bicolor, A. viridis and A. humilis and examples of allopatric semispecies such as A. bicolor and A. gabrielae and, A. rufus and A. pulcherrimus. There are parapatric hybridizing semispecies such as A. viridis and A. bicolor; sympatric hybridising semispecies such as A. humilis and A. kalbarriensis, A. manglesii and A. bicolor; and sympatric reproductively isolated biological species such as A. bicolor and A. flavidus, A. humilis and A. pulcherrimus. Speciation would appear to have been facilitated primarily by environmental fluctuations during the Quaternary in the transitional climatic zone, since recently evolved geographical variants and species are concentrated in the scrubland and woodland areas of the transitional climatic zone. In addition it has been proposed that speciation within this group is associated with differential adaptation to the foraging behaviour of nectar seeking honeyeaters leading to the development of pre-mating crossing barriers. The variation in perianth size and shape and the consequent effect on the site of pollen deposition on the pollinator supports this contention. Finally although geographical speciation at the diploid level seems to have been the predominant mode of evolutionary change in the kangaroo paws there is strong evidence to suggest that A. kalbarriensis is a stabilised hybrid derivative.

Recent studies in Eremaea (Myrtaceae), an endemic genus of outcrossing woody shrubs, again indicate the complexity of evolutionary patterns in the southwest flora (Coates and Hnatiuk, in prep.). This genus currently consists of eight described species yet morphological and allozyme studies indicate at least nine other taxa of which five are no doubt good biological species. All species within the genus with the exception of E. pauciflora, are restricted to the northern sand plain region between Perth and Shark Bay. E. pauciflora occurs within this region and throughout the wheatbelt as far south as the Fitzgerald River area. The

allozyme data indicates three distinct lineages; 1) the E. pauciflora lineage which consists of the E. pauciflora - E. beaufortioides species complex, the E. violaceae species complex, E. ebracteata and E. purpurea; 2) the E. brevifolia lineage which consists of the E. brevifolia species complex and E. sp.4 (considered to be of hybrid origin), and 3) the monotypic E. fimbriata lineage. The latter species is unique within the genus, being the only species requiring fire for seed release.

Typical patterns of population divergence and speciation within the genus can be readily demonstrated by examining the E. brevifolia species complex (Fig. 7). Here there is one allopatric taxon, E. brevifolia, north of Geraldton with the remaining taxa forming parapatric distributions. All three undescribed taxa are morphologically distinct although the genetic divergence between T1 and T2 is minimal as indicated by the genetic distance data from allozyme studies. It may be that T1 and T2 are continuously intergrading geographic races although the morphological data indicates otherwise. The other taxa T3 and E. acutifolia are both morphologically and allozymically distinct. There are no obvious eco-geographic boundaries delineating the parapatric distributions of these taxa which suggests that past climatic fluctuations resulting in restricted isolation, extinction and confluence of populations within this transitional climatic region may be the major factor contributing to speciation within this complex and the genus as a whole. However it should be stressed that further biosystematic investigations, including chromosome and breeding system studies, are needed for a more precise determination of modes of population divergence and speciation within Eremaea.

With the exception of Acacia anomala, detailed biosystematic data is not currently available on population divergence and speciation within the genus Acacia. Yet it is evident from phytogeographic studies that the southwest region has also been a major centre of speciation for Acacia in Western

that species such as E. kalganensis and E. chrysantha are hybrids or of hybrid origin and herbarium and field observations suggest that E. priessiana hybridises with at least five other species in the group. In addition species such as E. carnabyii and E. brachyphylla, originally considered to be extremely rare species are now presumed to be hybrids (Hopper pers comm).

In Eremaea allozyme and morphometric data has provided strong evidence to suggest that an undescribed taxon T4 (Fig 6) is a stabilised hybrid resulting from hybridization between E. violaceae and another new taxon T3.

Although hybridization does not appear to be common in the genus Stylidium, studies in the S. caricifolium species complex (Fig 5) indicate that hybridization has occurred on at least two separate occasions (Coates, 1981). Morphological and chromosome data suggest that individuals in one group of populations which occur in an ecological transition zone, between the wheatbelt and the Darling Scarp vegetation systems and which bridge the morphological discontinuities separating S. affine and S. caricifolium, are of hybrid origin. Evidence supporting this comes from studies which indicate that plants having an intermediate karyotype had pollen fertility reduced to as low as 58% whereas normal pollen fertility in the parental taxa was greater than 95%. Recent field studies have also provided evidence for hybrids between S. nungarinense and a new species S. sp. 2 (Fig 5) in the eastern wheatbelt. In this case the hybrids are found in a disturbed area where gravel mining occurs. Their presence is of particular interest given the marked chromosome differences between the parental taxa (n=8 and n=6).

Probably the most detailed accounts of hybridization in the southwest flora are those resulting from studies on the kangaroo paws (Hopper, 1977, 1979). Twenty four naturally occurring sympatric species combinations have been recorded for this group. Species found to form large hybrid swarms

with numerous partially fertile  $F_1$  hybrids and extensive backcrossing were A. viridis and A. bicolor, A. manglesii and A. viridis, A. manglesii and A. bicolor, A. humilis and A. kalbarriensis, A. humilis, and A. onycis, A. humilis and A. bicolor, and A. humilis and A. gabrielae. In addition species whose sympatric populations contain a low frequency of partially fertile  $F_1$  hybrids and occasional backcrosses are A. manglesii and A. humilis, and A. viridis and A. humilis. In nearly all cases hybridization occurs in areas which have been recently burnt or disturbed. Finally as mentioned previously A. kalbarriensis appears to be a stabilized diploid backcross derivative of natural hybridization between A. humilis and A. manglesii.

In the genus Conostylis natural hybridization and introgression has been documented in some detail for the three species of the Conostylis aculeata group C. candicans, C. aculeata and C. pauciflora (Hopper, 1977). Further, the evidence suggests that C. pauciflora is a stabilised diploid derivative of C. aculeata and the coastal ecotype of C. candicans.

Hybridization has also been reported for a number of orchid genera (Thelymitra, Caladenia, Microtis, Diuris, Drakea, Elythranthera and Prasophyllum; Brown, pers comm) and is extremely common in Caladenia and Microtis. In Microtis where the species are self compatible and also tend to undergo extensive clonal reproduction hybridization has resulted in large hybrid swarms in which hybrids and backcross derivatives are common whereas the original parental taxa are frequently rare (Brown pers. comm.) Studies to date also indicate that at least one undescribed Caladenia species is a stabilised hybrid derivative.

Although the number of detailed biosystematic studies on the southwest flora have been limited, particularly in terms of studying hybridization and its evolutionary significance it is perhaps surprising to note the number of cases which have been documented. It is also of interest to note that



Anigozanthos kalbarriensis, Conostylis pauciflora and two new species in the genera Eremaea and Caladenia appear to be stabilised diploid species resulting from natural hybridization.

#### CONCLUSIONS

Species richness and high endemism of the southwest flora is considered to have developed as a result of a combination of climatic and geohistorical events during the late tertiary and Quaternary. In particular Hopper (1979) has stressed the importance of climatic fluctuations in the transitional climatic region where conditions appear to have been particularly favourable for rapid evolutionary change and speciation over this period. This is supported by observations which show that the majority of species and species groups mentioned herein are undergoing active population differentiation and or have undergone recent speciation in this region. In the Stylidium crassifolium and S. caricifolium species complexes evolutionary patterns support this contention. Further speciation within these groups would appear to be associated with eco-geographic factors. However it is also clear that population differentiation and speciation in Stylidium in the southwest has been greatly influenced by chromosome repatterning and the development of a post-zygotic lethal system which promotes outcrossing. These and other biosystematic and evolutionary studies in the southwest flora indicate that climatic and geohistorical circumstances are not the only factors responsible for the prolific speciation observed in this region. Indeed in Isotoma petraea, Stylidium crosscephalum, to a lesser extent Acacia anomala and other species which have also been studied in some detail such as Dampiera linearis (Bousefield and James 1976; James, 1982) and Laxmannia sessiliflora (Keighery pers comm Paterson and James, 1973; James 1982) the breeding system and chromosome repatterning have been shown to have profound effects on the population genetic structure of a species. In the case of Isotoma petraea and Stylidium crosscephalum it has resulted

in the development of partial reproductive isolation between populations. It would appear that the effects of climatic fluctuations and active landscape changes on the transitional climatic zone have not only contributed directly to population isolation and speciation but have also been conducive to dramatic changes in the genetic system of many species resulting in population differentiation and speciation which in many instances has no obvious association and probably no casual relationship with present eco-geographic boundaries.

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Table 1. Number of relic and recently-evolved species or chromosome races of biosystematically studied genera occurring in the high rainfall and transitional rainfall zones of south-western Australia. <sup>a</sup>(Date of Hopper 1978, 1979).

	Number of taxa in			Total
	High rainfall zone	Transitional rainfall zone	Both or borderline	
Relict or parental taxa	11 (9) <sup>b</sup>	40 (42)	18	69
Recent or derived taxa				
diploids	0 (2)	9 (7)	6	15
low dysploids	2 (3)	13 (12)	8	23
polyploids	6 (5)	24 (25)	7	37
Total	8 (9)	46 (45)	21	75

<sup>a</sup>Species, chromosome races and authorities consulted are listed in Hopper (1978).

<sup>b</sup>Numbers in parenthesis indicate those expected on the basis of the relative areas of the two zones (the transitional rainfall zone occupies an area five times larger than that of the high rainfall zone).



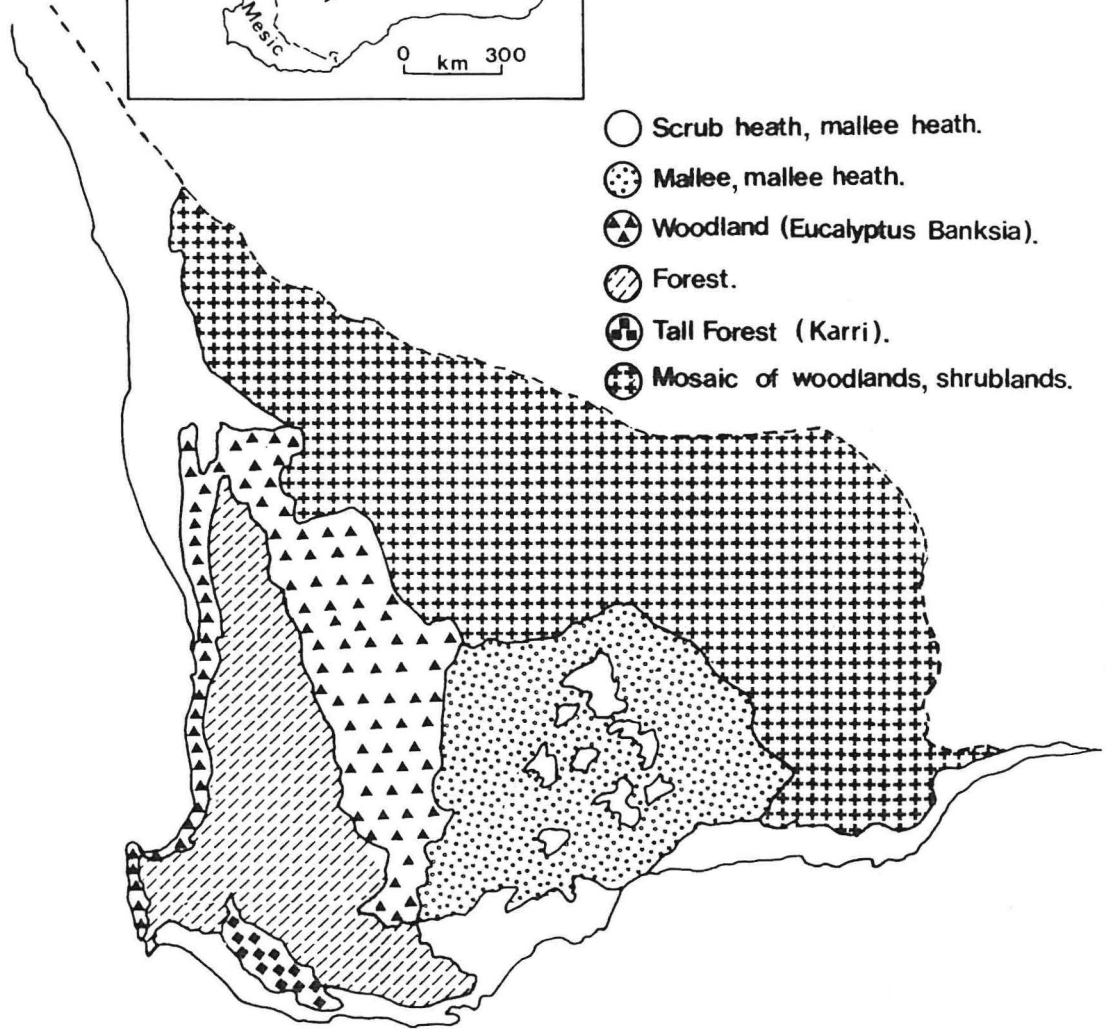
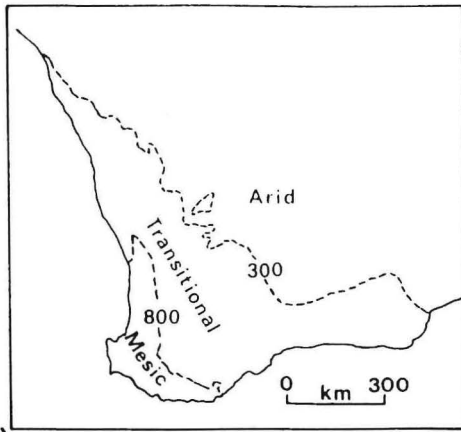
Table 2. Meiotic behaviour and the breeding system of interchange heterozygotes in Isotoma petraea (Data from James, 1970)

Population	Various	Various	Pigeon Rock	Berring-booding Rock	Muntagin	3 mile Rock	Bencubbin	Merredin	Mt Stirling
	II	" 4	" 6	2 " 6	2 " 6	" 10	" 12	" 14	" 14
% Disjunction of AI	100.0	90.2	58.8	65.0	46.8	29.5	23.2	22.5	16.3
%Pollen Fertility	>95	-	73.6	-	37.2	57.9	48.0	34.6	-
Breeding System	Mixed selfing and crossing		>99% selfing	High levels of selfing with a residual capacity for crossing					

II = 7 bivalents  
 " = a ring of

## Figure Legends

- Fig. 1. Distribution of dominant vegetation formations in southwestern Australia (From Hopper, 1979; Beard, 1981) and their relationship with the three major rainfall zones.
- Fig. 2. Distribution of the 16 different karyotypic forms found in Stylidium crossoiephalum (From Coates and James, 1979).
- Fig. 3. Phenogram based on Nei's genetic distance (D) between populations of Eucalyptus caesia sub sp. caesia and sub sp. magna (From Moran and Hopper 1983).
- Fig. 4. Phenogram based on Nei's genetic distance (D) between the Kalamunda (K) and Chittering (C) populations of Acacia anomala. (From Coates in press).
- Fig. 5. Distribution of the taxa in the Stylidium crassifolium species complex. Haploid chromosome numbers and ploidy levels are shown (From Banyard and James, 1979).
- Fig. 6. Distribution and karyotypes of the taxa in the Stylidium caricifolium species complex. T corresponds to the transition zone between S. affine and S. caricifolium (From Coates, 1981).
- Fig. 7. Distribution, phenogram and cladogram for the six taxa in the Eremaea brevifolia species complex. The phenogram and cladogram are based on Nei's genetic distance (From Coates and Hnatiuk in prep.).



- Scrub heath, mallee heath.
- Mallee, mallee heath.
- ▲ Woodland (Eucalyptus Banksia).
- ▨ Forest.
- ⊠ Tall Forest (Karri).
- ⊠ Mosaic of woodlands, shrublands.

