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Biogeographical patterns of zodariid spiders (Araneae: Zodariidae) in the wheatbelt region, Western Australia.

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Abstract – 117 zodariid species were recorded from the Wheatbelt region of Western Australia after 12 months of continuous pit trapping at 306 quadrats (12 landform types at each of 24 survey areas), with an average richness of 3.98 per quadrat. Analysis of the data at the landscape scale showed no significant relationships between species composition and substrate at each quadrat, other than a weak north-south changeover in composition. Strongly localised patterns of composition at the species level were overt, with a high proportion of short-range endemic species. However a regional-scale analysis (of species compositional patterns by survey area) showed a distinct relationship with precipitation in the driest period. Also, species richness for each survey area and each landform type revealed a correlation between low richness and both high rainfall and low drainage. Greater knowledge of zodariid ecology is required to determine the possible influence of microhabitats on species composition.

INTRODUCTION

The Zodariidae are medium-sized spiders, currently divided into five subfamilies and approximately 60 genera. They are ground-dwelling spiders, constructing a simple burrow with a silken retreat, although some Australian species construct a palisade around the burrow entrance (Main, 1975). The use of burrows by all species has not been substantiated. Zodariids are obligate ant-feeding spiders (Jocqué, 1991), many of which have behavioural attributes to capture prey. The lack of aerial dispersal by juveniles ensures that zodariids have potential for detailed biogeographic analyses of relictual organisms (Jocqué, 1993; Ramirez and Beckwitt, 1995). Of the five recognised subfamilies, only three have been recorded from Australia: Cyriocteinae (see Platnick and Griffin, 1988); Lachesaninae (Jocqué, 1991); and Storeninae (see Jocqué, 1991, 1992, 1995; Jocqué and Baehr, 1992, 1995).

The Australian fauna is reasonably well-known at the generic level and the publication of a key to subfamilies and genera (Jocqué, 1995) has allowed the rapid identification of adult males in museum collections to these ranks. However, most genera are unrevised and numerous species await description. Two genera have been revised. *Storena* Walckenaer now has 29 species (Jocqué and Baehr, 1992, 1995), and *Asteron* Jocqué has been split into 8 new genera with over 100 species (Baehr and Jocqué, 1996) of which 37 are described (Baehr and Jocqué, 2000, 2001). Revision of the *Asteron* complex is continuing. Prior to this survey only eight species of zodariids had been collected from the wheatbelt region, which is the main focus of the survey.

Only 26% of the wheatbelt region's area remains native vegetation, primarily consisting of small uncleared bushland remnants surrounded by wheat fields (George and Coleman, 2002). The large scale clearing of deep-rooted perennial vegetation, combined with land irrigation (Hart *et al.*, 1990), has resulted in an overall rise in the ground water and consequently an increase in the salinity of the valley floors and lower slopes. This increase in salinity causes death of vegetation (Mulcahy, 1978; Ruprecht and Schofield, 1991; George *et al.*, 1995).

In this paper, data collected during a detailed wet pitfall trap program, covering all major geomorphological units in the wheatbelt, are used to:

a. Examine diversity of zodariids at species level in an internationally recognised biodiversity hotspot.
b. Investigate patterns in zodariid species composition and richness across the wheatbelt in terms of environmental attributes.
c. Determine whether secondary salinisation is liable to affect zodariid assemblage composition.

METHODS

Study area

The wheatbelt study area comprises all or part of five biogeographical regions (Figure 1): the entire Avon Wheatbelt bioregion, western two-thirds of

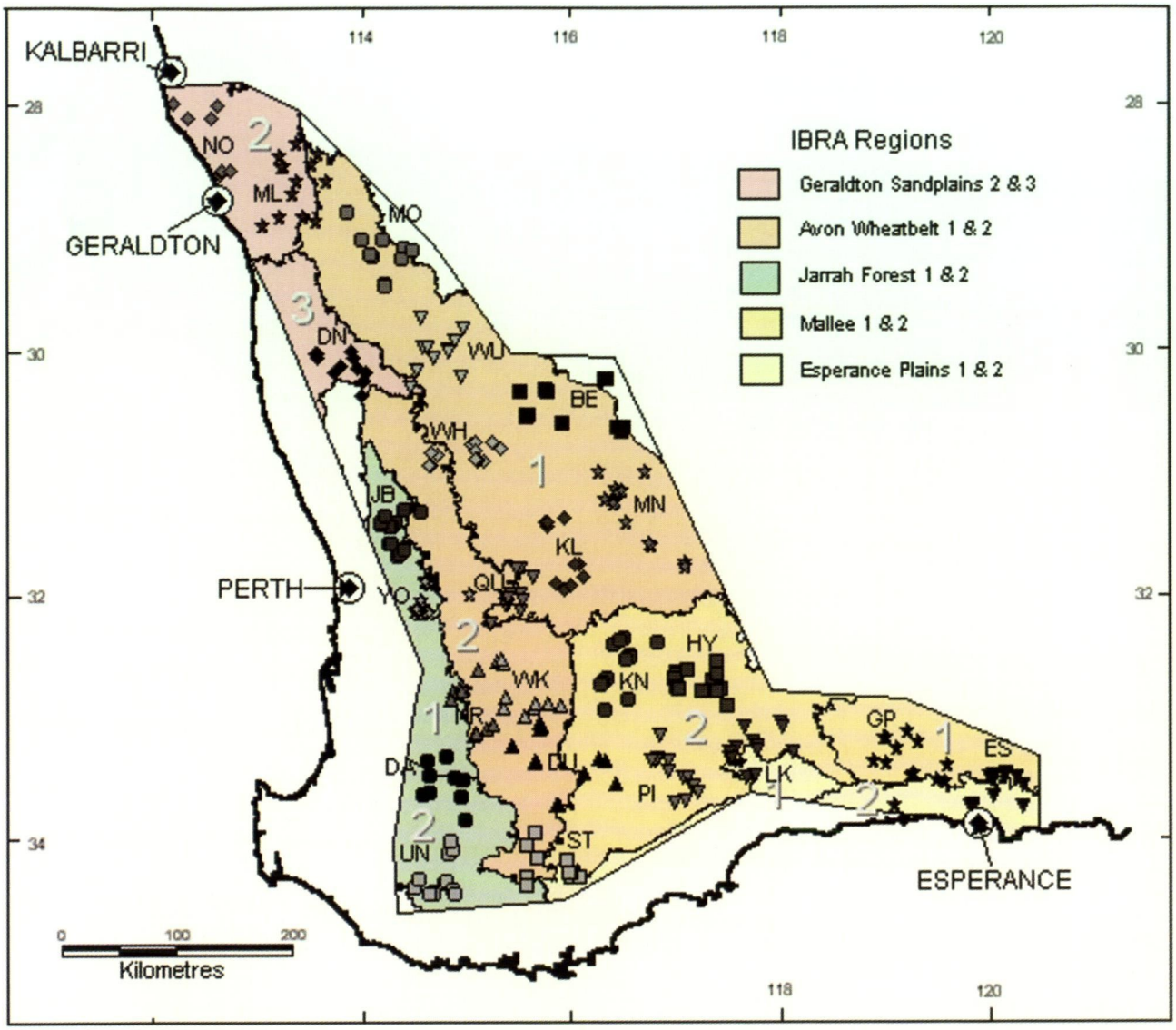


Figure 1 Wheatbelt study area, showing the 304 quadrats, and relevant IBRA biogeographical region boundaries (Thackway and Cresswell, 1995). The different symbols indicate the 12 to 13 quadrats in each of the 24 survey areas.

the Mallee, southern half of the Geraldton Sandplains, western edge of the Jarrah Forest and the central quarter of the Esperance Plains. It covers 205 000 km^2 and extends from Esperance to Hill River. For a more detailed explanation of the bioregions see McKenzie *et al.* (2004).

Field sampling

A three year survey was undertaken in 24 survey areas (304 sites) in three bands, northern, central and southern (Figure 1). The survey areas are: northern band; Beacon (BE), Julimar-Bolgart (JB), Mullewa (ML), Morawa (MO), Northampton (NO), Wongan Hills (WH), Wubin (WU); central band; Hyden (HY), Kellerberrin (KL), Kondinin (KN), Merredin (MN), Narrogin (NR), Quairading (QU), Wickepin (WK), York (YO); southern band; Darkin (DA), Dumblyung (DU), Esperence (ES), Grass Patch (GP), Lake King (LK), Pingrup (PI), Stirling Ranges (ST), Unicup (UN); and the Dandaragan Plain (DN).

Within each survey area, a quadrat was positioned as a typical example of each of the 10–12 landform units (Mulcahy and Hingston, 1961) comprising the wheatbelt landscape. One or two salt affected examples were also chosen resulting in 12 to 13 quadrats in each survey area; Dandaragan, Kellerberrin, Morawa, Narrogin, Northampton and Quairading had 12 each, the rest had 13. This decision was related to the number of salinised landforms present that could be used as pseudo-replicates of the non-salinised landforms. Quadrat locations are provided in Appendix 2. Three quadrats were removed from the analysis due to inundation of traps resulting in poor sampling (PI04, WK03 and UN13).

The survey areas served as pseudoreplicates because each of the landform units were sampled

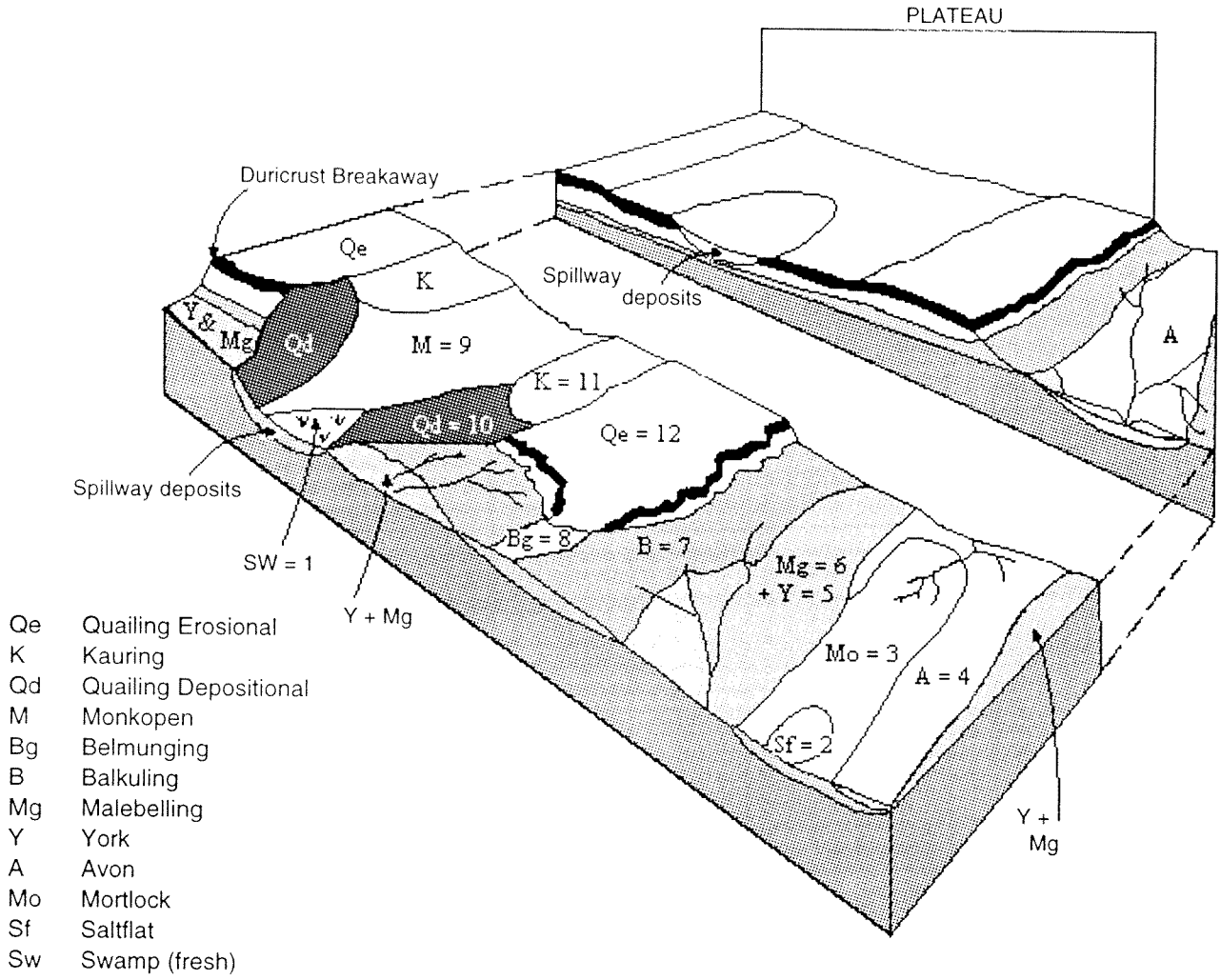


Figure 2 Wheatbelt landforms from McKenzie *et al.* (2004; modified from Mulcahy and Hingston, 1961). The plateau profile comprises the top five landforms (Qe, K, Qd, M and Bg), with the dissection profile the bottom seven (B, Mg, Y, A, Mo, Sf and Sw).

within each survey area; Sw (swamp), Sf (saltflat), Mo (Mortlock), A (Avon), Y (York), Mg (Malobellin), B (Balkuling), Bg (Belmungin), M (Monkopen), Qd (Quailing Depositional), K (Kauring) and Qe (Quailing Erosional) (Figure 2); for detailed explanation of landforms see McKenzie *et al.* (2004).

Traps were open for one calendar year (1825 pit trap nights per quadrat). Each band was sampled separately with the central band traps open from October 1997 to September 1998, northern band September 1998 to October 1999 and traps in the southern band and Dandaragan Plain open from October 1999 to October 2000. The effect of seasonal sampling bias was minimised because quadrats were sampled for an entire calendar year. However 1999 and 2000 were unusually dry years. This may have influenced study outcomes.

The five wet pitfall traps at each quadrat were positioned in different microhabitats and at least 5 metres apart. Each trap was a two litre plastic container (80 mm neck diameter and 25 cm deep) set flush with the ground surface. It contained 400 mL of preserving liquid, comprising 320 ml ethylene glycol, 64 ml tap water and 16 ml formaldehyde. It was protected with a square plate of wood (15 cm x 15 cm) set 5 cm above the pit mouth.

Samples were taken back to the laboratory, rinsed, sorted and then stored in 75% ethyl alcohol. All specimens were lodged with the W.A. Museum.

Data Analysis

The data matrix was constructed based on the presence and absence of species collected at each quadrat. The computer package PATN (Belbin, 1995) was used to explore and expose species composition patterns. Similarities in species composition between quadrats were compared using the Czekanowski association measure, and

the quantitative relationship between each pair of species was determined using the Two-step association measure. Dendrograms of the resulting association matrices were created using a modified unweighted pair group arithmetic averaging (UPGMA) hierarchical clustering strategy (Sneath and Sokal, 1973), which was also used to reorder the data matrix as a two-way table.

Twenty-three geographic, 13 climatic (ANUCLIM; McMahon *et al.*, 1995), 15 soil, four vegetation, and three geomorphic variables including salinity risk (see McKenzie *et al.*, 2004) were taken for each quadrat (Appendix 3). Significant correlations were identified between many of these physical attributes using Kendall's rank correlation coefficient (Kendall's tau). PATN's GSTA module was used to expose relationships between compositional patterns and the environmental attributes, and Kruskall-Wallis K-sample tests were used to test the significance of these relationships.

Species compositional patterns were also analysed at the survey area level, by combining species lists from the component quadrats and averaging their climatic and cartographic attributes (latitude, longitude and the 13 climatic variables). Analysis at this level was biogeographically valid because the survey areas were evenly distributed across the study area, and the quadrats in each survey area were positioned to provide a consistent cross-section of the landscape profile's main components. This nested stratification allowed the influence of substrate to be suppressed, exposing broad-scale patterns.

Differences in the species richness, drainage and salinity type of quadrats based on the twelve landform types was compared using ANOVA and then post-hoc Neuman-Keuls tests.

Taxonomy

The morphospecies and/or undescribed genera distinguished in this study were distinguished primarily on differences in male palpal morphology, a character-set used in existing zodariid revisions. New genera were distinguished on the basis of differences in the palpal tibia, tegulum and clypeus, while characters such as embolus shape and length, and tegular apophyses were used to separate species. Where problems have arisen, experienced zodariid taxonomists (B. Baehr, R. Jocque and R. Raven were consulted), so the species-level and generic separations are conservative.

RESULTS

Taxonomy

The zodariids collected from this survey represent the second most speciose group of spiders following the Salticidae. Of the 20 genera currently described from Australia, 11 have been previously collected in Western Australia. Six of these genera were collected in the wheatbelt. Thirteen taxa were consistent with existing species (Table 1) and 5 taxa were unable to be assigned to known genera. These were placed into 4 unknown genera based on current taxonomy. The other 89 undescribed species were placed in the fifteen genera with the largest additions being to the genera *Habronestes* and *Neostorena* with 39 and 27 new species, respectively. Of the 117 species that were identified across the 306 quadrats, 283 sites yielded between one and 12 species per site. Zodariids were absent from 21 sites. The average richness across all sites, including those with no zodariids, was 3.98 ± 2.49 (sd).

Table 1 List of recognised zodariid species identified from the survey.

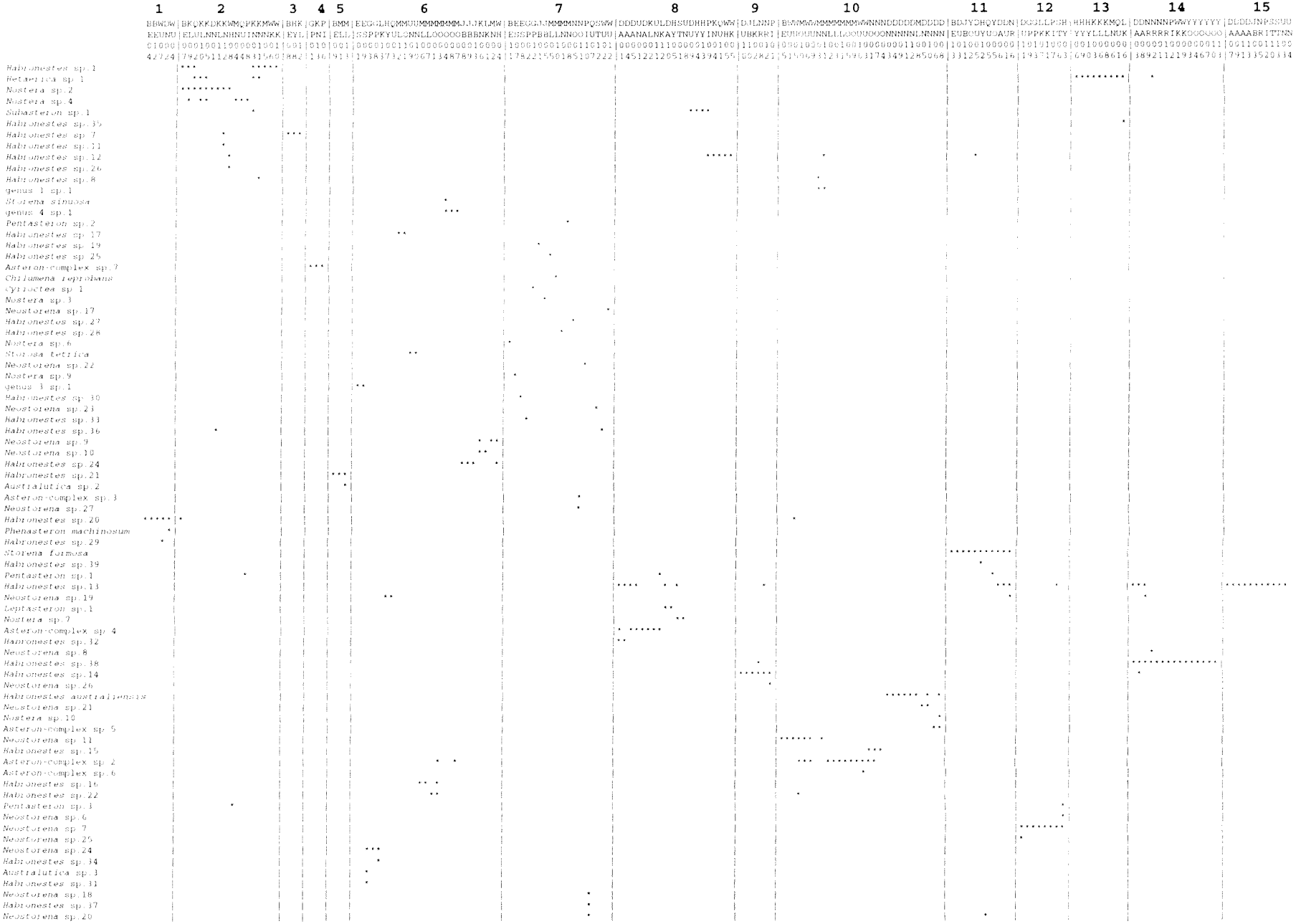
Species	Author
Australutica quaerens	Jocqué 1995
Chilumena reprobans	Jocqué 1995
Habronestes australiensis	(O.P.-Cambridge 1869)
Habronestes grimwadei	(Dunn 1951)
Hetaerica harveyi	Raven and Baehr 2000
Neostorena victoria	Jocqué 1991
Pentasteron intermedium	Baehr and Jocqué 2001
Phenasteron longiconductor	Baehr and Jocqué 2001
Phenasteron machinosum	Baehr and Jocqué 2001
Storena Formosa	Thorell 1870
Storena sinuosa	Jocqué and Baehr 1992
Storosa tetrica	(Simon 1908)
Zillimata scintillans	(O.P.-Cambridge 1869)

Analysis of quadrat composition.

Two types of species were initially identified from the complete data matrix, localised (geographically endemic) and widespread. Species that had a maximum distribution of greater than 390 km were assigned to the widespread type and those with smaller areas of occurrence were termed localised. Once the widespread species were isolated another split was apparent, So the dataset was again divided into two types of species, regularly widespread (an even distribution of sites) and disjunct (two or more localised occurrences not connected). These three types are dealt with separately below, beginning with the localised species.

The localised zodariids totalled 78 species and covered 182 sites. Of these nearly half (37) were species recorded at only a single quadrat. This accounted for nearly a third of all the zodariid species. The two-way table (Table 2) confirmed the strongly localised nature of their geographical distributions; ten of the 15 groups were defined by single species and nearly all were recorded at a set of adjacent or near-adjacent quadrats.

Table 2. Data matrix for localised zodariids reordered according to similarities in species composition. The groupings have been left in to show the reliance on single species in determining the groups. Quadrat codes are printed vertically with group numbers above each partition.



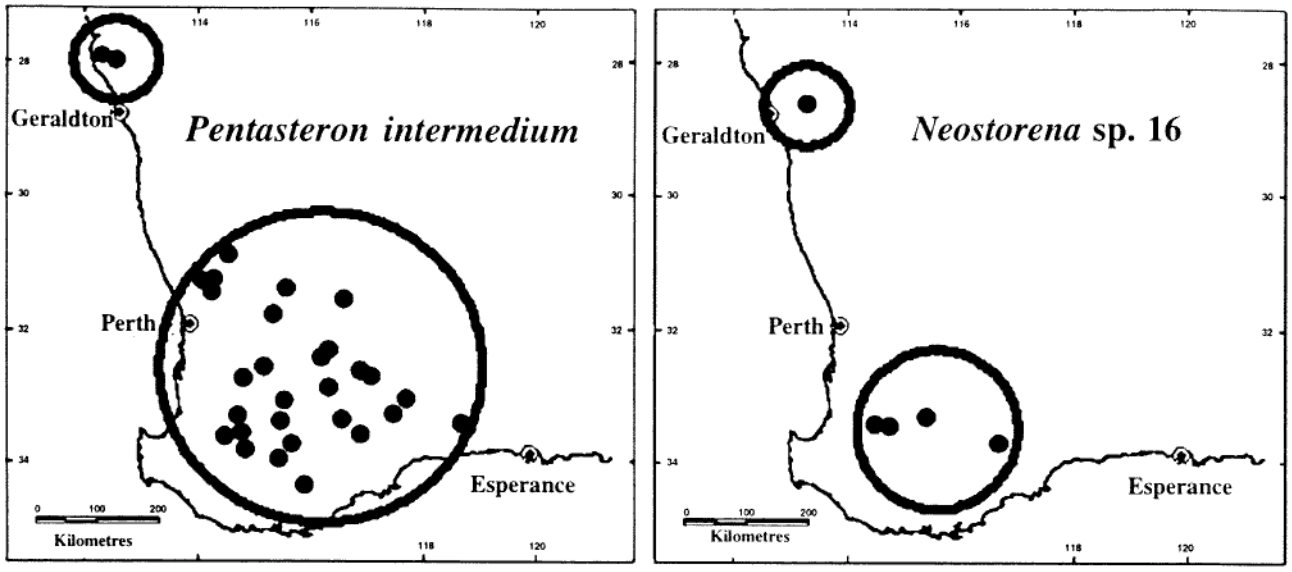


Figure 3 Maps of two zodariid species as examples of widespread, disjunct distributions.

The second type comprised of widespread, but geographically disjunct zodariids. Two examples are *Pentasteron intermedium* and *Neostorena* sp.16 (Figure 3). The two-way table (Table 3) showed that there was minimal overlap (generally, they were not found in the same parts of the study area) and that the groupings were primarily based on single species as in the localised two-way table.

Analysis did not yield well defined quadrat groups from the third type of zodariids (regularly widespread – Table 4). However, at the five classification group level, there were significant differences between groups one, three, four and five in terms of latitude and wettest quarter precipitation (Figure 4).

Analysis of survey area composition

Using all 117 species, compositional patterns were analysed after the quadrat lists were pooled for each survey area. The analysis involved only latitude, longitude and the 13 climatic variables because these were the only attributes relevant at the survey area level. In order to maintain an overall significance level of $\alpha = 0.05$, a Bonferroni correction was used so that the *P*-value used for each of the 15 individual tests was 0.003. Three distinct clusters were defined from the resulting

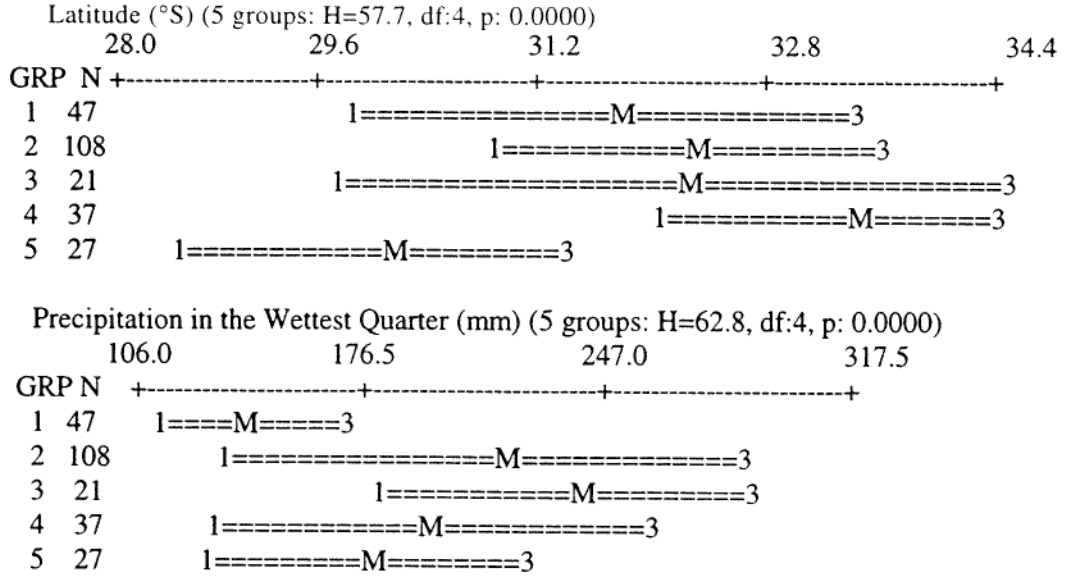


Figure 4 Physical attributes related to the partition structure at the 5-group level derived when quadrats were classified according to the presence/absence of regularly widespread zodariid species. [N= number of quadrats in each classification group (GRP); "1==M==3" indicates one standard deviation either side of the mean (M). H = Kruskall-Wallis coefficient; df = degrees of freedom; p = probability].

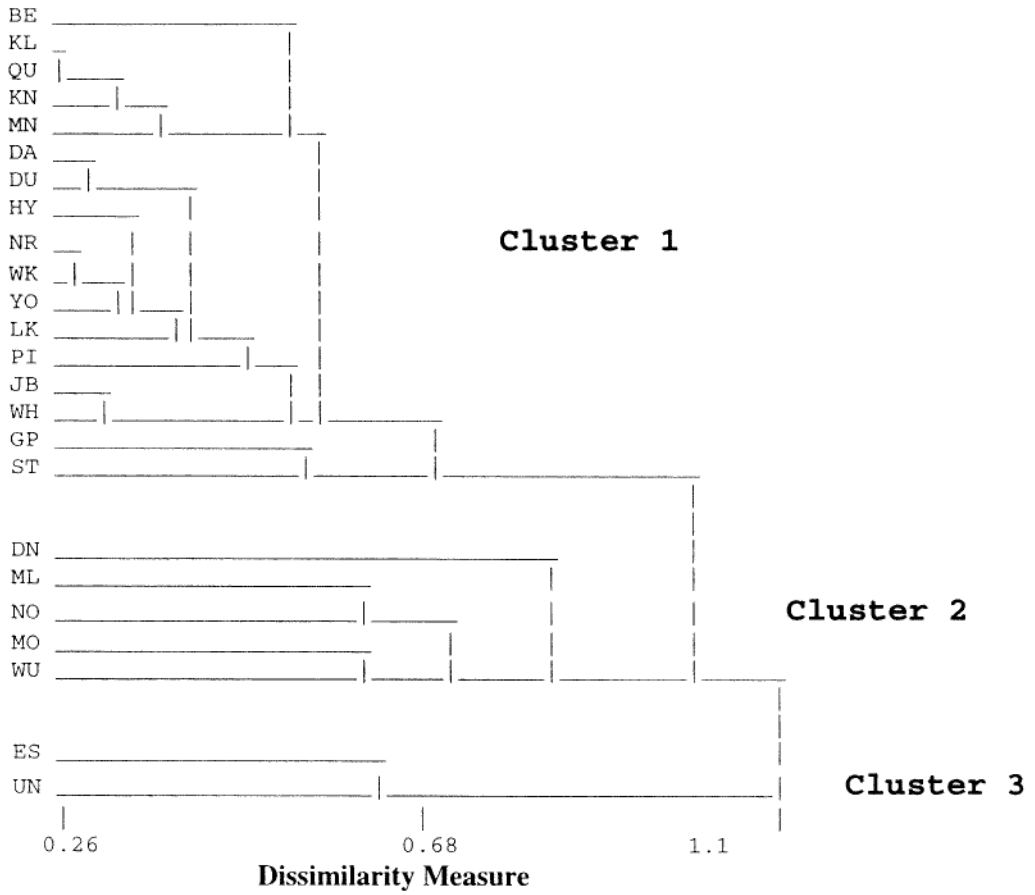


Figure 5 Dendrogram of survey areas grouped into three clusters based on species composition.

dendrogram (Figure 5). Of the environmental attributes tested, precipitation in the driest period provided the greatest separation of the three groups of quadrats with a *P*-value of 0.0006 (Figure 6). The three clusters are outlined below.

Cluster 1 comprises all the central and southern-central survey areas (Figure 7) and encompasses the greatest number of survey areas and species as well as the greatest variation in dry period precipitation, as seen in Figure 6. Seventeen survey areas and 92 species comprise this group. Cluster 2 comprises the five most northern survey areas, and involves 57 species. These areas have a distinct dry season of negligible precipitation. The last cluster has a comparatively wet dry season and comprises the south-west and south-east corners of the study region, the Unicup and Esperance survey areas respectively. Only 17 species were collected in these two areas.

Species richness

In terms of survey area species richness (Table 5), the four most southern survey areas (UN, ES, ST and GP) were significantly less rich than all the other sites. Examination of quadrat species richness based on landform type (Table 6) resulted in three groups (Table 7). The most obvious significance is that of the swamp (Sw) and saltflat (Sf) quadrats which both were poorer in species than all other landforms but not from each other. These surfaces are the lowest in the landscape which correlates with low drainage (Table 8) and other soil variables,

Precipitation in the Driest Period (mm) (3 groups: H=14.8, df:2, p: 0.0006)

	0.0	4.7	9.4	14.1	18.8
GRP	N	+---------+---------+---------+---------+			
1	17		1=========M=========3		
2	5	1M3			
3	2			1====M===3	

Figure 6 Physical attribute related to the partition structure at the 3-group level derived when survey areas were classified according to the presence/absence of all zodariid species. [N= number of quadrats in each classification group (GRP); "1===M===3" indicates one standard deviation either side of the mean (M). H = Kruskall-Wallis coefficient; df = degrees of freedom; p = probability].

particularly those associated with salinity. This gives their low richness an apparent relationship with these salinity related variables, but the equally low richness of quadrats in the freshwater swamps (non-saline) highlights the significance of soil moisture (and thus drainage). Table 9 shows that salinity at Sf and Sw are significantly different from each other, and Mo and A were in fact significantly more saline than Sw. Species compositions also differed between the saltflat and swamp areas but there was little species similarity between quadrats between each of the two landform types.

Vicariant patterns

The distribution patterns of each genus were checked for possible vicariance between two or more species. There were many examples of related species having different distributions however nearly all still overlapped with each other, with just the scale of the geographical range differing, i.e. a few species were widespread and some were highly localised or a single site record. The only genus where an allopatric pattern emerged at the species level was *Chilumena*. Only two species of *Chilumena* were recorded; *Chilumena* sp.1 was recorded along the south-south western edge of the wheatbelt from GP13 to NR03 without extending into the ST, UN or DN survey areas, whereas *C. reprobans* Jocqué had only a single occurrence at ML10 in the north-east corner of the study area.

DISCUSSION

Taxonomy

Prior to the survey the Australian Zodariidae had approximately 93 described species, of which most were described from eastern Australia. The most significant contributions are 39 new species in the genus *Habronestes* and 27 in *Neostorena*. Neither genus has been revised recently and either may turn out to be polyphyletic. As well, this study has captured a new species of *Cyrioctea*, the most primitive zodariid genus (considered the sister group to all zodariids) and only the second record from Australia (the other in Queensland), with the other species being found in Africa and South America.

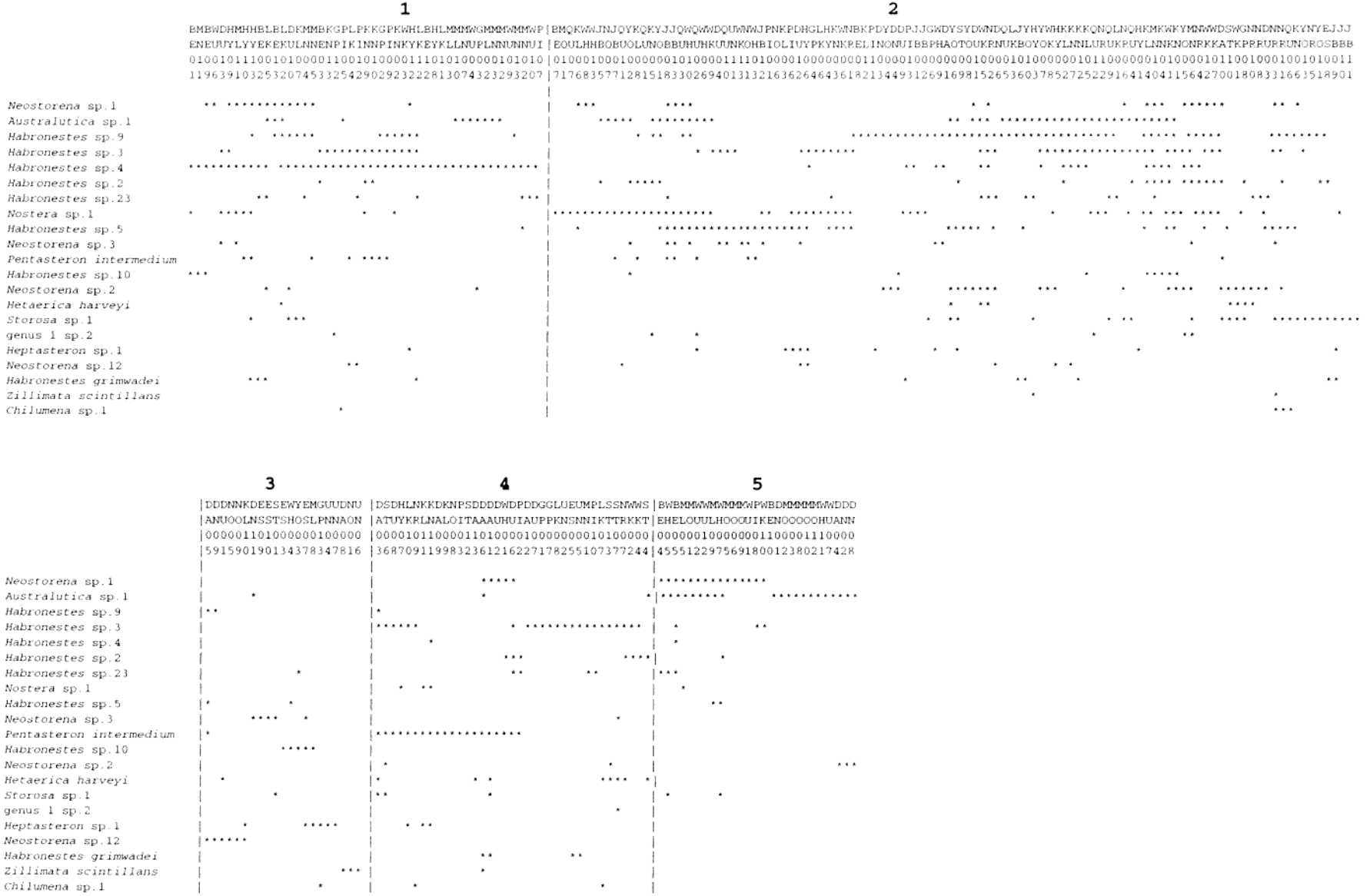
Species compositional patterns

Zodariid compositional patterns at the species level showed few significant relationships with the environmental factors recorded. The widespread subset showed relationships with aspects of climate, essentially a north-south changeover in composition. Furthermore the smaller-scale variables we measured, pertaining to soil and geology, appeared to have no significant influence on distribution patterns. This may be connected to

Table 3 Data matrix for disjunct zodariids reordered according to similarities in species composition. The groupings have been left in to show the reliance on single species in determining the groups. Quadrat codes are printed vertically with group numbers above each partition.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	BBDGHJJLMPQQWWY	BMBKMQ	KNNBBNMNDM	MPWMW	DD	DWK	JMMMNN	LMMYQ	DKNP	DDPD	HKNQWKWMWW	BBWBMW	DHPPPSDNN	DDEEEEEU	DDDDDEJJKMMWW	BBBDKKKKMMMMMMMMMQQQWWWYY
	EENPYBBKLIUUKKO	ELELNU	LOREEOOOAN	NIHNU	AN	NUN	BLLLOO	KLNOU	NNOI	AUIA	YLOUULUOUU	EEHELH	AYIIITUOO	UUSSSSSN	NNNN****BBNLLHH	EEEULLLNNOOOOOOOOOUUUUUUOO
	00001011001000	000000	0010101001	00110	00	110	000010	11000	1000	0010	0001000001	001101	000110011	00000011	0000100000000	01100010000000011001000100
	14660830013089 5	576225	4208371863	95227	27	023	956801	21444	2959	4527	1361399610	791043	582035721	68234602	1234111782928	21231722812345902792256112
Kerasteron sp.1		******	** ***	*	*			*		*	****	*		*		**********************************
Neostorena sp.4							*				**********					
Habronestes sp.6	**********	* ****	*	**							**		*			
Habronestes sp.18			*				*					******				
Cavasteron sp.1			*** *			**	*****	**						***		**********
Australutica quaerens	**						******		*							
Phenasteron longiconductor									****							
Nostera sp.9															*********	
Nostera sp.11			*		**											
Neostorena sp.14				*****		*										
Nostera sp.5						***										
Neostorena sp.13												*		*		
Asteron-complex sp.1													**********			
Neostorena sp.5			*****									*				
genus 2 sp.1			** **													
Neostorena victoria								****	*							
Neostorena sp.16								*		****						
Neostorena sp.15								*	*							

Table 4 Data matrix for regularly widespread zodariids reordered according to similarities in species composition at the optimal group level (5). Quadrat codes are printed vertically with group numbers above each partition.



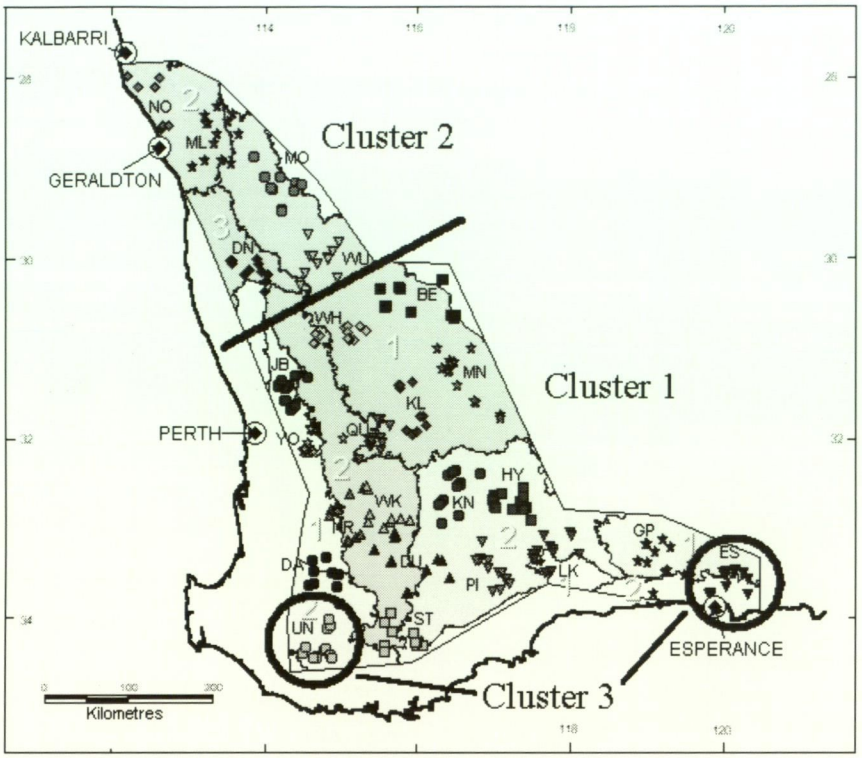


Figure 7 Study area showing the location of each of the clusters from Figure 4.

Table 5 ANOVA post-hoc test results (Neumann-Keuls) showing the significant differences between survey areas in terms of average quadrat species richness. Survey areas that share a letter are not significantly different from each other.

Survey Area	Richness	
UN	1.31	a
ES	1.62	ab
ST	2.38	abc
GP	2.46	abc
NO	3.25	abcd
MO	3.25	abcd
WH	3.46	abcd
ML	3.46	abcd
DN	3.50	abcd
WU	3.54	abcd
JB	3.77	abcd
LK	3.77	abcd
PI	3.85	abcd
BE	4.31	bcd
MN	4.62	cd
YO	4.85	cd
DA	4.85	cd
QU	4.92	cd
WK	4.92	cd
DU	5.08	cd
KL	5.25	cd
HY	5.31	cd
KN	5.92	d
NR	6.00	d

their high species diversity, because taxonomic diversity of spiders is believed to be highest in those groups which are environmentally tolerant and lack specialised feeding behaviour (Main, 1981). Adaptation to semi-arid and arid regions is indicative of the tolerance required for species diversity in Australia. Taxa that have a specialised behaviour tend to have less taxonomic diversity because of their inability to occupy numerous microhabitats (Main, 1981). The characterization of microhabitats involves topography, soil moisture and texture, canopy and litter cover, vegetation and prey potential (Main, 1996) of which most were included as part of this survey, albeit on a broader "quadrat" level. Main (1996) explains the variations that exist within a site, based on the microhabitat requirements of trapdoor spiders. The size and position of a microhabitat varies based on a species foraging behaviour and preference, which has allowed several species to coexist in non-competitive assemblages. Therefore species richness of trapdoor spiders could be determined by the degree of heterogeneity of a generalized habitat (Main, 1996). Whether this can be used to explain zodariid richness is uncertain given that variations in foraging behaviour within the group are unknown.

Most Australian zodariids are adapted for semi arid/arid regions, particularly areas with a distinct

Table 6 Number of quadrats in each landform type according to species richness.

	Dissection Profile Low in Landscape							Plateau Profile Top of Landscape					
Species Richness	Sw	Sf	Mo	A	Y	Mg	B	Bg	M	Qd	K	Qe	Total
0	6	7	4			1			1	3		1	23
1	2	4	10	1		1	2		6	1	2	2	31
2	3	2	7	3	3	1	4	2	3	7	3	1	39
3	1	2	12	3	3	6		2	4	1	3	3	40
4		1	6	5	3	8	2	2	6	7	5	6	51
5			4	6	8	5	4	1	2	12	2	5	49
6			5	3	4	4	3	1	3	1	1	4	29
7			2	3	2		2	1	1		1		12
8			1	2	1	1	3	1		3	2		14
9			3		1		1	1			1	1	8
10							3	1	1			1	6
11				1									1
12								1					1
Total	12	16	54	27	25	27	24	13	27	35	20	24	304

Table 7 ANOVA post-hoc test results (Neumann-Keuls) showing the significant differences in average quadrat species richness between each landform type. Landform types that share a letter are not significantly different from each other.

Landform	Richness	
Sw	0.92	a
Sf	1.12	a
Mo	3.39	b
M	3.44	b
Qd	3.89	bc
Mg	4.07	bc
K	4.25	bc
Qe	4.58	bc
Y	4.88	bc
A	4.89	bc
B	5.54	c
Bg	5.77	c

Table 8 ANOVA post-hoc test results (Neumann-Keuls) showing the significant differences in average quadrat drainage between each landform type. Landform types that share a letter are not significantly different from each other.

Landform	Drainage	
Sf	1.25	a
Sw	1.60	a
Mo	2.67	b
Mg	3.30	c
Y	3.32	bc
B	3.33	bc
A	3.63	cd
Qe	3.73	cd
Bg	3.92	cd
K	4.25	d
M	4.85	e
Qd	5.60	f

Table 9 ANOVA post-hoc test results (Neumann-Keuls) showing the significant differences in average quadrat salinity type between each landform type. Landform types that share a letter are not significantly different from each other.

Landform	Salinity	
Sf	4.00	a
Mo	2.80	b
A	2.70	b
Sw	2.20	c
B	2.04	c
Bg	1.38	d
Y	1.36	d
M	1.19	d
Mg	1.11	d
Qe	1.04	d
K	1.00	d
Qd	1.00	d

dry season (Jocqué and Baehr, 2001). They are extremely drought resistant and able to survive for periods of weeks to months without food or water (Jocqué, 1991). So they have adapted in a way that has allowed them to diversify. The compositional patterns revealed by the survey area analysis shows a distinct difference between those with a very dry summer period (DN, ML, NO, MO and WU) and those with a very wet one (ES and UN). ES and UN also had the two lowest levels of species richness.

Possibly the most influential aspects of zodariid natural history on their distribution patterns is poor dispersal. One of the main methods of dispersal in some but not all spiders is ballooning, using gossamer silk to disperse, usually as a juvenile, on wind currents. This method has not been recorded in the zodariidae, making them prone to endemism. The high proportion of localised species in this

study, 78 from 117, seems to support the view that the Zodariidae are unable to disperse far. Also 37 of the 78 were species recorded at only a single quadrat, indicating either short range endemism or sampling artefacts. This, along with the fragmentation of the wheatbelt region through both recent agricultural use and geoclimatic changes since the Tertiary, seems to have resulted in a large number of geographically restricted species.

Zodariids are also obligate ant feeders which, as a specialised feeding behaviour, would normally constrain their diversity. However the arid regions have the highest richness of ants in Australia, even compared to wetter regions in other countries (Shattuck, 1999). Therefore prey specificity does not appear to impinge on zodariid diversity. Ants were not looked at in this survey but previous work has shown that the highest richness of ants usually occurs in regions of rainfall transition (Shattuck, 1999), in this case the central wheatbelt

This family appears to have a level of diversity that would indicate a high dependence on microhabitats despite what, on first appearance, would seem a diversity constraining diet. The broad scale of the environmental and geological variables used in this study does little to explain overall species composition, particularly among the localised and disjunct types. Microhabitat surveys may help determine factors affecting species composition.

Species Richness

Differences in species richness were also significant, both between survey areas and landform types. The central wheatbelt, identified in this survey as having higher richness than the southern and northern parts, is included in an area referred to as the transitional rainfall zone (Hopper, 1979). This region, which does not include the wetter southern and drier north eastern wheatbelt, has been subjected to the greatest environmental and geological modification imposed by early Tertiary geoclimatic changes. This has resulted in a mosaic pattern of soils allowing high levels of speciation combined with the retention of relictual species (Hopper, 1979). Although this work originally dealt with botanical species, Main (1996) used the concept as a basis for discussing the biogeography of trapdoor spiders at Durokoppin (in the central wheatbelt). Main explained that certain spider groups have speciated alongside climatic and geological changes leading to very high species richness and the coexistence of relictual and derived taxa. Given that the Zodariidae are a Gondwanan taxonomic group, which have a similar life history to the Mygalomorphae, they may have speciated in a similar way.

A distinct trend exists between quadrats and soil attributes correlated with landform level and drainage, e.g. salinity, exchangeable Na, electrical conductivity. There was also minor correlation with a few climatic variables including minimum coldest period temperature, temperature annual range and average annual rainfall. It is clear that a much lower level of species richness exists in areas where the water table is close to or on the surface (i.e. low drainage). This could also be attributed to the lack of microhabitat variation, but given that the level of microhabitat richness of the valley floors would vary greatly between saline and freshwater quadrats, this is unlikely

Burrowing within the Zodariidae is well documented, but data on burrow architecture are known for very few species. All of the species from this survey had at least light spination (still very noticeable but fewer in numbers and generally shorter and thinner) on the third and fourth legs, and most had moderate to heavy spines, a character associated with burrowing (Jocqué, 1991). As well, those with only light spination had at least moderately heavy spines on the distal edge of the palp, another character that is likely associated with digging, although only one species had a large, terminal palpal claw, like that of the genus *Cavasteron*, which is possibly used to break lichen-crusted sand for digging (Baehr and Jocqué, 2000). Whether soil structure has an affect on their ability to burrow is unknown. The moist soils may be difficult to construct burrows in, or allow them to bury themselves like the primitive genera *Cyrioctea* (Platnick, 1986) and *Lutica* (Ramirez and Beckwitt, 1995), compared to either the loose, dry sand of the plateaus or the firmer soils of the lower and middle landforms. Also, unlike other burrowing families (e.g. Lycosidae and Mygalomorphae), few zodariids may have developed the ability to build burrows to withstand flooding. This would be a necessity for ground dwelling spiders in low drainage areas, particularly those with high rainfall such as the UN, ES, GP and ST survey areas which had the lowest species richness.

The availability of prey is another factor worth considering. Ant species richness is greatest in semi-arid regions of Australia, particularly near transition zones where the arid and temperate/tropical species overlap (Shattuck, 1999). The low drainage saline areas would almost certainly have low ant species richness because of the low vegetation diversity, lack of nectar flow (no flowering plants and thus little prey activity) and few microhabitats. However the freshwater swamps, which have much greater vegetation diversity and structure, would likely have very good ant species richness (B. Heterick, pers. comm.). Therefore it is unlikely that ant richness is a major factor, at least in the freshwater swamp areas.

A number of factors could be seen to be influencing zodariid species richness and

distribution patterns within the wheatbelt although from this survey no one factor stands out consistently. It does seem, however, that general habitat variables have less influence than the factors involved in microhabitat determination. The biggest hurdle is our lack of knowledge of zodariid taxonomy and ecology, particularly dispersal, food preference and burrowing.

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REFERENCES

Baehr, B. and Jocqué, R. (1996). A revision of *Asteron*, starring male palpal morphology (Araneae, Zodariidae). *Revue Suisse de Zoologie, hors série*: 15–28.

Baehr, B. and Jocqué, R. (2000). Revisions of genera in the *Asteron*-complex (Araneae, Zodariidae). The new genera *Cavasteron* and *Minasteron*. *Records of the Western Australian Museum* **20**: 1–30.

Baehr, B. and Jocqué, R. (2001). Revisions of genera in the *Asteron*-complex (Araneae: Zodariidae): new genera *Pentasteron, Phenasteron, Leptasteron* and *Subasteron*. *Memoirs of the Queensland Museum* **46**: 359–385.

Belbin, L. (1995). *PATN technical reference*. CSIRO, Canberra.

George, R.J., Clarke, C.J. and Hatton, T.J. (2001). Computer modelled groundwater response to recharge management for dryland salinity control in Western Australia. *Advances in Environmental Monitoring and Modelling* **2**: 3–35.

George, R. and Coleman, M. (2002). Hidden menace or opportunity – groundwater hydrology, playas and commercial options for salinity in wheatbelt valleys. *In* V. Read & Associates (ed.), Dealing with sailinity in wheatbelt valleys: processes, prospects and practical options: 1–21. Water and Rivers Commission, Perth. (Available on CD)

Guthrie, N.A. and Waldock, J.M. (2004). Patterns in the composition of the jumping spider (Araneae: Salticidae) assemblage from the Wheatbelt region, Western Australia. *Records of the Western Australian Museum Supplement* **67**: 187–200.

Hart, B.T., Bailey, P., Edwards, R., Hortle, K., McMahon, A., Meredith, C. and Swadling, K. (1990). Effects of salinity on river, stream and wetland ecosystems in Victoria, Australia. *Water Research* **24**, 1103–1117.

Hopper, S.D. (1979). Biogeographical aspects of speciation in the south-west Australian flora. *Annual Review of Ecological Systematics* **10**: 399–422.

Jocqué, R. (1991). A generic revision of the spider family Zodariidae (Araneae). *Bulletin of the American Museum of Natural History* **201**: 1–160.

Jocqué, R. (1992). A new species and the first males of *Suffasia*, with a redilimitation of the subfamilies of the Zodariidae (Araneae). *Revue Suisse de Zoologie* **99**: 3–9.

Jocqué, R. (1993). "We'll meet again", an expression remarkably applicable to the historical biogeography of Australian Zodariidae (Araneae). *Memoirs of the Queensland Museum* **33**: 561–564.

Jocqué, R. (1995). Notes on Australian Zodariidae (Araneae), I. New taxa and key to the genera. *Records of the Australian Museum* **47**: 117–140.

Jocqué, R. and Baehr, B. (1992). A revisions of the Australian spider genus *Storena* (Araneae, Zodariidae). *Invertebrate Taxonomy* **6**: 953–1004.

Jocqué, R. and Baehr, B. (1995). A supplement to the revision of the Australian spider genus *Storena* (Araneae, Zodariidae). *Records of the Western Australian Museum* Supplement **52**: 135–144.

McKenzie, N.L., Gibson, N., Keighery, G.J. and Rolfe, J.K. (2004). Patterns in the biodiversity of terrestrial environments in the Western Australian wheatbelt. *Records of the Western Australian Museum Supplement* **67**: 277–319.

McMahon, J.P., Hutchinson, M.F., Nix, H.A. and Ord, K.D. (1995). *ANUCLIM users guide, version 1*. Centre for Resource and Environmental Studies, Australian National University, Canberra.

Main, B.Y. (1976). *Spiders*. Collins Sydney.

Main, B.Y. (1981). Australian spiders: Diversity, distribution and ecology. *In* A. Keast (ed.), Ecological biogeography of Australia, vol. 2: 807–852. Dr W. Junk, The Hague.

Main, B.Y. (1996). Microcosmic biogeography: trapdoor spiders in a time warp at Durokoppin. *In* S.D. Hopper, J.A. Churchill, M.S. Harvey and A.S. George (eds), *Gondwanan Heritage: Past, Present and Future of the Western Australian Biota: 163–171*. Surrey Beatty, Sydney.

Mulcahy, M.J. (1978). Salinisation in the southwest of Western Australia. *Search* **9**, 269–272.

Mulcahy, M.J. and Hingston, F.J. (1998). The Development and Distribution of the soils of the York-Quairading Area, Western Australia, in Relation to Landscape Evolution. Soil Publication 17. CSIRO, Canberra.

Platnick, N.I. (1986). A review of the spider genus *Cyrioctea* (Araneae, Zodariidae). *American Museum Novitates* **2858**: 1–9.

Platnick N.I. and Griffin, E. (1988). On the first African and Australian spiders of the genus Cyrioctea (Araneae: Zodariidae). *Journal of the New York Entomological Society* **96**: 359–362.

Ramirez, M.G. and Beckwitt, R.D. (1995). Phylogeny and historical biogeography of the spider genus *Lutica* (Araneae, Zodariidae). *Journal of Arachnology* **23**: 177–193.

Ruprecht, J.R. and Schofield, N.J. (1991). Effects of partial deforestation on hydrology and salinity in high salt storage landscapes. I. block clearing. *Journal of Hydrology* **129**: 19–38.

Shattuck, S.O. (1999). *Australian Ants: their biology and identification*. CSIRO, Collingwood.

Sneath, P.H.A. and Sokal, R.R. (1973). *Numerical taxonomy. The principles and practice of numerical classification*. W.H. Freeman, San Francisco.

Thackway, R. and Cresswell, I.D. (eds) (1995). *An interim biogeographic regionalisation for Australia: A framework for setting priorities in the National Reserves Cooperative Program, version 4.0*. Australian Nature Conservation Agency, Canberra.

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