

SCORPION DIVERSITY AND DISTRIBUTION IN SOUTHERN AFRICA: PATTERN AND PROCESS

Lorenzo Prendini

Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA, E-mail: lorenzo@amnh.org

Abstract: Patterns of scorpion diversity and distribution in southern Africa (south of 15° latitude), and the processes that produced them, are reviewed. A georeferenced presence-only dataset, comprising 6766 point locality records for the 140 scorpion species currently recognised in the subregion, is compiled and analysed with a geographical information system. Hotspots of scorpion species richness and endemism in southern Africa are mapped at the level of a quarter-degree square. The taxonomic composition of the southern African scorpion fauna is assessed and found to comprise distinct western and eastern components. Hotspots of species richness and endemism are concentrated in arid regions with rugged topography, complex geology, or substratal heterogeneity. The distributions of genera and species are discussed in terms of their ecological requirements and modes of speciation within the context of historical events. Historical changes in the geomorphology and climate of southern Africa, coupled with the specific ecological requirements of most southern African scorpions, are proposed as primary causes for their speciation and, ultimately, their high species richness and endemism.

Key words: Chelicerata; Scorpiones; southern Africa; diversity; endemism; distribution; GIS; hotspot; taxonomy; evolution; speciation; biogeography

1. INTRODUCTION

Predictable, non-random patterns characterise the spatial distribution of most taxa (MacArthur, 1972; Myers and Giller, 1988), and scorpions are no exception. The distribution of scorpions has interested arthropod biogeographers for more than a century (Pocock, 1894, Kraepelin, 1905;

Birula, 1917a, 1917b, 1925; Hewitt, 1925; Lawrence, 1952; Lamoral, 1980a; Stockwell, 1989; Sissom, 1990; Nenilin and Fet, 1992; Lourenço, 1996, 1998, 2000; Soleglad and Fet, 2003). Scorpions allow opportunities for ecological and historical biogeographic investigation almost unparalleled among Arthropoda. One reason for using scorpions as model taxa in biogeographic studies is the antiquity of the group. Fossil records show that scorpions have existed in the terrestrial environment since the middle Silurian, over 400 MYA, and are almost unchanged today (Jeram, 1990a, 1990b, 1994a, 1994b; Selden, 1993; Sissom, 1990). Scorpion distribution patterns often reveal evidence of continental drift (Koch, 1977, 1981; Lourenço, 1984a, 1991a, 1996, 1998, 2000; Stockwell, 1989; Sissom, 1990) or palaeoclimatic change (Lourenço, 1994a, 1994b, 1996). A similarity in the habits and ecological requirements of fossil and modern scorpions may be inferred from their morphological conservatism (Jeram, 1990b). It is thus reasonable to assume that the ecological factors determining scorpion distributions today are similar to those which determined their distributions in the past.

Scorpions are also useful for biogeographic studies because of their diversity (Lourenço, 1994c). Scorpions occur on all major landmasses except Antarctica, and on many oceanic islands, in all terrestrial habitats – including high-elevation mountaintops, caves, and the intertidal zone – except tundra and high-latitude taiga (Polis, 1990; Gromov, 2001). Diverse communities of scorpions (4–13 species) occur in habitats as different as desert (Williams, 1980) and tropical rainforest (González-Sponga, 1978, 1984, 1996; Lourenço, 1983a). Many ecological factors influence the spatial distribution of scorpions, including temperature, precipitation, soil or rock characteristics, stone or litter cover, topography, vegetation, and environmental physiognomy (Polis, 1990). Some of these factors, e.g. the substratum, may be important determinants of their evolution and may underpin broad patterns of geographical distribution (Lamoral, 1978a; Prendini, 2001a). For example, the sedentary nature of most scorpion species, together with their often narrow physiological and ecological tolerances (Polis, 1990), may have limited their vagility and promoted allopatric speciation by vicariance during periods of palaeoclimatic change (Lamoral, 1978b; Prendini, 2001a), in turn creating high levels of endemism in certain areas, e.g. Baja California (Williams, 1980).

The prevalence of relictual, endemic scorpion species in certain areas may warrant their biogeographic investigation as models for arthropod conservation (Lourenço, 1991b). The importance of knowing the distribution of venomous scorpions, from a medical perspective, is yet another reason to study their biogeography (Newlands, 1978b; Newlands and Martindale, 1980). The ecological abundance and medical importance of scorpions has also ensured their good representation in museum

collections. The taxonomic diversity of scorpions is thus better understood, worldwide, than that of many other arthropod taxa. Both factors, in turn, guarantee greater accuracy in biogeographic investigations of the distributions of species or higher taxa.

The rich scorpion fauna of the southern African subregion was recognised at the turn of the previous century. Hewitt (1925) identified a difference between the scorpion species composition of the northeastern and southwestern parts of the subregion, and proposed that the most southerly species were primitive, species further north being more advanced. Hewitt's work was published before the theories of continental drift and plate tectonics were widely accepted, and concentrated on dispersalist rather than vicariance arguments. It also failed to address the ecology of the group. Lawrence (1942, 1952) noted the same distinction between the eastern and western scorpion faunas, but attributed the relative paucity of the eastern fauna entirely to ecological factors, while neglecting the role of history. Later theories about scorpion distribution patterns in southern Africa (Newlands, 1972a, 1972b, 1978a, 1978b, 1980; Lamoral, 1978b, 1979) also failed to accommodate ecological explanations within a historical context.

Such criticisms are not reserved solely for studies of scorpion biogeography, but extend to biogeographic studies of many other taxa. Few authors (see, for example, references in Werger (1978) and Keast (1981)) consider patterns of distribution in terms of ecology and history, despite the undeniable influence of both (Haydon et al., 1994). Myers and Giller (1988: 3) warn that "to progress, biogeography must attempt to ... determine how speciation, adaptation, extinction and ecological processes interact with one another and with geology and climate to produce distributional patterns in the world's biota through time."

In this contribution, a distributional dataset for the southern African scorpion species is compiled and analysed with a geographical information system (GIS). Using evidence from the literature, the observed patterns of diversity and distribution are interpreted as the outcome of two interacting sets of circumstances: (1) ecological factors, i.e. the distribution of environmental gradients, the ecological requirements of the species, and the biotic component of species interactions; (2) historical factors, i.e. past, often chance events that have determined the occurrence of a species in particular localities, e.g. dispersal, vicariance, and speciation (Koch, 1977).

2. METHODS

2.1 Taxonomic considerations

Traditionally, all southern African scorpions were placed into Buthidae C.L. Koch, 1837 or Scorpionidae Latreille, 1802 (Hewitt, 1918, 1925; Lawrence, 1955; Lamoral and Reynders, 1975; Lamoral, 1978b, 1979; Newlands, 1978a, 1978b, 1980; Newlands and Martindale, 1980; Newlands and Cantrell, 1985). Today, they are divided among Bothriuridae Simon, 1880, Buthidae, Liochelidae Fet and Bechly, 2001, and Scorpionidae.

Bothriuridae are represented in southern Africa by two genera: *Brandbergia* Prendini, 2003; *Lisposoma* Lawrence, 1928. Although previously known to share similarities with the bothriurids (Vachon, 1974), *Lisposoma* was retained in Scorpionidae, in a unique subfamily, Lisposominae Lawrence, 1928 (Lawrence, 1955; Lamoral, 1978b, 1979), until Francke (1982) transferred it to Bothriuridae. Lourenço's (2000) creation of a unique family, Lisposomidae Lawrence, 1928, for the genus is unsupported by cladistic analysis (Prendini, 2000a, 2003a, 2003b). *Lisposoma* was revised by Prendini (2003b).

Six genera of Buthidae were recognised in southern Africa (*Buthotus* Vachon, 1949; *Karasbergia* Hewitt, 1913; *Lychas* C.L. Koch, 1845; *Parabuthus* Pocock, 1890; *Pseudolychas* Kraepelin, 1911; *Uroplectes* Peters, 1861) until a seventh, *Afroisometrus* Kovařík, 1997, was created to accommodate a species of *Lychas* from Zimbabwe (FitzPatrick, 1994a). Francke (1985) demonstrated that *Buthotus* is a junior synonym of *Hottentotta* Birula, 1908. Southern African *Parabuthus* have been studied intensively in recent years and 20 species are currently recognised from the subregion (FitzPatrick, 1994b; Prendini 2000b, 2001b, 2003c, 2004a). The species composition of *Karasbergia* and *Pseudolychas* remains unaltered following recent revisions (Prendini 2004b, in press). *Uroplectes* currently contains 19 southern African species (FitzPatrick, 1996, 2001; Fet and Lowe, 2000), but requires extensive revision; the genus is undoubtedly more diverse than *Parabuthus*.

Liochelidae, until recently known as Ischnuridae Simon, 1879, contains three southern African genera formerly assigned to subfamily Ischnurinae Simon, 1879 of Scorpionidae (Lourenço, 1989; Sissom, 1990): *Cheloctonus* Pocock, 1892; *Hadogenes* Kraepelin, 1894; *Opisthacanthus* Peters, 1861. A fourth genus, *Iomachus* Pocock, 1893, with one species, *Iomachus politus* Pocock, 1896, widespread in eastern Africa (Ethiopia, Kenya, Tanzania, Uganda and the Democratic Republic of Congo), and also recorded from northeastern Mozambique (Kraepelin, 1913; Werner, 1936), has not been confirmed as occurring south of 15° latitude; records of *I. politus* from Beira

(Werner, 1936; Aguiar, 1978) are almost certainly erroneous. *Opisthacanthus* was revised by Lourenço (1987a) but the validity of several southern African species remains questionable, as does the validity of *Cheloctonus* and its component species, which remain to be addressed (Prendini, 2000a). *Hadogenes*, presently containing 16 species, is the subject of ongoing revision by the author (Newlands and Prendini, 1997; Prendini, 2001c, in press). Lourenço's (1999, 2000) proposals to transfer this genus to Scorpionidae, or to create a unique family, Hadogenidae Lourenço, 2000, to accommodate it, are unsupported by cladistic analysis (Prendini, 2000a, 2001c).

Opisthophthalmus C.L. Koch, 1837 remains the sole representative of Scorpionidae in southern Africa. This diverse genus, also under revision by the author, currently contains 59 valid species (Prendini, 2000c, 2001d; Harington, 2002). The actual number is closer to 80 (Prendini et al., 2003). To date, no records of *Pandinus viatoris* (Pocock, 1890), a scorpionid widespread in central Africa (recorded from the Democratic Republic of Congo, Malawi, Tanzania, Zambia, and northwestern Mozambique), have been confirmed as occurring south of 15° latitude. Alleged records of this species from Zimbabwe (Lamoral and Reynders, 1975; Fet, 2000a) are actually in Zambia (Prendini et al., 2003). A single record from Maputo (Aguiar, 1978) is erroneous.

The status of many southern African scorpion species and subspecies, particularly within *Uroplectes* and the liochelid genera, remains contentious in spite of intensive taxonomic work. However, for the purpose of this study, the taxonomy reflected by the most recent published treatments was employed, according to which 140 species are presently recognised from Africa south of 15° latitude (Appendix 1). Subspecies were not considered, although some will certainly be elevated to species in future revisions.

2.2 Distributional data

Point locality data for each species were collated from available published locality records. Lamoral and Reynders' (1975) catalogue of the scorpions described from the Afrotropical Region up to December 1973 was used for all the early records. Remaining (post-1975) records were obtained from the following works: Eastwood (1977a, 1977b, 1978a, 1978b); Harington (1978, 1984, 2002); Lamoral (1978b, 1979, 1980b); Lourenço (1981, 1987a); Newlands (1980); Newlands and Martindale (1980); Newlands and Cantrell (1985); Fitzpatrick (1994a, 1994b, 1996, 2001); Newlands and Prendini (1997); Prendini (2000b, 2000c, 2001b, 2001c, 2003a, 2003b, 2003c, 2004a, 2004b, in press).

Literature records were supplemented with records of personally identified specimens deposited in the following collections: Austria: Zoologisches Institut und Naturhistorisches Museum, Universität Wien; Belgium: Musée Royal de l'Afrique Centrale, Tervuren; Denmark: Zoological Museum, University of Copenhagen; France: Museum National d'Histoire Naturelle, Paris; Germany: Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt; Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; Zoologisches Institut und Zoologisches Museum, Universität Hamburg; Zoologisches Museum, Universität Humboldt, Berlin; Namibia: Desert Research Foundation of Namibia, Gobabeb; National Museum of Namibia, Windhoek; South Africa: Albany Museum, Grahamstown; Kruger National Park Reference Collection, Skukuza; KwaZulu-Natal Nature Conservation Service, Pietermaritzburg; McGregor Museum, Kimberley; Natal Museum, Pietermaritzburg; National Collection of Insects and Arachnids, Plant Protection Research Institute, Pretoria; National Museum, Bloemfontein; South African Museum, Cape Town; Transvaal Museum, Pretoria; University of Natal, Pietermaritzburg; Sweden: Göteborgs Naturhistoriska Museet, Göteborg; Naturhistoriska Riksmuseet, Stockholm; Zoologiska Institutionen, Lunds Universitet; Switzerland: Musée d'Histoire Naturelle, La-Chaux-de-Fond; Muséum d'Histoire Naturelle, Genève; The Netherlands: Zoologisch Museum, Universiteit van Amsterdam; U.S.A.: American Museum of Natural History, New York; California Academy of Sciences, San Francisco; Field Museum of Natural History, Chicago; Museum of Comparative Zoology, Harvard University, Cambridge, MA; U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC; U.K.: The Natural History Museum, London; Zimbabwe: Natural History Museum of Zimbabwe, Bulawayo.

2.3 Georeferencing

All records of sufficient accuracy were collated to create a point locality geographical dataset for mapping distributional ranges. Only a small proportion of the records were initially accompanied by geographical coordinates or quarter-degree squares (QDS). Localities defined in degrees and minutes latitude and longitude (accurate to within 1.7 km²) were used preferentially, whenever possible, owing to their high level of spatial resolution. All such localities were, in turn, converted to decimal-degree format for GIS input. Many localities were, however, only available in QDS notation (de Meillon et al., 1961). A decimal-degree approximation for the centroid of the QDS was used for these records, as a centroid would always be situated nearest to the average locality. For example, a locality registered

as occurring in QDS SE1927Ac would be recorded as -19.375/27.125. As a QDS covers an area of approximately 26 km² in southern Africa (Poynton, 1964), this may result in some loss of resolution. Augmenting accurate locality records with QDS centroids yields distribution maps at least as accurate as maps using the QDS notation system (Newlands, 1980; Newlands and Martindale, 1980).

Available georeferences were checked for accuracy and an attempt was made to trace coordinates for as many remaining records as possible by reference to gazetteers, the official 1:250 000 and 1:500 000 topo-cadastral maps of Namibia, Botswana, Lesotho, South Africa and Swaziland published by the Government Printer of South Africa, and the GEONet Names Server: http://164.214.2.59/gns/html/cntry_files.html. This database is based on gazetteers published by U.S. National Imagery and Mapping Agency for the U.S. Board on Geographic Names, which contain the standard names approved for official use, unapproved variant names, designations (cities, mountains, rivers, etc.) and coordinates: <http://geonames.usgs.gov/bgngaz.html>. The following regional gazetteers and lists of place-names were consulted: Gross (1920); Doidge (1950); Webb (1950); National Place Names Committee (1951, 1978, 1988); Ministry of Land and Natural Resources (1959); Gonçalves (1962); Davis & Misonne (1964); Poynton (1964); Copeland (1966); Ministry of Land and Mines (1967); SWALU (1967); Postmaster-General (1970); Surveyor-General (1970, 1988); Coaton and Sheasby (1972); Skead (1973); Haacke (1975); Penrith (1975, 1977, 1979, 1981a,b, 1987); Leistner and Morris (1976); Lamoral (1979); Bamps (1982); Raffle (1984); Poynton and Broadley (1985a,b, 1987); Raper (1987); Irish (1988); Polhill (1988); *Flora Zambesiaca: Gazetteer of Localities* (unpublished document, Bolus Herbarium Library, University of Cape Town); Herpetology Department, Transvaal Museum (unpublished records); Entomology Department, South African Museum (unpublished records).

Doubtful localities, discussed in the literature, and single, highly disjunct records that could not be verified, were omitted. After screening for errors, the final species presence-only dataset (*sensu* Mugo *et al.* 1995) was submitted to the GIS for mapping and spatial analysis. A total of 6 766 data points were collated.

2.4 Spatial analysis

Digital distribution maps were produced for each species by superimposing point locality records on a dataset representing the political boundaries of southern Africa (south of 15° latitude), using ArcView GIS Version 3.2 (Environmental Systems Research Institute, Redlands, CA). A

spatial join was then conducted by superimposing scorpion distributions on a dataset representing the QDS grid of southern Africa, to determine scorpion hotspots, i.e. areas of high species richness and endemism (Myers et al., 2000), at the scale of a QDS (Lombard, 1995a, 1995b). Hotspots were based on measures of species richness (all 140 species) and endemism (including only southern African endemics), which may reflect centres of endemism, or regions of speciation, given that most scorpion species are sedentary (Polis, 1990; Harington, 1984), and probably experience minimal range-shifting.

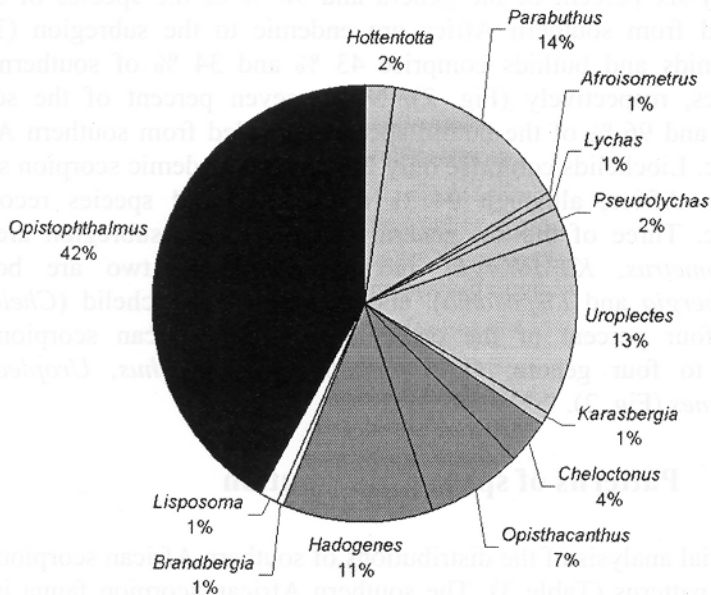
Spatial joins were also conducted to determine to what extent scorpion distributions are explained by topography, major sand systems and river drainage in southern Africa. A topographic contour dataset was created from the GTOPO30 raster grid, obtained from the website of the U.S. Government Public Information Exchange Resource: <http://edcdaac.usgs.gov/gtopo30/gtopo30.html>. The dataset of sand systems was created by clipping and merging relevant polygons extracted from a dataset of African geology from the Department of Marine Geoscience, University of Cape Town, with polygons extracted from a dataset of Namibian landforms from the Namibian National Biodiversity Task Force (Barnard, 1998), downloaded from: <http://www.dea.met.gov.na/programmes/biodiversity/countrystudy.htm>. A dataset of major rivers in southern Africa was created by merging polygons extracted from a dataset of Namibian rivers from the website of the Namibian National Biodiversity Task Force (Barnard, 1998) with a dataset of South African rivers from the *Surface Water Resources of South Africa 1990* (WR90) database (Midgley et al., 1994), of the Water Research Commission, South Africa.

3. RESULTS

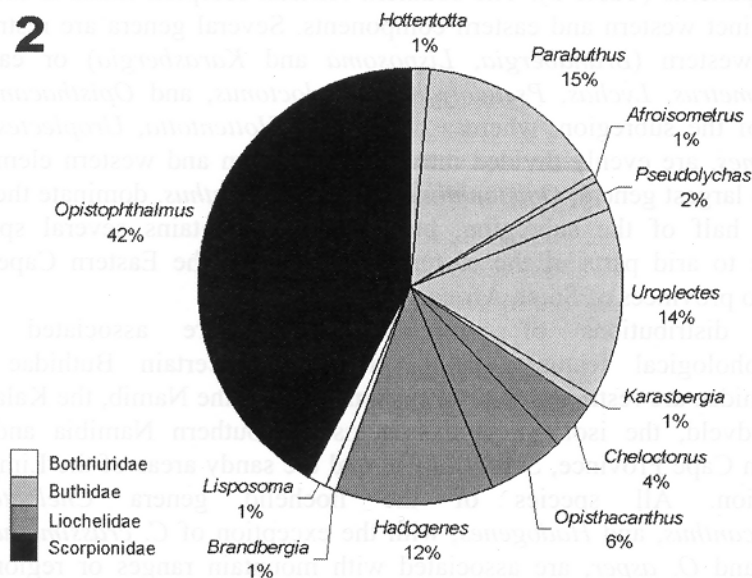
3.1 Composition of the fauna

Scorpionidae and Buthidae respectively comprise 42 % and 34 % of the southern African scorpion species, whereas Liochelidae and Bothriuridae respectively comprise 22 % and 2 % thereof (Fig. 1; Table 1). Despite a similar proportion of species, buthids comprise 54 % of the southern African scorpion genera, whereas scorpionids comprise only 8 %; liochelids and bothriurids respectively comprise 22 % and 15 % thereof. Eighty-one percent of the southern African scorpion species belong to four genera: *Opisthophthalmus*, *Parabuthus*, *Uroplectes*, and *Hadogenes*.

1



2



Figures 1,2. 1. Proportion of species in the families and genera of southern African scorpions. 2. Proportion of endemic species in the families and genera of southern African scorpions.

Forty-six percent of the genera and 96 % of the species of scorpions recorded from southern Africa are endemic to the subregion (Table 2). Scorpionids and buthids comprise 43 % and 34 % of southern African endemics, respectively (Fig. 2). Ninety-seven percent of the scorpionid species and 96 % of the buthid species recorded from southern Africa are endemic. Liochelids comprise only 21 % of the endemic scorpion species in southern Africa, although 94 % of the liochelid species recorded are endemic. Three of the six genera endemic to the subregion are buthids (*Afroisometrus*, *Karasbergia* and *Pseudolychas*), two are bothriurids (*Brandbergia* and *Lisposoma*), and the last is a liochelid (*Cheloctonus*). Eighty-four percent of the endemic southern African scorpion species belong to four genera: *Opisththalmus*, *Parabuthus*, *Uroplectes*, and *Hadogenes* (Fig. 2).

3.2 Patterns of species distribution

Spatial analysis of the distributions of southern African scorpions reveals several patterns (Table 3). The southern African scorpion fauna is divided into distinct western and eastern components. Several genera are restricted to the western (*Brandbergia*, *Lisposoma* and *Karasbergia*) or eastern (*Afroisometrus*, *Lychas*, *Pseudolychas*, *Cheloctonus*, and *Opisthacanthus*) halves of the subregion, whereas others, e.g. *Hottentotta*, *Uroplectes* and *Hadogenes*, are evenly divided into distinct eastern and western elements. The two largest genera, *Opisththalmus* and *Parabuthus*, dominate the arid western half of the subregion, but each also contains several species endemic to arid parts of the eastern half, such as the Eastern Cape and Limpopo provinces of South Africa.

The distributions of particular species are associated with geomorphological features of the landscape. Certain Buthidae and Scorpionidae are restricted to sand systems such as the Namib, the Kalahari, the Sandveld, the isolated sand systems of southern Namibia and the Northern Cape Province, South Africa, and the sandy areas of the Limpopo Depression. All species of the liochelid genera *Cheloctonus*, *Opisthacanthus*, and *Hadogenes*, with the exception of *C. crassimanus*, *C. jonesii* and *O. asper*, are associated with mountain ranges or regions of rugged topography, as are many species in the scorpionid genus *Opisththalmus*. *Hadogenes* is absent from the Kalahari and vast areas of the Cape Middleveld, the Free State, and the Karoo, as well as from the Springbok flats of the Limpopo Province, the sandy Mozambique plains and Makatini flats of northern KwaZulu-Natal Province, and the sandy areas of

Table 1. Scorpion diversity in southern African countries, south of 15° latitude. Percentages of the total are provided in parentheses. Questionmarks reflect suspected occurrences that remain to be verified. Abbreviations as follows: A (Angola); B (Botswana); L (Lesotho); Ma (Malawi); Mo (Mozambique); N (Namibia); SA (South Africa); S (Swaziland); Za (Zambia); Zi (Zimbabwe); E (Extralimital).

Family	Genus	Sth. Africa	A	B	L	Ma	Mo	N	SA	S	Za	Zi	E
Bothriuridae	<i>Brandbergia</i>	1 (1)						1 (100)					
	<i>Lisposoma</i>	2 (1)						2 (100)					
	Total	3 (2)						3 (100)					
Buthidae	<i>Afroisometrus</i>	1 (1)						?	1 (100)			1 (100)	
	<i>Hottentotta</i>	3 (2)	1 (33)	1 (33)	?		1 (33)	2 (67)	2 (67)		1 (33)	1 (33)	1 (33)
	<i>Karasbergia</i>	1 (1)						1 (100)	1 (100)				
	<i>Lychas</i>	1 (1)				1 (100)	1 (100)	1 (100)	1 (100)				1 (100)
	<i>Parabuthus</i>	20 (14)	4 (20)	7 (35)	?		2 (10)	15 (75)	15 (75)		1 (100)	3 (15)	5 (25)
Liochelidae	<i>Pseudolychas</i>	3 (2)					1 (33)		3 (100)				
	<i>Uroplectes</i>	19 (14)	3 (16)	5 (26)	2 (11)	1 (5)	6 (32)	10 (53)	15 (79)	4 (21)	4 (21)	6 (32)	
	Total	48 (34)	8 (17)	13 (27)	2 (4)	2 (4)	11 (23)	28 (58)	38 (79)	5 (10)	9 (19)	14 (29)	2 (4)
	<i>Cheloctonus</i>	5 (4)		?			1 (20)		5 (100)	1 (20)	?	?	
Scorpionidae	<i>Hadogenes</i>	16 (11)	1 (6)	2 (13)	?		2 (13)	4 (25)	12 (75)	1 (6)	1 (6)	2 (13)	
	<i>Opisthacanthus</i>	10 (7)		1 (10)	2 (20)	2 (20)	2 (20)		6 (60)	3 (30)	?	2 (20)	2 (20)
	Total	31 (22)	1 (3)	3 (10)	2 (6)	2 (6)	5 (16)	4 (13)	23 (74)	5 (16)	1 (3)	4 (13)	2 (6)
Total	<i>Opisththalmus</i>	59 (42)	5 (8)	6 (10)	1 (2)	1 (2)	3 (5)	28 (47)	39 (66)	?	2 (3)	4 (7)	2 (3)
	Genera	13	5 (38)	6 (46)	3 (23)	5 (38)	9 (69)	8 (62)	11 (85)	5 (38)	6 (46)	7 (54)	7 (54)
	Species	140	9 (6)	22 (16)	5 (4)	5 (4)	19 (14)	63 (45)	100 (71)	10 (7)	12 (9)	22 (16)	6 (4)

Table 2. Scorpion endemism in southern African countries, south of 15° latitude. Percentages of the total are provided in parentheses. Abbreviations as follows: A (Angola); N (Namibia); SA (South Africa).

Family	Genus	Sth. Africa	A	N	SA
Bothriuridae	<i>Brandbergia</i>	1 (1)		1 (100)	
	<i>Lisposoma</i>	2 (1)		2 (100)	
	Total	3 (2)		3 (100)	
Buthidae	<i>Afroisometrus</i>	1 (1)			
	<i>Hottentotta</i>	2 (1)			
	<i>Karasbergia</i>	1 (1)			
	<i>Parabuthus</i>	20 (15)		5 (25)	3 (15)
	<i>Pseudolychas</i>	3 (2)			2 (67)
	<i>Uroplectes</i>	19 (14)		3 (16)	4 (21)
	Total	46 (34)		8 (17)	9 (20)
	Liochelidae	<i>Cheloctonus</i>	5 (4)		
<i>Hadogenes</i>		16 (12)		1 (6)	8 (5)
<i>Opisthacanthus</i>		8 (6)			3 (3)
Total		29 (22)		1 (3)	15 (52)
Scorpionidae	<i>Opisthophthalmus</i>	57 (43)	1 (2)	19 (32)	27 (46)
Total	Genera	6 (46)		2 (15)	
	Species	134 (96)	1 (1)	31 (22)	51 (36)

the Namib. The scorpion faunas occurring to the north and south of the Orange River are also distinctly different, sharing only 20 species that occur on both sides.

Most southern African scorpion species show discrete restricted distributional ranges (less than 50 QDS), with the exception of a few widespread species, e.g. *P. granulatus*, *O. carinatus* and *O. wahlbergii*. The distributional ranges of closely related species are invariably allopatric or parapatric, especially in the non-buthid genera *Cheloctonus*, *Opisthacanthus*, *Hadogenes*, and *Opisthophthalmus*. The distributions of *Opisthacanthus* and *Hadogenes* are almost mutually exclusive, *Opisthacanthus* occupying the length of the eastern escarpment and the Cape Fold Mountains (excluding the Cedarberg) and *Hadogenes* occupying the interior plateau and the Cedarberg.

3.3 Hotspots

Hotspot analysis of species richness indicates that most parts of southern Africa contain at least one scorpion species (Fig. 3). The apparent absence of scorpions from large parts of Mozambique, northern Zimbabwe, and the central Kalahari in Botswana is a sampling artefact. Despite the bias caused by undersampling in these areas, coverage of southern Africa is fairly complete for an arthropod group.

Table 3. Patterns of scorpion distribution in southern Africa, expressed as the number of species with distributions in the west, east or centre of southern Africa; north, south or extending across the Orange River; associated with major sand systems or mountain ranges; and intersecting up to 400 quarter-degree squares (QDS), an index of range size. Percentages of the total are provided in parentheses. Abbreviations as follows: *Brandbergia* (B); *Lisposoma* (Li); *Afroisometrus* (A); *Lychas* (Ly); *Pseudolychas* (Ps); *Hottentotta* (Ho); *Karasbergia* (K); *Parabuthus* (Pa); *Uroplectes* (U); *Cheloctonus* (C); *Opisthacanthus* (Oh); *Hadogenes* (Ha); *Opisthophthalmus* (Oo).

	B, Li	A, Ly, Ps	Ho	K	Pa	U	C, Oh	Ha	Oo	Total
Sth. Africa	3 (2)		2 (1)	1 (1)	15 (11)	8 (6)		6 (4)	43 (31)	78 (56)
Eastern		5 (4)	1 (1)		3 (2)	9 (6)	15 (11)	9 (6)	10 (7)	52 (37)
Central					3 (2)	2 (1)			6 (4)	11 (8)
Namib					4 (3)				7 (5)	11 (8)
Kalahari					5 (4)				4 (3)	9 (6)
S Namibia-N Cape			1 (1)		4 (3)				4 (3)	9 (6)
Sandveld					3 (2)				4 (3)	4 (3)
Limpopo					2 (1)				2 (1)	5 (4)
Escarpment		1 (1)					7 (5)	9 (6)	9 (6)	28 (20)
Cape Fold						3 (2)	4 (3)	1 (1)	7 (5)	15 (11)
Other	2 (1)		1 (1)		2 (1)	1 (1)	1 (1)	8 (6)	12 (9)	27 (19)
North	3 (2)		1 (1)		8 (6)	5 (4)		2 (1)	24 (17)	43 (31)
South					3 (2)	4 (3)		3 (2)	22 (16)	32 (23)
Transvserine			1 (1)	1 (1)	8 (6)	2 (1)		2 (1)	6 (4)	20 (14)
1-20	2 (1)	2 (1)	1 (1)		7 (5)	7 (5)	10 (7)	9 (6)	36 (26)	74 (53)
20-50	1 (1)	3 (2)		1 (1)	2 (1)	3 (2)	2 (1)	2 (1)	16 (11)	30 (21)
50-100			2 (1)		7 (5)	5 (4)	3 (2)	3 (2)	4 (3)	24 (17)
100-200					4 (3)	2 (1)		1 (1)		7 (5)
200-300					1 (1)	2 (1)			2 (1)	4 (3)
300-400									1 (1)	2 (1)

Twenty-four primary hotspots (11-16 species) occur in the western third of southern Africa. Most are concentrated in northwestern, central, and southern Namibia, and the Richtersveld and Namaqualand regions of the Northern Cape Province, South Africa, with an isolated hotspot in the Breede River Valley, Western Cape Province, South Africa. Secondary hotspots (7-10 species) are concentrated in the same parts of Namibia, as well as the Richtersveld, Namaqualand, and the Western Cape. Additional secondary hotspots occur in Bushmanland and the southern Kalahari, Northern Cape Province, South Africa, the Eastern Cape, Limpopo and Mpumalanga provinces of South Africa, and the Eastern Highlands of Zimbabwe.

Hotspots of endemic species show a similar pattern (Fig. 4). Six primary hotspots (9-12 endemics) occur along the Aus Mountains and the Huib-Hoch Plateau of southern Namibia, the western escarpment, Namaqualand and Breede River Valley in the Northern and Western Cape provinces of South Africa, and the Eastern Cape Province. Secondary hotspots (6-8 endemics) are concentrated in central and southern Namibia, the Richtersveld, Namaqualand and Bushmanland, the Western Cape, Eastern Cape, Limpopo and Mpumalanga provinces.

Most regions of southern Africa contain at least one endemic species, except for Mozambique, northern Zimbabwe, and most of the Kalahari (no scorpion species are endemic to Botswana). The absence of endemics from northern Zimbabwe and the Kalahari cannot be attributed simply to collector bias, however, as some of these areas, particularly eastern Namibia, northern Botswana, and the northeastern border of Zimbabwe have been fairly well sampled. The distributions of several species in these areas extend beyond the boundaries of southern Africa.

Two trends will be noted from the hotspot analyses. Firstly, most hotspots occur in the arid western half of southern Africa, or in arid parts of the eastern half, e.g. the Eastern Cape and the Lowveld of the Limpopo and Mpumalanga provinces, suggesting the influence of climate. Secondly, all hotspots occur in regions of rugged topography, complex geology, or substratal heterogeneity. The Namibian hotspots occur along the Skeleton Coast, the mountainous Kaokoveld and Damaraland, at the interface of the Central Namib Sand Sea and the western escarpment, and in the highlands on the interior plateau (e.g. the Khomas Hochland, the Karasberg, and the Huib-Hoch Plateau). The South African hotspots in the mountainous Richtersveld, Namaqualand and Bushmanland, the sand dunes of the southern Kalahari, and the western escarpment are further evidence of this pattern. Remaining hotspots are associated with the Cape Fold Mountains, the escarpment in Mpumalanga and the Eastern Highlands of Zimbabwe, the Lebombo Mountains, the Magaliesberg, the Waterberg-Soutpansberg

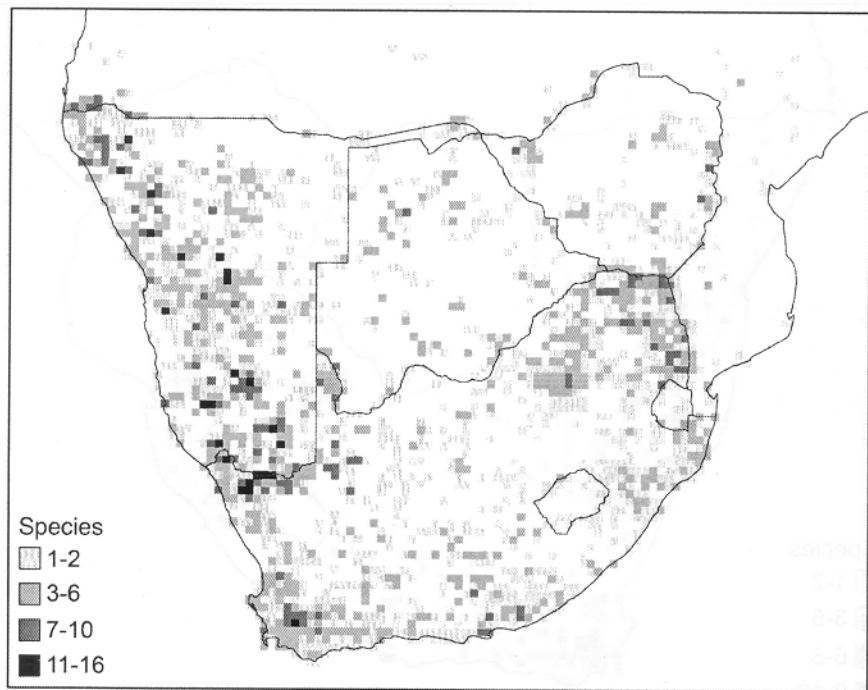


Figure 3. Hotspots of scorpion species richness in Africa, south of 15° latitude, expressed as the total number of species per quarter-degree square.

complex, and the sandy areas of the Limpopo Depression. The hotspot representing the Breede River Valley occurs at the junction of the north-south and east-west axes of the Cape Fold Mountains, and at a transition zone between fynbos and karoo vegetation types, respectively associated with higher and lower rainfall regimes. Notwithstanding the bias caused by undersampling in central Botswana and Mozambique, hotspots are in general poorly represented in areas of uniform topography, geology, and substratum, e.g. the Karoo, the Highveld, the central and northern Kalahari, and the Mozambique plain.

4. DISCUSSION

4.1 Models of speciation

Biogeography should explain the distribution of extant taxa in terms of historical factors together with the use of their contemporary ecology

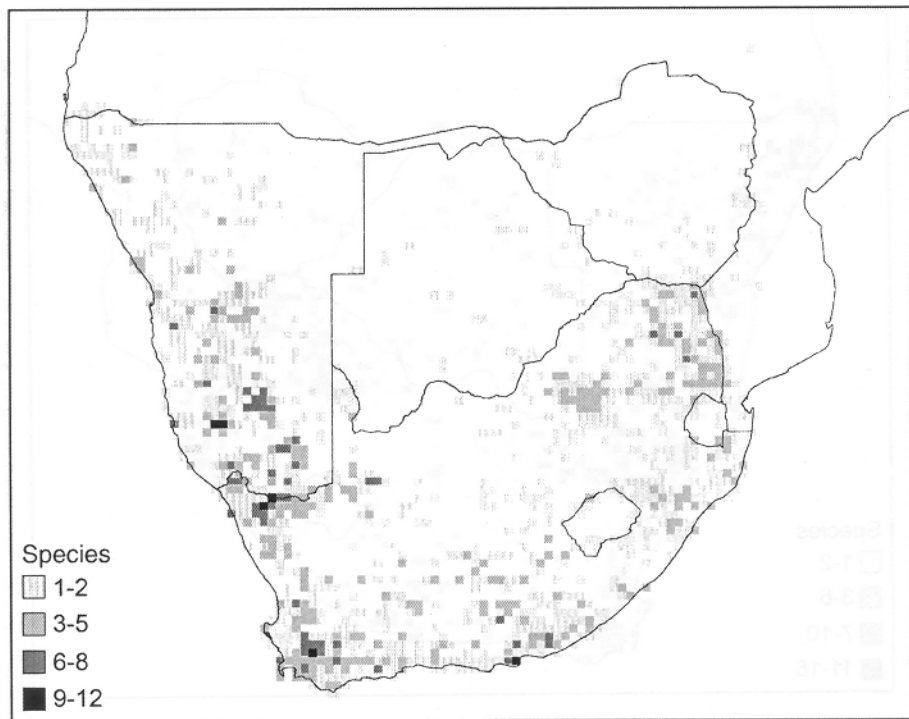


Figure 4. Hotspots of scorpion endemism in Africa, south of 15° latitude, expressed as the number of endemic species per quarter-degree square.

(Myers and Giller, 1988; Haydon et al., 1994). As fossil evidence is absent, biogeographic considerations of southern African scorpions must be derived primarily from ecological sources (Lamoral, 1978b). This approach is considered valid, however, as the habits of scorpions appear to have altered little over time (Jeram, 1990b; Sissom, 1990). The high species richness and endemism of southern African scorpions may be attributed to two main factors: a variable climate and a topographically diverse landscape (associated with complex geology). These factors, together with the specialised ecological requirements of most scorpion species, appear to have promoted speciation, especially during periods of palaeoclimatic change.

Speciation is most often explained by the allopatric model: species evolve from components of larger populations isolated in refugia by a cessation of gene flow between them (Mayr, 1942, 1963). Cessation of gene flow between populations may result from dispersal or vicariance. Although the existence of a physical barrier to gene flow is implied by both, vicariance and dispersal constitute distinct models of disjunction differentiated as follows: vicariance implies that the splitting of an ancestral population was caused by the appearance of a barrier; dispersal implies that

the splitting occurred by movement across a pre-existing barrier (Platnick and Nelson, 1978). Neither dispersal nor vicariance explanations should be discarded *a priori* as irrelevant for any particular group of organisms. Biogeographic analysis should allow us to choose objectively between these two types of explanations for particular taxa.

Scorpion dispersal is limited to terrestrial vagility. As aquatic and aerial dispersal are improbable, barring unusual circumstances such as transoceanic rafting and synanthropy (Newlands, 1973, 1978a), the biogeography of scorpion faunas separated by barriers is best explained through a vicariance model, terrestrial dispersal in turn being controlled at any time by various ecological requisites (Lamoral, 1978b). Given the specialised ecological requirements of southern African scorpions, it is feasible to construct a scenario of how repeated speciation might have produced current levels of diversity and endemism in the subregion, in a similar manner to that proposed by Koch (1977, 1981) for the scorpions of Australasia. The remainder of this paper is devoted to a discussion of the ecological and historical factors determining the distribution of southern African scorpions, insofar as these account for their diversity and endemism.

4.2 Ecological factors

4.2.1 Climate

Different genera and species of scorpions have adapted to xeric and mesic habitats in southern Africa, as elsewhere. At the broadest level, the distinct western and eastern elements of the southern African fauna confirm the importance of climate as a determinant of scorpion distribution in the subregion. Two components of climate are thought to affect scorpion distribution, viz. rainfall (relative humidity) and temperature. Rainfall has a noticeable effect on scorpion distribution in Israel (Warburg and Ben-Horin, 1978; Warburg et al., 1980), whereas temperature appears to be the primary factor limiting the southward expansion of tropical scorpion species on the east coast of Australia (Koch, 1977, 1981). The absence of scorpions from higher latitudes may be indicative of the importance of temperature on a global scale (Gromov, 2001); few species occur where snow is a common occurrence (Williams, 1987; Polis, 1990).

Previous authors (Hewitt, 1925; Lawrence, 1942, 1952; Newlands, 1978a, 1978b) observed that several scorpion genera are restricted to, or dominant in, the arid to semi-arid western half of southern Africa, whereas others are restricted to the humid east, a pattern confirmed in the present investigation. The distributions of *Hottentotta* and *Parabuthus* have been related to the 600 mm isohyet, as these genera are generally absent from

areas receiving more than 600 mm of annual rainfall (Newlands, 1978b). In contrast, *Afroisometrus*, *Lychas*, *Pseudolychas*, *Cheloctonus* and *Opisthacanthus* require high rainfall, and several species in these genera are endemic to Afromontane forests (Lawrence, 1942, 1953). Their limited distributions may be partly indicative of their relative humidity requirements. *Lisposoma josehermanorum* is restricted to humid subterranean habitats such as caves, and leaf litter under boulders on south and east-facing slopes in the Otavi Highlands, which receive the highest rainfall in Namibia (Lamoral, 1978b, 1979; Prendini, 2003b). The restricted distributions of certain silvicolous *Uroplectes* (e.g. *U. insignis* on the forested eastern slopes of Table Mountain) may likewise be related to their narrow climatic requirements.

The distinction between the western and eastern components of the southern African scorpion fauna is repeated within more widespread genera such as *Opisthophthalmus*, *Parabuthus*, *Hottentotta*, *Hadogenes* and *Uroplectes*, each of which contains particular species or groups of related species that are restricted to either the humid east or the arid west of southern Africa. Newlands (1978a: 688) stated “water is probably the most important single factor affecting the distribution of scorpions in southern Africa in that it is largely responsible for the type of vegetation in any given region and, to an extent, the daily temperature fluctuation of the soil surface.”

4.2.2 Substratum

The importance of the substratum in scorpion ecology and distribution is well known (San Martín, 1961; Smith, 1966; Lamoral, 1978a, 1978b, 1979; Bradley, 1986, 1988; Bradley and Brody, 1984; Polis and McCormick, 1986; Fet et al., 1998, 2001; Prendini, 2001a). Lamoral (1978a, 1978b, 1979) established that the distribution of *Opisthophthalmus* in southern Africa is determined primarily by soil hardness and, to a lesser degree, by soil texture, each species being restricted to soils within a certain range of hardness, rather than to a particular soil type. Lamoral (1978b: 305) concluded that “the nature of the substratum, taken in its broadest possible definition, is probably the most important single factor that has and still determines the distribution of scorpions ... the nature of the substratum is affected to a greater or lesser extent by vegetation, which is in turn partly the result of prevailing climatic conditions.”

Newlands (1978a) and Lamoral (1979) independently classified the southern African scorpions according to their habitat predilections, both recognising a distinction between arboreal, rock-dwelling and burrowing species. Rock-dwelling species were further subdivided into species that inhabit crevices and species that shelter under stones, whereas burrowing

species were subdivided according to their occurrence in soft or hard substrata. Bradley (1988) and Polis (1990) redefined these ecomorphotypes for all scorpions (see also Tikader and Bastawade, 1983; Fet et al., 1998). Prendini (2001a) introduced the concept of substratum-specialization and identified stenotopic vs. eurytopic ecomorphotypes, which were then applied to the southern African scorpion species.

Most species of *Parabuthus*, *Opisthophthalmus*, and *Cheloctonus* are fossorial. They are divided into psammophilous and pelophilous species (Lawrence, 1969; Newlands, 1972a; Prendini, 2001a). Psammophilous and semi-psammophilous species of *Parabuthus* and *Opisthophthalmus* display ecomorphological adaptations to increase locomotor and burrowing efficiency in loose sand (Lawrence, 1969; Newlands, 1972a, 1978a; Polis, 1990; Prendini, 2001a). These adaptations are exaggerated in ultra-psammophilous species (Newlands, 1972a) that occupy shifting sand dune environments (e.g. *O. flavescens* and *O. holmi*). All psammophilous scorpions are specialists, poorly adapted to life outside their sandy habitats. They are unable to burrow in harder or coarser substrata (Polis, 1990), and their distributions are restricted to sand systems. In southern Africa, such habitats occur in the northern and southern Namib, the Kalahari, southern Namibia, the Northern Cape Province, and the Limpopo Province. As species that burrow in soft, sandy soils tend to be restricted to a smaller range of substratum hardness than those burrowing in harder substrata, only a few (e.g. *P. granulatus*) are widely distributed, tracking generalised sandy environments across southern Africa.

Pelophilous species burrow in sandy loam and clay soils, and display ecomorphological adaptations to assist with loosening these compacted substrata (Newlands, 1972a, 1972b, 1978a; Polis, 1990; Prendini, 2001a). Pelophilous species of *Opisthophthalmus* are cheliceral burrowers (Newlands, 1972b; Eastwood, 1978b). In contrast, *Cheloctonus jonesii*, a liochelid common in black turf soils (Newlands, 1978a), is a pedipalpal burrower that uses its large, rounded pedipalp chelae for burrowing in this extremely hard clayey substratum (Harington, 1978). Several pelophilous species, e.g. *O. glabrifrons*, are widely distributed, presumably because they are able to burrow in a greater range of soil hardness than is possible for psammophilous species.

Substratum hardness is carried to the extreme in the rock habitats of lithophilous scorpion species, specialists adapted to life in the narrow cracks and crevices of rocks (Newlands, 1972b, 1978a; Polis, 1990; Prendini 2001a, 2001b). The ecomorphological adaptations that characterise lithophilous scorpions facilitate locomotion on rock but hinder locomotion on other substrata. These scorpions are therefore usually restricted to regions of mountainous or rugged topography, their distributions often closely matching the boundaries of mountain ranges and geological

formations (Newlands, 1972b, 1978a, 1980; Prendini, 2001b). Lithophilous adaptations are exaggerated in the southern African genus *Hadogenes*, all species of which inhabit the cracks and crevices of weathered outcrops consisting usually of fine-grained quartzite or igneous rocks such as granite, norite, syenite, diorite, and gabbro (Newlands, 1980). *Hadogenes* are absent from vast areas of southern Africa that are either rockless or contain unsuitable geology. Most *Cheloctonus* and *Opisthacanthus* are generalist lithophiles, sheltering under rocks or logs, in addition to occupying crevices (Lawrence, 1953; Newlands, 1972b). Their requirement for higher humidity appears to have restricted their distributions to the eastern escarpment, the Cape Fold Mountains, and the southern and eastern coastal plains. *Hadogenes*, which tolerate lower rainfall, are more widely distributed in the interior (Lawrence, 1942; Newlands, 1980). Males of certain *Opisththalmus* that excavate shallow scrapes under rocks, or between slabs of rock (e.g. *O. austerus*, *O. karrooensis*, and *O. pallipes*), show similar ecomorphological adaptations to *Hadogenes* (Eastwood, 1978b; Prendini, 2001a). Such semi-lithophilous species are characterised by discrete, allopatric distributions in particular mountain ranges.

Only four obligate corticolous species, that shelter in holes or under the loose bark of trees, often several metres above the ground, occur in southern Africa (Lamoral, 1979; Newlands, 1978a; Newlands and Martindale, 1980; Prendini, 2001b): *Lychas burdoi*; *Uroplectes otjimbinguensis*; *U. vittatus*; *Opisthacanthus asper*. Corticolous species display few ecomorphological adaptations and are widely distributed. All except *U. otjimbinguensis* are restricted to the eastern half of southern Africa.

Lapidicolous scorpions, which shelter under stones or any other available cover, are habitat generalists (Newlands, 1978a; Lamoral, 1978b, 1979; Prendini, 2001a), displaying few ecomorphological adaptations and varied, often widespread distributions (e.g. *U. planimanus* and *U. triangulifer*), governed primarily by climate. In southern Africa, most species of *Hottentotta*, *Pseudolychas*, and *Uroplectes* are lapidicolous. Several normally ground-dwelling species occasionally shelter in arboreal habitats (e.g. *H. conspersus*, *P. villosus*, *U. formosus*, *U. insignis*, *U. lineatus*, and *U. olivaceus*) or are epigeic on vegetation while foraging nocturnally (e.g. *P. villosus* and *U. gracilior*) (Lamoral, 1978b, 1979).

4.2.3 Biotic interactions

Scorpion-scorpion interactions affect the distributions of many scorpion species (Williams, 1970, 1980; Koch, 1977, 1978, 1981; Lamoral, 1978a, 1978b; Shorthouse and Marples, 1980; Bradley and Brody, 1984; Polis and McCormick, 1986, 1987). The exact nature of these interactions is controversial, two main hypotheses with similar predictions having been

presented (Polis, 1990): exploitation competition for prey or homesites and interference, manifested as aggression or intraguild predation among potential competitors. Exploitation competition for limited resources selects for ecological divergence of species from one another in resource use, whereas interference competition selects for subordinate species' avoidance of dominant species (Simberloff, 1983). Divergence and avoidance may decrease habitat overlap and even produce competitive exclusion in certain regions, thereby resulting in geographical allopatry or parapatry; e.g. in Australia, *Urodacus* Peters, 1861 species are almost totally absent where *Liocheles waigiensis* (Gervais, 1843) is abundant (Koch, 1977, 1981). Alternatively, the decrease in habitat overlap caused by divergence or avoidance may allow coexistence, resulting in sympatry; e.g. *Hadrurus arizonensis* Ewing, 1928, *Paruroctonus luteolus* (Gertsch and Soleglad, 1966), *Paruroctonus mesaensis* (Stahnke, 1957), and *Vaejovis confusus* Stahnke, 1940 in California (Polis and McCormick, 1986, 1987). In addition, intraguild predation may allow coexistence by preventing exclusion of competitively inferior species through differential exploitation of competitively superior species (Polis and Holt, 1992).

Competition theory predicts that coexistence, and thus sympatry, will be associated with niche differences and "resource partitioning" (Simberloff, 1983): decreased overlap in the use of critical resources, different spatio-temporal patterns, and differences in body size. Evidence suggests that niche differences exist in space and time, but not in the use of food (Polis, 1990). Although there are exceptions (Main, 1956; Koch, 1977, 1981; Lourenço, 1983b), most scorpion species are generalists, eating any prey they are able to capture (Polis, 1979; McCormick and Polis, 1990). Size differences may divide prey eaten by adults of different sizes. For example, in southern Africa, sympatric species of *Opisthophthalmus* often differ in size (e.g. *O. flavescens* and *O. holmi* of the Namib, or *O. wahlbergi* and *O. concinnus* of the Kalahari), as do sympatric species of *Hadogenes* (e.g. *H. tityrus* and *H. taeniurus* or *H. zumpti*), implying a difference in ecological niche. However, as adults of large species must grow from a small size at birth, all species overlap in size (and associated size-related prey use) during some part of their lives and such developmental overlap greatly limits the effectiveness of body size differences to divide resources among those species that show a wide range in size during development (Polis, 1990).

Size is nonetheless of paramount importance in interference among scorpions. Intraguild predation is known to occur among at least 30 pairs of scorpion species at six North American sites (Polis et al., 1981; Bradley and Brody, 1984; Polis and McCormick, 1986, 1987; Polis, 1990), and has personally been recorded in southern Africa between *Parabuthus granulatus* and *Opisthophthalmus wahlbergi*, *Parabuthus transvaalicus* and *Hadogenes troglodytes*, *H. troglodytes* and *Opisthophthalmus boehmi*, *H. troglodytes* and

Opisthophthalmus glabrifrons. In California, the impact of intraguild predation by *Paruroctonus mesaensis* and *Hadrurus arizonensis* is reflected in niche shifts among the smaller prey species (*Paruroctonus luteolus* and *Vaejovis confusus*), which are relatively uncommon in the habitats occupied by the intraguild predators (Polis and McCormick, 1986, 1987). The subordinate species occupy microhabitat refuges, avoiding ground predation by foraging primarily from burrow entrances (*P. luteolus*) or on vegetation (*P. luteolus* and *V. confusus*). This is also seen in southern Africa, where smaller species of *Uroplectes* and *Opisthophthalmus*, as well as juveniles of larger species (e.g. *Parabuthus*) forage on vegetation, avoiding predation by larger *Parabuthus* and *Opisthophthalmus*, including adult conspecifics.

The effect of substratum hardness is an important spatial factor governing the coexistence of different scorpion species. Koch (1977, 1978, 1981) argued that the distribution of species of the fossorial Australian genus *Urodacus* is determined by competition for homesites, citing differential burrow construction among different species as evidence of decreased habitat overlap. Lamoral (1978a, 1978b) argued similarly that specific soil-hardness preferences decrease competition for burrow sites and allow coexistence among southern African *Opisthophthalmus*. Species with overlapping hardness preferences tend to be allopatric or parapatric, sympatry usually occurring only when two or more species occupy substrata of very different hardness within the same geographical locality (in which case they are allotopic), as shown in the Kalahari species *O. carinatus* and *O. wahlbergi*, which burrow in calcrete and aeolian sand, respectively (Lamoral, 1978a, 1978b). This may, in part, account for the discrete distributions of most species of *Opisthophthalmus*. Sympatric species of *Opisthophthalmus* may also coexist by differential burrow location: in northern Namaqualand, *O. granifrons* burrows on sandy-loam flats at the base of inselbergs where *O. peringueyi* occupies a semi-lithophilous niche under stones. Similarly, *O. boehmi* burrows in sandy-loam flats at the base of the northern slopes of the Soutpansberg, where *O. lawrencei* burrows under stones on the lower slopes (Newlands, 1969).

More fossorial buthid species are observed in sympatry than is the case among non-buthids, but this may be due to more subtle size differences and spatio-temporal microhabitat utilisation. In the southern Kalahari, five fossorial *Parabuthus* species (*P. granulatus*, *P. kalaharicus*, *P. kuanyamarum*, *P. laevifrons*, and *P. raudus*) coexist on the same sand dunes by means of differences in size and spatial occurrence on the dune. Sympatric scorpion species may also differ in foraging station: some hunt in vegetation, others forage on the ground, some “doorkeep” at their burrow entrance; some move constantly during foraging, and others are sit-and-wait foragers (Polis, 1990). In the Kalahari, *P. granulatus*, *P. kalaharicus* and *P.*