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SCORPION DIVERSITY AND DISTRIBUTION IN SOUTHERN AFRICA: PATTERN AND PROCESS

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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: Muséum 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/bgn gaz.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

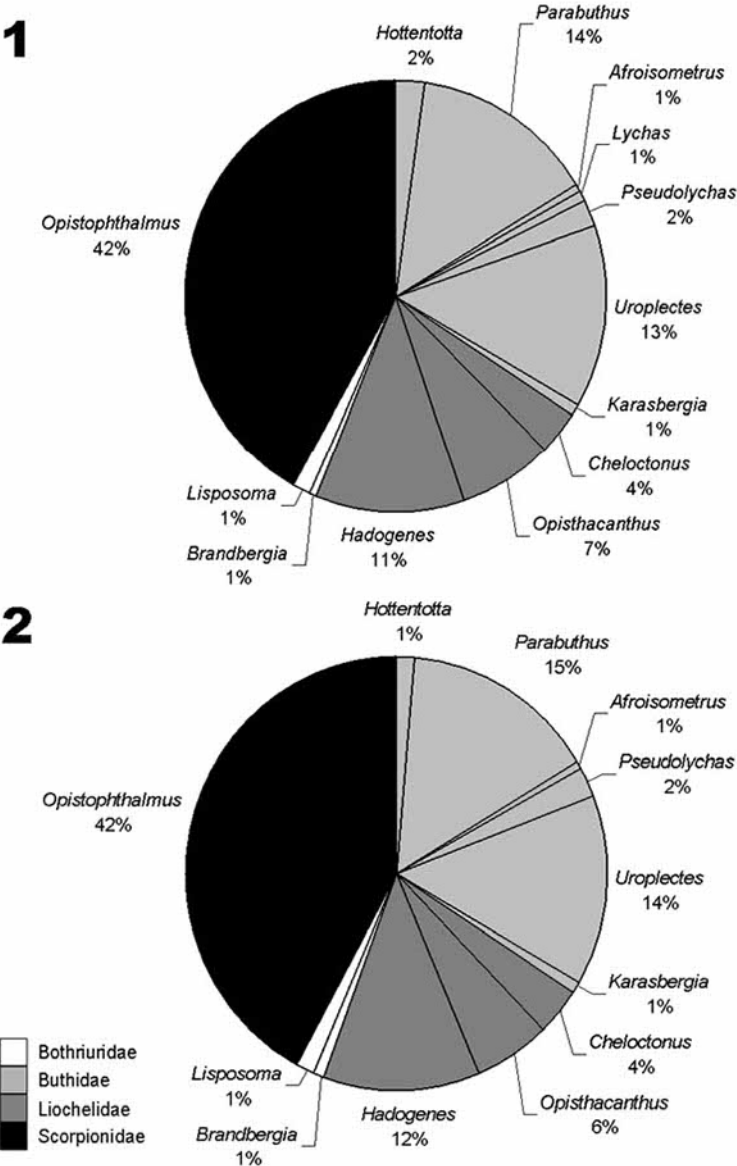
spatial join was then conducted by superimposing scorpion distributions on a dataset representing the QDS grid of southern Africa, to determine scorpion hotspots, i.e. areas of high species richness and endemism (Myers et al., 2000), at the scale of a QDS (Lombard, 1995a, 1995b). Hotspots were based 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, bothrids 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*.



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: *Opisthophthalmus*, *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, *Opisthophthalmus* 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 *Opisthophthalmus*. *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)	1 (100)	1 (100)
	<i>Parabuthus</i>	20 (14)	4 (20)	7 (35)	?		2 (10)	15 (75)	15 (75)		3 (15)	5 (25)	
	<i>Pseudolychas</i>	3 (2)					1 (33)	3 (100)	3 (100)				
Liochelidae	<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)	5 (100)		?	?	
	<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)	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)
Scorpionidae	<i>Opistophthalmus</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	Brandbergia	1 (1)		1 (100)	
	Lisposoma	2 (1)		2 (100)	
	Total	3 (2)		3 (100)	
Buthidae	Afroisometrus	1 (1)			
	Hottentotta	2 (1)			
	Karasbergia	1 (1)			
	Parabuthus	20 (15)		5 (25)	3 (15)
	Pseudolychas	3 (2)			2 (67)
	Uroplectes	19 (14)		3 (16)	4 (21)
	Total	46 (34)		8 (17)	9 (20)
Liochelidae	Cheloctonus	5 (4)			4 (8)
	Hadogenes	16 (12)		1 (6)	8 (5)
	Opisthacanthus	8 (6)			3 (3)
	Total	29 (22)		1 (3)	15 (52)
Scorpionidae	Opisthophthalmus	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); *Opistophthalmus* (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)
Western			1 (1)		3 (2)	9 (6)	15 (11)	9 (6)	10 (7)	52 (37)
Eastern		5 (4)			3 (2)	2 (1)			6 (4)	11 (8)
Central					4 (3)				7 (5)	11 (8)
Namib					5 (4)				4 (3)	9 (6)
Kalahari			1 (1)		4 (3)				4 (3)	9 (6)
S Namibia-N Cape									4 (3)	4 (3)
Sandveld					3 (2)				2 (1)	5 (4)
Limpopo		1 (1)			2 (1)		7 (5)	9 (6)	9 (6)	28 (20)
Escarpment						3 (2)	4 (3)	1 (1)	7 (5)	15 (11)
Cape Fold							1 (1)	8 (6)	12 (9)	27 (19)
Other	2 (1)		1 (1)		2 (1)	1 (1)		2 (1)	24 (17)	43 (31)
North	3 (2)		1 (1)		8 (6)	5 (4)		3 (2)	22 (16)	32 (23)
South					3 (2)	4 (3)		2 (1)	6 (4)	20 (14)
Transriversine			1 (1)	1 (1)	8 (6)	2 (1)		9 (6)	36 (26)	74 (53)
1-20	2 (1)	2 (1)	1 (1)		7 (5)	7 (5)	10 (7)	2 (1)	16 (11)	30 (21)
20-50	1 (1)	3 (2)		1 (1)	2 (1)	3 (2)		3 (2)	4 (3)	24 (17)
50-100			2 (1)		7 (5)	5 (4)		1 (1)		7 (5)
100-200					4 (3)	2 (1)				4 (3)
200-300						2 (1)			2 (1)	4 (3)
300-400					1 (1)				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

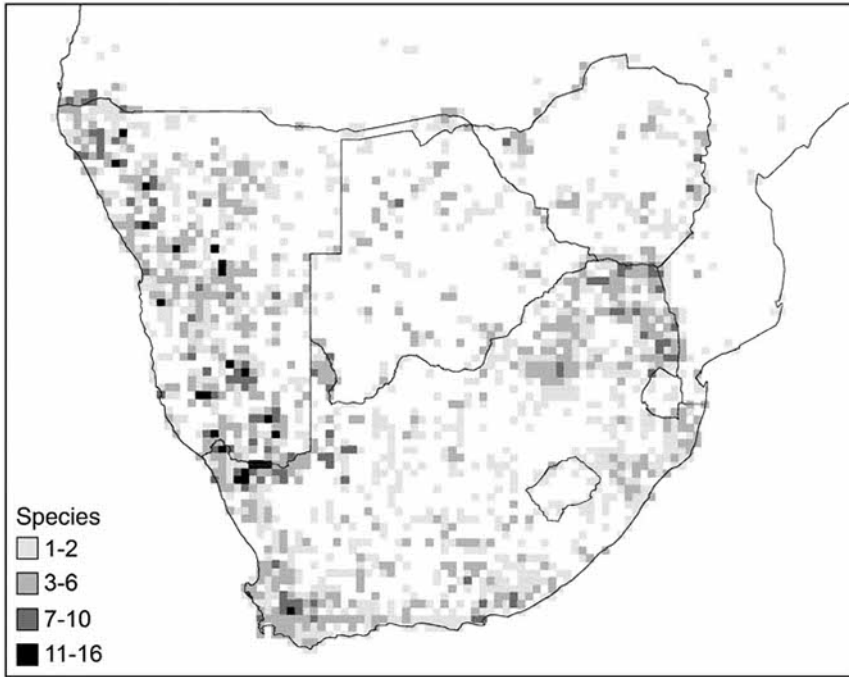


Figure 3. Hotspots of scorpion species richness in Africa, south of 15° latitude, expressed as the total number of species per quarter-degree square.

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

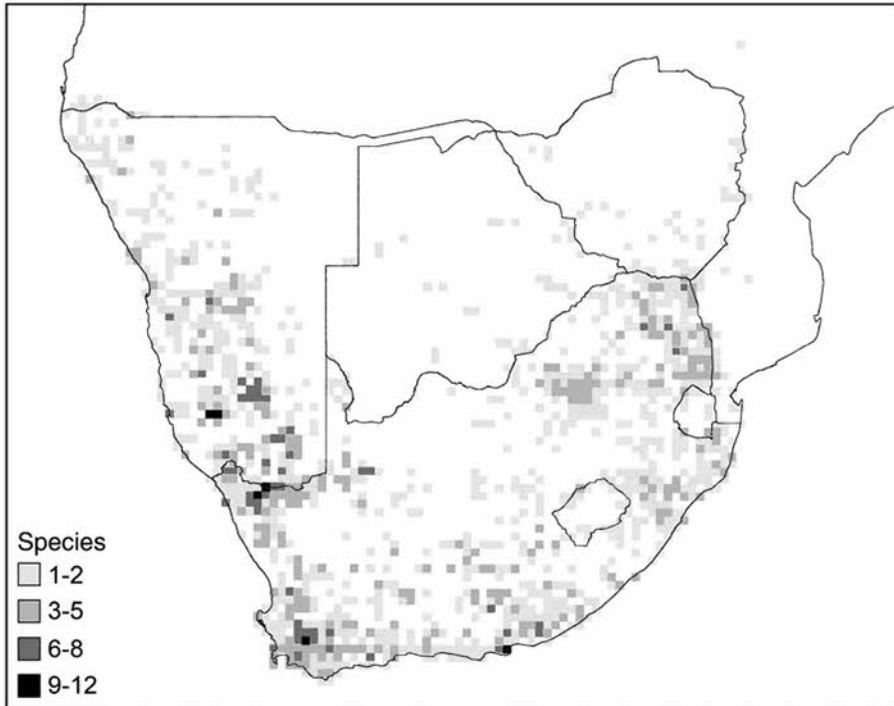


Figure 4. Hotspots of scorpion endemism in Africa, south of 15° latitude, expressed as the number of endemic species per quarter-degree square.

(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 joseehermanorum* 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 pedipalpal 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 *Opisthophthalmus* 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.*

kuanyamarum are active ground-surface foragers, *P. laevifrons* is epigeic on vegetation, and *P. raudus* is a sit-and-wait forager.

Presumably, exploitation competition for the restricted, two-dimensional rock crevice habitat, or interference through intraguild predation by the larger *Hadogenes* has prevented coexistence with the lithophilous species of *Cheloctonus* and *Opisthacanthus*, the distributions of which are almost entirely allopatric with *Hadogenes*. Exceptions are observed only when there are niche differences. For example, the pelophilous *C. jonesii* is sympatric with the lithophilous *H. newlandsi* and the corticolous *O. asper* in Limpopo Province, South Africa. Generally, species of *Hadogenes* occupy hotter, drier habitats than the smaller lithophilous *Opisthacanthus* and *Cheloctonus*, suggesting that there is also a difference in microclimatic requirements between them. In the Mpumalanga Province, South Africa, *H. bicolor* and *O. validus* occur in sympatry (e.g. at Blyderivierspoort and Haenertsburg), but they are allotopic, *H. bicolor* inhabiting exposed rock outcrops and *O. validus* inhabiting outcrops under forest cover (Newlands, 1980). However, climatic differences fail to explain the replacement, by *Hadogenes minor* in the Cedarberg, of *Opisthacanthus*, which occurs throughout the rest of the Cape Fold Mountains, where geology and climate are largely similar. Exploitation competition or intraguild predation seems a more plausible explanation. Almost all congeneric species of *Hadogenes*, *Cheloctonus* and *Opisthacanthus* occupy discrete, allopatric or parapatric distributional ranges, presumably for the same reason (Newlands, 1980). Exceptions are observed only when there are niche differences. For example, the pelophilous *C. jonesii*, lithophilous *O. laevipes* and corticolous *O. asper* are sympatric in Swaziland and the Mpumalanga and KwaZulu-Natal provinces, South Africa.

4.3 Historical factors

4.3.1 Continental drift

As Gondwanaland fragmented, each of the southern continents carried with it a sample of the ancestral biota. This is well illustrated by several groups (MacArthur, 1972), including scorpions. Bothriurid scorpions, also known from South America, Australia and India, are represented in southern Africa by the genera *Brandbergia* and *Lisposoma* (Francke, 1982; Prendini, 2000a, 2003a, 2003b). Each contains species endemic to northern Namibia that display distributions typical of deserticolous palaeogenic elements (Stuckenberg, 1962). Lamoral (1978b, 1979) suggested that *Lisposoma* is a relict of a formerly tropical forest-dwelling ancestral element that survived the onset of aridification in Miocene times by resorting to a semi-endogean

existence, and offered the euedaphic habitat of *L. joseehermanorum* as supporting evidence. The subsequent adoption of a lapidicolous habitat by *L. elegans* may have contributed to its present broader distribution and occurrence in habitats considerably drier than those inhabited by *L. joseehermanorum* (Prendini, 2003b).

A similar evolutionary scenario is proposed for the monotypic buthid genus *Karasbergia*, a fossorial endemic of rocky desert habitats in southern Namibia and the Northern Cape Province, South Africa (Lamoral, 1978b, 1979; Prendini, in press). This species, possibly related to *Charmus* Karsch, 1879 from India and Sri Lanka (Prendini, in press; E.S. Volschenk, pers. comm.), may also be considered a deserticolous palaeogenic element.

Taking possible vicariance and dispersal into account, few affinities exist between the scorpion faunas of the Afrotropical and Neotropical regions. There are, however, three notable exceptions. The first of these is the buthid genus *Ananteris* Thorell, 1891, with 19 species in Central and South America (including the island of Trinidad), and a single species from Guinea and Guinea-Bissau in West Africa, formerly placed in a monotypic genus, *Ananteroides* Borelli, 1911 (Gonzalez-Sponga, 1972, 1980; Lourenço, 1982, 1984b, 1985, 1987b, 1991c, 1993; Lourenço and Flórez, 1989; Fet and Lowe, 2000). The transfer of *Ananteroides feae* Borelli, 1911 to *Ananteris* by Lourenço (1985) was not justified phylogenetically and the monophyly of *Ananteris* remains to be tested.

The second exception is the diplocentrid genus *Heteronebo* Pocock, 1899, currently comprising 15 species. Thirteen species of *Heteronebo* are endemic to the Greater and Lesser Antilles in the Caribbean (Francke, 1978; Francke & Sissom, 1980; Armas, 1981, 1984, 2001; Stockwell, 1985; Armas & Marciano Fondeur, 1987; Prendini, 2000a; Sissom & Fet, 2000). However, two species inhabit Abd-el-Kuri Island off the Horn of Africa, east of Somalia and south of Yemen (Pocock, 1899; Francke, 1979; Sissom, 1990; Prendini, 2000a). Additional records of *Heteronebo*, probably representing undescribed species, were recently obtained from the nearby island of Socotra (W. Wranik & B. Striffler, pers. comm.). Whether the New and Old World species of *Heteronebo* are congeneric remains unclear. Prendini's (2000a) phylogenetic analysis confirmed the monophyly of *Heteronebo* based on the monophyly of a New and an Old World exemplar species of the genus. However, the grouping of New and Old World *Heteronebo* was weakly supported and may not withstand analysis with additional taxa and characters.

The liochelid genus *Opisthacanthus* (Lamoral, 1978b, 1980a) is the third exception. *Opisthacanthus* currently contains seven species in northern South America, southern Central America, the Cocos Islands off the coast of Costa Rica, and Hispaniola Island in the Caribbean, twelve species in Africa, and two species in Madagascar (Lourenço, 1980, 1981, 1987a, 1988,

1991a, 1995, 1997, 2001; Fet, 2000b; Lourenço & Fé, 2003). The origin of the Neotropical species is contentious. Newlands (1973, 1978a) proposed that they dispersed from Africa by trans-Atlantic rafting. However, a more parsimonious conclusion is that they are Gondwana relicts, which reached the Neotropics prior to the African disjunction in the late Cretaceous, and subsequently evolved in isolation (Francke 1974; Lamoral, 1980a; Lourenço, 1984a, 1989; Sissom, 1990). Both hypotheses rest on the assumption that *Opisthacanthus* is monophyletic, an assumption that was questioned on the basis of morphological evidence (Prendini, 2000a). Most of the African species of *Opisthacanthus* appear to be more closely related to other African liochelid genera (e.g., *Cheloctonus*), than to the Neotropical species. The African species of *Opisthacanthus* are not monophyletic either. *Opisthacanthus lecomtei* is more closely related to the South American species, placed in subgenus *Opisthacanthus*, whereas the others, traditionally placed in subgenus *Nepabellus*, are more closely related to *Cheloctonus* (Prendini, 2000a). The relationships of the Malagasy species of *Opisthacanthus*—for which a new subgenus, *Monodopisthacanthus* Lourenço, 2001, was recently erected—to the other species of the genus, also remain unclear. Determining the phylogenetic relationships of the species of *Opisthacanthus* to the other liochelid genera has implications for understanding the biogeography of Liochelidae as a whole.

Opisthacanthus and the related genus *Cheloctonus* conform closely to the criteria proposed for montane palaeogenic elements by Stuckenberg (1962), reiterating a distribution pattern displayed by many other groups of southern African invertebrates. Species of both genera occur in humid habitats at high altitude, on the south- and east-facing slopes of the Drakensberg escarpment (including the Eastern Highlands of Zimbabwe), and the Cape Fold Mountains. *Lychas burdoi* and the related buthids *Afroisometrus* and *Pseudolychas* have similar ecological requirements, and distributional ranges, suggesting that these may also be montane palaeogenic elements.

The genera *Brandbergia*, *Lisposoma*, *Afroisometrus*, *Karasbergia*, *Pseudolychas*, *Cheloctonus*, and *Opisthacanthus* are all relatively basal in their respective clades, and represent an ancient, relictual element in a fauna otherwise characterised by highly derived and speciose genera, e.g., *Parabuthus*, *Hadogenes*, and *Opisthophthalmus*, which probably radiated fairly recently in post-Miocene or Pliocene times (Lamoral, 1978b, 1979; Prendini, 2000, 2001b, 2003a, 2003b, 2004b; Prendini et al., 2003).

4.3.2 Geomorphology and climate

Mountain ranges exert a significant influence on rainfall, temperature and vegetation, and may thus have indirectly promoted speciation in taxa

with restricted climatic tolerances during periods of palaeoclimatic change. For example, species of *Cheloctonus*, *Opisthacanthus*, *Pseudolychas*, and *Uroplectes* requiring high humidity probably experienced vicariance when formerly continuous patches of Afromontane forest or fynbos became isolated along the eastern escarpment during dry periods from the Pliocene to the Pleistocene (van Zinderen Bakker, 1962, 1976, 1978), and speciated in consequence. The sister species *O. validus* and *O. lamoralis*, from the Drakensberg of South Africa and Eastern Highlands of Zimbabwe, respectively, separated by at least 300 km of dry savanna in the Limpopo Depression, are one of several examples. Speciation by vicariance associated with climate-induced expansion and contraction of montane forest or fynbos habitats (e.g. in "Pleistocene refugia") is the favoured explanation for high levels of endemism among montane palaeogenic elements (Stuckenberg, 1962). Most southern African species of *Cheloctonus*, *Opisthacanthus*, and *Pseudolychas*, and several southern African species of *Uroplectes*, may be products of such processes.

Expansion and contraction of the "arid corridor", connecting arid southwestern and northeastern Africa during successive wet and dry phases from the Pliocene to the Pleistocene (Balinsky, 1962; van Zinderen Bakker, 1969) could similarly have induced speciation among arid-adapted species, explaining the existence of *Parabuthus*, *Hadogenes* and *Opisthophthalmus* in northeastern Africa (Prendini, 2001b, 2001c; Prendini et al., 2003).

Topography may also be responsible for speciation in scorpions by acting as barriers to dispersal (Koch, 1977). Some of the more important mountain barriers in southern Africa include the Great Escarpment, the Namaqua Highlands, Cape Fold Mountains, Lebombo Mountains, Magaliesberg, Waterberg, and Soutpansberg of South Africa, and the highlands of Namibia, e.g. the Khomas Hochland, Aus Mountains, Huib-Hoch Plateau, Otavi Highlands, and Karasberg. Many of these mountain ranges separate related scorpion species (Lamoral, 1978b).

There is also evidence that sand systems constitute barriers to non-psammophilous scorpions. Lamoral (1978b, 1979) hypothesised that, since the Pliocene, the Kalahari has acted as an agent of vicariance preventing migration of scorpion species along the "arid corridor". Lamoral (1978b) provided an example of how mountains and sand systems may have contributed to the present distribution of *Hottentotta*, a largely Palaearctic genus, in southern Africa. By the end of the Oligocene, the ancestral species of this genus had migrated as far south as their present distributions, facilitated by prevailing tropical and subtropical climates and vegetation. The emergence of the Kalahari sand system during the Pliocene (van Zinderen Bakker, 1975) induced the vicariance of the southwestern and northeastern species groups, resulting in the speciation of *H. trilineatus* in the northeast. Western expansion of the Kalahari forced the ancestral

southwestern group to migrate west. Once the western front of the Kalahari sands had reached the Central Highlands up to the 1 500 m contour, presumably in the Pleistocene when climate was generally colder, the ancestral range was effectively bisected and a vicariance established that caused the speciation of *H. conspersus* in the north and *H. arenaceus* in the south. A similar scenario was proposed to account for the distributions of various species of *Parabuthus*, *Uroplectes*, and *Opisthophthalmus* north (*P. gracilis*, *P. kraepelini*, *U. otjimbinguensis*, *U. planimanus*, *O. brevicauda*, *O. cavimanus*, *O. coetzeei*, and *O. ugabensis*) and south (*P. laevifrons*, *P. nanus*, *P. schlechteri*, *U. gracilior*, *U. longimanus*, *U. schlechteri*, *U. tumidimanus*, *O. fitzsimonsi*, *O. gigas*, *O. haackei*, *O. intercedens*, *O. opinatus* and *O. schultzei*) of the Namibian Central Highlands (Lamoral, 1978b). This hypothesis rests on the assumption that the species in question are intolerant of sandy environments and fails to account for the distributions of semi-psammophiles such as *P. gracilis*, *P. laevifrons*, *P. nanus*, *O. coetzeei*, *O. fitzsimonsi*, and *O. intercedens*. Moreover, there is no reason to expect that, for the full duration of the Pleistocene, with its fluctuating warm and cold periods (van Zinderen Bakker, 1962, 1975, 1978), the Central Highlands would have constituted an ecological barrier to the ancestors of pelophilous *Opisthophthalmus* which burrow under stones (e.g. *O. cavimanus*, *O. opinatus* and *O. schultzei*), or to species with semi-lithophilous adults (e.g. *O. brevicauda*, *O. ugabensis*, *O. gigas*, and *O. haackei*).

4.3.3 Substratum-specialization

Hotspots of species richness are located primarily in regions of complex topography and geology. The large number of species restricted to particular mountain ranges suggests that speciation often occurs in mountainous areas, rather than adjacent to them. Thus it appears as though intermontane valleys and depressions commonly act as barriers, rather than the other way around.

This may be related to the substratum-specialization of many scorpions, discussed extensively elsewhere (Prendini, 2001a). For example, the erosion of a mountain range, inhabited by a lithophilous scorpion species, would create isolated populations on the resultant inselbergs and ridges. Gene flow would cease once there were no longer rocky outcrops between adjacent inselbergs or ridges, owing to the substratum-specialization of the scorpion species. Observations for *Hadogenes* suggest that very narrow valleys or plains may interrupt gene flow between adjacent populations (Newlands, 1978a, 1980; Newlands and Cantrell, 1985). In the Pretoria area, *H. gunningi* inhabits the Magaliesberg and ridges to the south, whereas *H. gracilis* occurs on a series of ridges running parallel 2-3 km north; the narrow valley between them is free of rock outcrops, and thus acts as a

complete barrier to gene flow. The parapatric distribution patterns of *H. trichiurus* in the southern and eastern escarpment and *H. zuluanus* in the Lebombo reveal a similar process: the geomorphology of the hills in the area between differs in that the boulders are composed of basaltic rock, without cracks and crevices, and there are thus no suitable habitats for *Hadogenes* (Newlands, 1980).

Parts of mountain ranges may also have become separated by the invasion of aeolian sand during the Miocene or Pliocene (van Zinderen Bakker, 1975) leading to speciation in the isolated scorpion populations. For example, the Uri-Hauchab Mountains of the southern Namib are separated from the escarpment by a narrow belt of sand which blew in from the coast (Newlands, 1972c, 1978a, 1980). The isolation of these mountains probably took several million years, during which the isolated population of *Hadogenes* evolved into a new species, *H. lawrencei*, morphologically and genetically distinct from its sister species, *H. tityrus*, on the escarpment. As there are no rocks in the area between the Uri-Hauchab Mountains and the escarpment, the 26 km stretch of soft sand provides an insurmountable barrier to their dispersal.

Restricted ecological requirements probably account for the limited distributional ranges of most *Hadogenes*. Presumably, *Hadogenes*, which displays a suite of apomorphic character states, evolved from liochelid ancestors similar to *Opisthacanthus* and *Cheloctonus* (Lamoral, 1978b; Newlands, 1980), most of which occupy a similar, but more generalist lithophilous niche. Specialization in the lithophilous niche and the development of a greater tolerance for high temperatures and low rainfall may have enabled *Hadogenes* to exploit the arid to semi-arid interior of southern Africa, facilitating speciation by vicariance and, ultimately, producing a greater proportion of range-restricted endemics.

Speciation promoted by substratum-specialization may also be extended to fossorial taxa. Psammophilous and semi-psammophilous species, tracking deposits of a particular hardness, may have experienced vicariance when pockets of aeolian sand became separated from larger sand systems – a frequent occurrence during past periods of increased aridity such as the Pliocene, when wind action was believed to have transported vast quantities of sand over the western interior of southern Africa (van Zinderen Bakker, 1975; Lancaster, 1990). The occurrence of isolated populations of psammophilous species in areas of aeolian Kalahari sand support this notion: *P. granulatus*, *P. kuanyamarum* and *O. wahlbergii* occur in sandy areas northwest of the Soutpansberg, several hundred kilometers east of the main Kalahari sand system, but are not found on the intervening calcrete (Newlands, 1969, 1974).

Numerous similar examples of isolated psammophilous and semi-psammophilous *Parabuthus* and *Opisthophthalmus* populations occur in

Namibia, especially the sandy regions of the south, and in the Richtersveld and Namaqualand of South Africa, where numerous small dunes or dune-fields, of mixed Namib or Kalahari sand origins, are isolated from the main sand systems against mountains or on sandless plains. Lamoral (1978b) suggested that psammophilous species probably evolved as a result of dispersal into the sand systems, rather than as a result of vicariance. Phylogenetic analyses show that psammophilous and semi-psammophilous species of *Parabuthus*, *Uroplectes* and *Opisthophthalmus* are derived and must, therefore, have evolved after the sand systems became well established, speciating after dispersal into an environment that had previously constituted a barrier (Lamoral, 1978b, 1979; Prendini, 2001b). Post-Pliocene adaptation to the sandy substrata was proposed to account for species inhabiting the Kalahari, the Namib, and the sandy areas of southern Namibia and the Northern Cape Province, South Africa. Although it is certainly correct that the psammophilous and semi-psammophilous lineages in these genera evolved after colonising these sandy environments, the actual speciation events that gave rise to current species must have involved vicariance. If cessation of gene flow is an assumed prerequisite for allopatric speciation, the only manner in which populations of a psammophilous or semi-psammophilous scorpion species, unable to burrow in harder soils, could become isolated is through vicariance, i.e. by translocation on small sand dunes or dune-fields that gradually became separated from larger sand systems. Even in historical time, crescent dunes, e.g. barchans, have been found to travel considerable distances over sandless plains, carrying their associated arthropod fauna with them (Penrith, 1979; Endrödy-Younga, 1982). Speciation by vicariance among psammophilous and semi-psammophilous scorpions probably contributed to the high diversity and endemism of *Parabuthus* and *Opisthophthalmus*, and may, in part, explain the larger number of hotspots in the arid, sandy western half of southern Africa.

Pelophilous species are capable of utilising a greater range of substratum hardness than other fossorial scorpions (Lamoral, 1978a). Accordingly, they may be less easily isolated and less prone to speciation. The wide distributions of several pelophilous species (e.g. *O. glabrifrons*) contrast markedly with the often highly restricted distributions of most lithophilous and psammophilous species. Nevertheless, many pelophilous species of *Opisthophthalmus* also display markedly discrete distributions. Such species tend to be concentrated in the mountainous regions of Namibia and the Northern, Western, and Eastern Cape provinces of South Africa, related species invariably occupying adjacent, but separate mountain ranges, or the intervening valleys. This is particularly clear among semi-lithophilous species of *Opisthophthalmus* (Prendini, 2001a). The adults of such species construct shallow scrapes under rocks (Eastwood, 1978b), and may have speciated in a manner similar to that proposed for the lithophilous

Hadogenes, where the ecological requirement for rock cover promoted speciation by vicariance in the various discrete mountain ranges.

4.3.4 Drainage patterns

The most important agents of vicariance in the evolution of southern African scorpions, besides the sand systems and mountain ranges, are represented by major rivers, especially the Orange, the largest river crossing the arid interior and western coastline of southern Africa. The scorpion faunas occurring to the north and south of this river are distinctly different, sharing only 20 species that occur on both sides. All remaining species are endemic to the region north or south of the river and, given their low vagility, are probably autochthonous. The present disjunction is so complete that although several species can be found right up to the northern and southern banks of the river, they do not occur on the opposite sides, a pattern mirrored by flightless tenebrionid and scarabaeid beetles, and lepidistomatid silverfish (Penrith 1975, 1977; Irish 1990; Harrison 1999).

Other rivers that appear to have acted as agents of vicariance in the evolution of southern African scorpions include the Curoca, Kunene, Hoanib, Huab, Ugab, Swakop, Kuiseb, Koichab, Olifants and Berg rivers of the west coast, the Fish River, a major tributary of the Orange in the southern interior of Namibia, the Breë River of the south coast, and the Limpopo and Zambezi rivers of the east coast. In addition to the Limpopo and the Zambezi, the presence of numerous large, fast-flowing rivers emanating from the Natal Drakensberg section of the eastern escarpment might explain the absence of *Opisthophthalmus* species from the region of South Africa between the Natal Drakensberg, the Kei River (Eastern Cape Province) and the Tugela River (KwaZulu-Natal Province). The Kei and Tugela rivers have both incised deep valleys that are inhabited by endemic species of *Opisthophthalmus*, but no *Opisthophthalmus* species are found in between them. The effects of river drainage on the evolution and biogeography of southern African scorpions are currently under further investigation by the author.

5. CONCLUSIONS

The southern African scorpion fauna contains the following components: ancient elements comprising endemic Gondwanaland relicts (*Brandbergia*, *Lisposoma*, *Karasbergia*, *Opisthacanthus*) and their endemic southern African derivatives (*Cheloctonus*); old elements now widespread in the Afrotropical and Oriental regions (*Hottentotta*, *Lychas* and *Uroplectes*),

many of which are also endemic to the southern African subregion, and their endemic derivatives (*Afroisometrus*, *Pseudolychas*); recent elements derived in and largely endemic to the Afrotropical region (*Parabuthus*) or the southern African subregion (*Hadogenes* and *Opisthophthalmus*).

Combined effects of geomorphology and palaeoclimatic change have acted as agents of vicariance in determining the evolution of the southern African scorpions, with their restricted climatic and substratal requirements, and are primarily responsible for the high species richness and endemism in the subregion (Prendini, 2001a). The progressive spatial restriction of groups of taxa, such as an entire genus, groups of related species, or single species, is the result of vicariance, in turn facilitated by limited vagility due to narrow ecological tolerances. In many cases, agents of vicariance are still in existence (e.g. mountain ranges, sand systems and palaeodrainage channels), and coincide with disjunct distribution patterns. Specialist lithophilous (*Hadogenes*), semi-psammophilous or psammophilous (*Parabuthus* and *Opisthophthalmus*), and pelophilous (*Opisthophthalmus*) taxa have speciated extensively, producing a high proportion of range-restricted endemics. *Opisthophthalmus*, in particular, with 42 % of the southern African species, has radiated in a similar manner to the burrowing scorpionoid genus *Urodacus* in Australia (Koch, 1977, 1978, 1981). Presumably specialisation into psammophilous, pelophilous, and semi-lithophilous ecomorphotypes promoted rampant speciation by vicariance in both genera (Prendini, 2001a). This pattern contrasts with that observed in the relictual genera (e.g., *Lisposoma*, *Karasbergia*, *Pseudolychas*, *Cheloctonus*, and *Opisthacanthus*), which contain relatively few species.

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Appendix 1. Scorpion genera and species recorded from southern African countries, south of 15° latitude. 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).

Species	A	B	L	Ma	Mo	N	SA	S	Za	Zi	E
Bothriuridae											
<i>Brandbergia haringtoni</i> Prendini, 2003						+					
<i>Lisposoma elegans</i> Lawrence, 1928						+					
<i>Lisposoma josephermanorum</i> Lamoral, 1979						+					
Buthidae											
<i>Afroisometrus minshullae</i> (FitzPatrick, 1994)							+			+	
<i>Hottentotta arenaceus</i> (Purcell, 1901)						+	+				
<i>Hottentotta conspersus</i> (Thorell, 1876)	+					+					
<i>Hottentotta trilineatus</i> (Peters, 1861)		+		?	+		+		+	+	+
<i>Karasbergia methueni</i> Hewitt, 1913						+	+				
<i>Lychas burdoi</i> (Simon, 1882)				+	+		+		+	+	+
<i>Parabuthus brevimanus</i> (Thorell, 1876)	+					+	+				
<i>Parabuthus calvus</i> Purcell, 1898							+				
<i>Parabuthus capensis</i> (Ehrenberg, 1831)						+	+				
<i>Parabuthus distridor</i> Lamoral, 1980							+				
<i>Parabuthus gracilis</i> Lamoral, 1979						+					
<i>Parabuthus granulatus</i> (Ehrenberg, 1831)	+	+				+	+			+	
<i>Parabuthus kalaharicus</i> Lamoral, 1977		+				+	+				
<i>Parabuthus kraepelini</i> Werner, 1902		?				+					
<i>Parabuthus kuanjamarum</i> Monard, 1937	+	+				+	+		+	+	
<i>Parabuthus laevifrons</i> (Simon, 1888)		+				+	+				
<i>Parabuthus mossambicensis</i> (Peters, 1861)		+		?	+		+		+	+	
<i>Parabuthus muelleri</i> Prendini, 2000						+					
<i>Parabuthus namibensis</i> Lamoral, 1979						+					
<i>Parabuthus nanus</i> Lamoral, 1979						+	+				
<i>Parabuthus planicauda</i> (Pocock, 1889)							+				
<i>Parabuthus raudus</i> (Simon, 1888)	+	+				+	+		+	+	
<i>Parabuthus schlechteri</i> Purcell, 1899						+	+				
<i>Parabuthus stridulus</i> Hewitt, 1913						+					
<i>Parabuthus transvaalicus</i> Purcell, 1899		+			+		+			+	
<i>Parabuthus villosus</i> (Peters, 1862)	?					+	+				
<i>Pseudolychas ochraceus</i> (Hirst, 1911)		?	?				+			?	
<i>Pseudolychas pegleri</i> (Purcell, 1901)					+		+	+			
<i>Pseudolychas transvaalicus</i> Lawrence, 1961							+				
<i>Uroplectes carinatus</i> (Pocock, 1890)	+	+				+	+			+	
<i>Uroplectes chubbi</i> Hirst, 1911		+			+		+		+	+	
<i>Uroplectes flavoviridis</i> Peters, 1861				+	+		+		+	+	?
<i>Uroplectes formosus</i> Pocock, 1890			+		+		+	+			
<i>Uroplectes gracilior</i> Hewitt, 1914						+	+				
<i>Uroplectes insignis</i> Pocock, 1890							+				
<i>Uroplectes lineatus</i> (C. L. Koch, 1844)							+				
<i>Uroplectes longimanus</i> Werner, 1936						+					
<i>Uroplectes marlothi</i> Purcell, 1901							+				
<i>Uroplectes olivaceus</i> Pocock, 1896					+		+	+		+	
<i>Uroplectes otjimbinguensis</i> (Karsch, 1879)	+					+					

Appendix 1. (continued).

Species	A	B	L	Ma	Mo	N	SA	S	Za	Zi	E
Buthidae (continued)											
<i>Uroplectes planimanus</i> (Karsch, 1879)	+	+			+	+	+		+	+	?
<i>Uroplectes schlechteri</i> Purcell, 1901						+	+				
<i>Uroplectes teretipes</i> Lawrence, 1966						+					
<i>Uroplectes triangulifer</i> (Thorell, 1876)			+				+	+			
<i>Uroplectes tumidimanus</i> Lamoral, 1979		+				+	+				
<i>Uroplectes variegatus</i> (C. L. Koch, 1844)							+				
<i>Uroplectes vittatus</i> (Thorell, 1876)		+			+	+	+	+	+	+	
Liocchelidae											
<i>Cheloctonus anthracinus</i> Pocock, 1899							+				
<i>Cheloctonus crassimanus</i> (Pocock, 1896)							+				
<i>Cheloctonus glaber</i> Kraepelin, 1896							+				
<i>Cheloctonus intermedius</i> Hewitt, 1912							+				
<i>Cheloctonus jonesii</i> Pocock, 1892		?			+		+	+	?	?	
<i>Hadogenes bicolor</i> Purcell, 1899							+				
<i>Hadogenes gracilis</i> Hewitt, 1909							+				
<i>Hadogenes granulatus</i> Purcell, 1901		+			+				+	+	
<i>Hadogenes gunningi</i> Purcell, 1899							+				
<i>Hadogenes lawrencei</i> Newlands, 1972						+					
<i>Hadogenes longimanus</i> Prendini, 2001							+				
<i>Hadogenes minor</i> Purcell, 1899							+				
<i>Hadogenes newlandsi</i> Prendini, 2001							+				
<i>Hadogenes phyllodes</i> Thorell, 1876						+	+				
<i>Hadogenes taeniurus</i> (Thorell, 1876)	+					+					
<i>Hadogenes tityrus</i> (Simon, 1888)						+	+				
<i>Hadogenes trichiurus</i> (Gervais, 1843)							+				
<i>Hadogenes troglodytes</i> (Peters, 1861)		+			+		+			+	
<i>Hadogenes zuluani</i> Lawrence, 1937							+	+			
<i>Hadogenes zumpti</i> Newlands, 1985							+				
<i>Opisthacanthus asper</i> (Peters, 1861)		+			+		+	+	?	+	+
<i>Opisthacanthus basutus</i> Lawrence, 1955			+								
<i>Opisthacanthus capensis</i> Thorell, 1876							+				
<i>Opisthacanthus diremptus</i> (Karsch, 1879)							+				
<i>Opisthacanthus laevipes</i> (Pocock, 1893)					+		+	+			
<i>Opisthacanthus lamorali</i> Lourenço, 1981										+	
<i>Opisthacanthus piscatorius</i> Lawrence, 1955							+				
<i>Opisthacanthus rugiceps</i> Pocock, 1897				+							+
<i>Opisthacanthus rugulosus</i> Pocock, 1896				+							
<i>Opisthacanthus validus</i> Thorell, 1876			+				+	+			
Scorpionidae											
<i>Opisthophthalmus adustus</i> Kraepelin, 1908						+					
<i>Opisthophthalmus ammopus</i> Lamoral, 1980							+				
<i>Opisthophthalmus ater</i> Purcell, 1898							+				
<i>Opisthophthalmus austerus</i> Karsch, 1879							+				
<i>Opisthophthalmus boehmi</i> (Kraepelin, 1896)		+			+		+			+	+
<i>Opisthophthalmus brevicauda</i> Lawrence, 1928						+					
<i>Opisthophthalmus capensis</i> (Herbst, 1800)							+				
<i>Opisthophthalmus carinatus</i> (Peters, 1861)	+	+			+	+	+		+	+	
<i>Opisthophthalmus cavimanus</i> Lawrence, 1928						+					

Appendix 1. (continued).

Species	A	B	L	Ma	Mo	N	SA	S	Za	Zi	E
Scorpionidae (continued)											
<i>Opisthophthalmus chrysites</i> Lawrence, 1967						+					
<i>Opisthophthalmus coetzeei</i> Lamoral, 1979						+					
<i>Opisthophthalmus concinnus</i> Newlands, 1972		+				+	+				
<i>Opisthophthalmus crassimanus</i> Purcell, 1899							+				
<i>Opisthophthalmus fitzsimonsi</i> Hewitt, 1935		+				+	+				
<i>Opisthophthalmus flavescens</i> Purcell, 1898						+					
<i>Opisthophthalmus fossor</i> Purcell, 1898							+				
<i>Opisthophthalmus fuscipes</i> Purcell, 1898							+				
<i>Opisthophthalmus gibbericauda</i> Lamoral, 1979	+					+					
<i>Opisthophthalmus gigas</i> Purcell, 1898						+	+				
<i>Opisthophthalmus glabrifrons</i> Peters, 1861		+		+	+		+	?		+	+
<i>Opisthophthalmus granicauda</i> Purcell, 1898							+				
<i>Opisthophthalmus granifrons</i> Pocock, 1896							+				
<i>Opisthophthalmus haackei</i> Lawrence, 1966						+	+				
<i>Opisthophthalmus harpei</i> Harington, 2001						+					
<i>Opisthophthalmus holmi</i> (Lawrence, 1969)						+	+				
<i>Opisthophthalmus intercedens</i> Kraepelin, 1908						+					
<i>Opisthophthalmus intermedius</i> Kraepelin, 1894							+				
<i>Opisthophthalmus jenseni</i> (Lamoral, 1972)						+					
<i>Opisthophthalmus karrooensis</i> Purcell, 1898							+				
<i>Opisthophthalmus keilandsi</i> Hewitt, 1914							+				
<i>Opisthophthalmus lamorali</i> Prendini, 2000						+					
<i>Opisthophthalmus laticauda</i> Purcell, 1898							+				
<i>Opisthophthalmus latimanus</i> C. L. Koch, 1841							+				
<i>Opisthophthalmus latro</i> Thorell, 1876							+				
<i>Opisthophthalmus lawrencei</i> Newlands, 1969							+				
<i>Opisthophthalmus leipoldti</i> Purcell, 1898							+				
<i>Opisthophthalmus litoralis</i> Lawrence, 1955	+					+					
<i>Opisthophthalmus longicauda</i> Purcell, 1899							+				
<i>Opisthophthalmus lornae</i> Lamoral, 1979						+	+				
<i>Opisthophthalmus luciranus</i> Lawrence, 1959	+										
<i>Opisthophthalmus macer</i> Thorell, 1876							+				
<i>Opisthophthalmus nitidiceps</i> Pocock, 1896							+				
<i>Opisthophthalmus opinatus</i> (Simon, 1888)						+					
<i>Opisthophthalmus pallipes</i> C. L. Koch, 1842						+	+				
<i>Opisthophthalmus pattisoni</i> Purcell, 1899							+				
<i>Opisthophthalmus penrithorum</i> Lamoral, 1979						+					
<i>Opisthophthalmus peringueyi</i> Purcell, 1898							+				
<i>Opisthophthalmus pictus</i> Kraepelin, 1894							+				
<i>Opisthophthalmus pluridens</i> Hewitt, 1918							+				
<i>Opisthophthalmus praedo</i> Thorell, 1876							+				
<i>Opisthophthalmus pugnax</i> Thorell, 1876			+				+				
<i>Opisthophthalmus pygmaeus</i> Lamoral, 1979						+					
<i>Opisthophthalmus scabrifrons</i> Hewitt, 1918						+					
<i>Opisthophthalmus schlechteri</i> Purcell, 1898							+				
<i>Opisthophthalmus schultzei</i> Kraepelin, 1908						+					
<i>Opisthophthalmus setifrons</i> Lawrence, 1961						+					
<i>Opisthophthalmus ugabensis</i> Hewitt, 1934						+					
<i>Opisthophthalmus wahlbergii</i> (Thorell, 1876)	+	+				+	+		+	+	