

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 & Marcato Fondour, 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. lamorali*, 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 *Opisththalmus* 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 lepismatid 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 josehermanorum</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 kuanyamarum</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)	+				+	+	+	+	+	+	
Liochelidae											
<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 zuluanus</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 I. (continued).

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