

## Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited

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### Summary

Current biogeography seeks to explain the distribution of extant taxa in terms of historical factors and contemporary ecology. The link between history and ecology is a central tenet of Vrba's (1980) "effect hypothesis of macroevolution", in which macroevolutionary trends, e.g. adaptive radiation, are viewed as an effect of stenotopy. This paper reviews the role of stenotopic substratum requirements (termed "substratum specialization") as a determinant of distribution and speciation in southern African arthropods. The scorpions (Chelicerata, Scorpiones), a diverse group ecologically and phylogenetically, are used to illustrate how stenotopic substratum requirements might have promoted rampant allopatric speciation by vicariance during evolutionary time, in accordance with the Effect Hypothesis. Extant southern African scorpion species are classified into five ecomorphotypes, representing a range of substratum specialists (stenotopes) and substratum generalists (eurytopes). The patterns of distribution and species richness observed in these stenotopic vs eurytopic ecomorphotypes are compared, and found to support the predictions of the Effect Hypothesis. Substratum specialists are more speciose and more range-restricted than substratum generalists. The paper concludes with a survey of other speciose groups of substratum specialist arthropods that might confirm the predictions of the Effect Hypothesis, e.g. Coleoptera, Neuroptera, Orthoptera, Thysanura, Solifugae and fossorial Araneae. The complex geomorphology of southern Africa, with concomitant substratum diversity, is suggested as an explanation for the high species richness and endemism of substratum specialist southern African arthropods.

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*"The availability of a wide variety of substrata . . . and the genetic plasticity of the Adesmiini [Tenebrionidae], which has enabled them to develop features appropriate to the utilization of the various substrata, for example fossorial adaptations for sand, have resulted in the considerable diversification of the tribe with increased aridity of their environment."* (Penrith, 1979: 82)

### Introduction

In 1980, Elisabeth Vrba proposed the "effect hypothesis of macroevolution", based on earlier work by Eldredge (1979). Vrba (1980: 79) predicted that "one would expect lineages with relatively narrow species-specific adaptations (stenotopes) to be more prone to diversification than broadly adapted generalists (eurytopes) . . . so particularly rapid speciation may be seen as an

effect of particularly narrow environmental specialisation".

A corollary of this faster rate of speciation among stenotopes is the prediction of a net increase in the number of stenotopic species through time (Vrba, 1980), manifest in macroevolutionary trends such as "adaptive radiation" and observed among such diverse taxa as Galapagos finches and Hawaiian drosophilids. Such trends have long been the focus of attention for biogeographers and evolutionary biologists, e.g. see the debates surrounding the origin of species flocks of haplochromine cichlids in the East African Great Lakes (Avisé, 1990; Owen *et al.*, 1990; Fryer, 1991; Sturmbauer & Meyer, 1992; Meyer, 1993).

Although the Effect Hypothesis (hereafter referred to as EH) has received considerable discussion (Cracraft, 1982; Vrba, 1983, 1984a,

1989a; Vrba & Gould, 1986; Kellogg, 1988; Stanley, 1990; Masters & Rayner, 1993; Grantham, 1995; Lieberman & Vrba, 1995), there have been few case studies apart from Vrba's (1984b, 1987, 1989b) classic investigations of speciation rates in the Alcelaphini–Aepycerotini sister group of African antelope. Pelvic reduction in sticklebacks (Bell, 1987), molar morphology in marsupial carnivores (Werdelin, 1987), differential extinction of marine diatoms at the end of the Cretaceous (Kitchell *et al.*, 1986) and differential extinction of trilobites at the end of the Ordovician (Chatterton & Speyer, 1989) have been cited as cases of effect macroevolution. Recently, Kammer *et al.* (1997, 1998) provided an elegant example of differential species richness in Osagean–Meramecian crinoid clades. Kammer *et al.* (1998) demonstrated high species richness in the stenotopic camerates and cladids, but low species richness in the eurytopic disparids and cladids, confirming Eldredge's (1979) and Vrba's (1980, 1984a, b, 1987) predictions.

Grantham (1995) attributed the paucity of examples of effect macroevolution to the problems of extracting information from the fossil record. However, this is only a partial explanation, because effect macroevolution may also be tested with extant taxa by an assessment of species richness in stenotopic *v.* eurytopic clades. Moreover, the EH would enhance an understanding of causal mechanisms behind the existence of many speciose groups of extant taxa.

The EH, with its emphasis on the effects of ecology projected over evolutionary time, also has much to offer biogeographers. This is particularly true if their aim is to explain the distribution of extant taxa in terms of historical factors together with contemporary ecology, as advocated by Myers & Giller (1988: 3): "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".

Perhaps the paucity of examples proposed by neontologists concerned with the study of speciation is nothing more than a reflection of the general disjunction between those interested in ecology and those interested in history. In this paper, I attempt to bridge that disjunction by providing an example of how the EH can enhance an understanding of the biogeography and evolution

of a speciose group of extant taxa, namely the southern African scorpions.

The southern African scorpion fauna is well studied and fairly speciose. According to the world catalogue of Fet *et al.* (2000), the subregion contains 8% of the world's genera and at least 10% of the world's species. This is a high proportion when compared with similar values for larger temperate regions such as North Africa, with 12% and 3% (based on data in Vachon, 1952), and Australo-Papua, with 5% and 3% (based on data in Koch, 1977). Southern African values are also high in comparison with the values of tropical regions such as India, with 15% and 9% (based on data in Tikader & Bastawade, 1983), and Venezuela, with 15% and 6% (based on data in González-Sponga, 1996). Moreover, 38% of the genera and at least 86% of the species of southern African scorpions are endemic to the subregion.

Three genera—*Opisthophthalmus* C. L. Koch, 1837 (Scorpionidae), *Parabuthus* Pocock, 1890 (Buthidae) and *Hadogenes* Kraepelin, 1894 (Ischnuridae)—are remarkable for several reasons.

First, these genera dominate the southern African scorpion fauna, together comprising approximately 67% of the described species; this percentage will be even greater when based on forthcoming revisions of *Opisthophthalmus* and *Hadogenes*, in which additional species are to be recognized (Prendini, in prep.).

Second, each is characterized by numerous morphological apomorphies, compared with related genera. For example, *Opisthophthalmus* and *Parabuthus* possess autapomorphic stridulatory organs on the chelicerae and metasomal segments respectively (Prendini, 2000a, b, 2001a). *Hadogenes* exhibits the highest trichobothrial counts of any known scorpion (Newlands, 1980; Newlands & Cantrell, 1985), and some species of *Opisthophthalmus* display the lowest pectinal tooth counts (Prendini, in prep.).

Third, all three genera are characterized by a preponderance of unusually large species, although each genus also includes species of "average" size. *Hadogenes* includes the world's longest scorpions, e.g. *H. troglodytes* (Peters, 1861), which reaches a length of 210 mm and a mass of 32 g (Newlands, 1972c). *Parabuthus* includes the world's largest buthid scorpions—*Parabuthus villosus* (Peters, 1862), *P. transvaalicus* Purcell, 1899 and *P. schlechteri* Purcell, 1899,

which can reach a length of 140 mm and a mass of 14 g (Newlands, 1974a, 1978). Several species of *Opisthophthalmus* are also exceptionally large, e.g. *O. gigas* Purcell, 1898 commonly reaches 160 mm in length (Lamoral, 1979; Prendini pers. obs.).

Fourth and finally, many species in these genera are characterized by exaggerated sexual dimorphism. Species of *Opisthophthalmus* often display marked dimorphism in the shape of pedipalp chelae (Newlands, 1972a; Eastwood, 1978b; Prendini, 2000c) and the pectinal tooth counts (Newlands, 1972a; Lamoral, 1979), whereas many species of *Hadogenes* are characterized by marked dimorphism in metasomal length (Newlands, 1980; Newlands & Cantrell, 1985; Newlands & Prendini, 1997; Prendini, 2001b).

Although the richness of the southern African scorpion fauna has been the subject of discussion for more than a century (Purcell, 1899; Hewitt, 1918, 1925; Lawrence, 1942, 1955; Lamoral, 1978a, 1979; Newlands, 1978), there is still little consensus on the mechanisms that generated it. Below, I propose that the stenotopic substratum requirements (hereafter referred to as “substratum specialization”) of southern African scorpions have played an integral role in their speciation, and hence their diversity, as predicted by the EH.

I start with a review of the concept of substratum specialization and its importance in the ecology of scorpions and other arthropods. Next, I classify the southern African scorpions into substratum specialist (stenotopic) and substratum generalist (eurytopic) ecomorphotypes, and discuss possible modes of speciation. By comparing the patterns of distribution and species richness of extant ecomorphotypes, and assuming that the ecological requirements of scorpions have changed little over time, as inferred from the morphology of fossil forms (Jeram, 1990a, b, 1994a, b; Selden, 1993), I then illustrate how substratum specialization might have promoted speciation in evolutionary time. This discussion is supported by a quantitative test and confirmation of the prediction by the EH that substratum specialists are more speciose and more range-restricted than substratum generalists. Finally, I extend this theory to other groups of substratum specialist arthropods in southern Africa, thereby demonstrating the general applicability

of the concepts of substratum specialization and effect macroevolution.

### The definition of substratum specialization

Substratum specialization is a form of habitat stenotopy. It can be defined as the dependence of different species on substrata of specific hardness, texture or composition for survival. The substratum is the medium on or in which an animal lives, and thus constitutes its refuge from the ravages of climate and predation, and is the place where it locates food and mates. Substrata vary greatly in hardness, texture and composition—from rock to sand, and from leaf litter to tree bark. Accordingly, different substrata exert different selection pressures on the animals living on or in them, resulting in the evolution of specialized ecomorphological adaptations<sup>1</sup>. The more physically unfavourable the substratum, the more specialized the adaptations required for colonization and survival. When placed on a foreign substratum, many specialized animals are incapable of survival. For example, Fet *et al.* (1998) listed some unfavourable characteristics of sand-dune habitats for their occupants. Dunes are formed by aeolian deposition, hence individuals that inhabit them may suffer abrasion by windblown sand, and the instability and movement of sand may bury their burrows. Mechanical difficulties hinder locomotion and burrowing in sand, so that mobile organisms usually require specialized adaptations to move and, unless supported by an expanded surface area on the tips of legs, many species would be unable to travel over it. Finally, the angle of repose (slope angle where sand cascades on itself) prevents burrows from being built in the energetically most efficient way, i.e. as a vertical tube (Polis *et al.*, 1986). Similarly, unique challenges face taxa inhabiting bare rock faces, leaf litter or compacted soil.

The idea of substratum specialization has long been recognized in arthropods. Koch (1961: 10) introduced the term “ultra-psammophilous = loving vegetationless (ultra-desertic) sand” to describe the habitat preferences of tenebrionid beetles occupying the vegetationless sand dunes of the Namib desert, and discussed the importance of edaphic factors in governing the distribution of these species. Koch (1961) provided abundant evidence of “morpho-ethological

- Ants** Marsh (1990)
- Collembolans** Coineau & Massoud (1977); Thibaud & Christian (1989, 1997); Thibaud & Lee (1994); D'Haese (2000)
- Crickets** Irish (1986a, 1990)
- Scarabs** Holm & Scholtz (1979); Mostert & Holm (1982)
- Scorpions** Lawrence (1967, 1969); Williams (1969, 1980); Lamoral (1972, 1977, 1979, 1980); Newlands (1972a); Eastwood (1977, 1978a,b); Fet (1980, 1987, 1994); Levy & Amitai (1980); Newlands & Martindale (1980); Tikader & Bastawade (1983); Bradley (1988); Polis (1990); Fet *et al.* (1998)
- Silverfish** Irish (1986b, 1987, 1988a, 1989, 1990); Irish & Mendes (1988); Watson & Irish (1988)
- Solifuges** Lawrence (1963, 1966a, 1969, 1972); Lamoral (1972, 1973, 1974); Wharton (1981); Griffin (1990)
- Spiders** Lawrence (1962, 1965a,b, 1966b); Reiskind (1965, 1969); Dippenaar & Meyer (1980); Cloudsley-Thompson (1982, 1983); Dippenaar-Schoeman (1990); Henschel (1990a,b, 1994, 1995, 1997); Jocqué (1990); Platnick & Griffin (1990); Henschel & Lubin (1992, 1997); Peters (1992a,b)
- Tenebrionids** Penrith (1979, 1981a,b, 1982, 1984a,b, 1986a–c, 1987); Coineau *et al.* (1982); Louw (1983); Seely (1983); Endrödy-Younga (1986); Irish (1990)

Table 1: Selected references to psammophilous arthropods.

adaptations” in Namib tenebrionids to support his notion of “positive psammotropism”.

Koch (1961) observed that strictly thino-philous species are unable to migrate to adjacent, extra-dune soil surfaces which, even if formed by sand, may differ from the coarse dune sand in composition, compactness and granularity. Many of these Namib tenebrionids have evolved ecomorphological adaptations and behavioural habits that prevent them from entering different substrata such as consolidated sand, coarse sand, or gravel flats (Endrödy-Younga, 1982a). Unfavourable substratum conditions prohibit their typical behavioural pattern of avoiding exposure and predation by diving into loose sand, and the fine bristles and hypertrophic claws, promoting their movement on sand dunes, break on coarse substrata, resulting in a disadvantage when re-entering their optimal habitat. Reproduction, from oviposition to emergence of the adult generation, is also severely hampered on hard substrata.

According to Endrödy-Younga (1982a), individuals of such species will perish if accidentally carried onto a foreign substratum and have little chance to reproduce. Hence it is unsurprising that there is not a single record of an ultrapsammophilous tenebrionid species being found alive outside of its sand-dune habitat (Endrödy-Younga, 1982a).

Koch (1962) tested some of these observations experimentally and found that dune tenebrionids, kept in an insectarium on river sand, soon damaged the armatures of legs and lost the tactile sense bristles and lateral cilia of the body. Subsequent authors refined these concepts of psammophily and positive psammotropism in tenebrionids, and extended them to ants, collembolans, schizodactylid crickets, scarabs, scorpions, lepismatid silverfish, solifuges, and spiders (Table 1).

Other forms of substratum specialization, e.g. lithophily, have received less attention, although Newlands (1972b, 1980) provided evidence for what might be termed “positive lithotropism” in flat rock scorpions, *Hadogenes*. Newlands (1980) noted that sand forms a positive ecological barrier to species of *Hadogenes*, because their tarsi are adapted to providing grip on rock surfaces (Newlands, 1972b). Whereas psammophilous scorpions have long setae on the tarsi, which serve to increase the effective surface area and enable these species to move easily over soft sand, in laboratory conditions it is evident that species of *Hadogenes* experience great difficulty in walking over soft sand (Newlands, 1980). Therefore, Newlands (1980) suggested that it is unlikely that an individual *Hadogenes* could move more than a few hundred metres over soft sand in a night and the sun would certainly kill these heat-sensitive scorpions unless shelter could be found during the day.

#### Substratum specialization and ecomorphotypes in scorpions

Experimental and comparative support for the notion of substratum specialization in scorpions is widespread, because substratum selection is intimately linked to burrowing biology (Table 2). Lamoral's (1978a,b, 1979) experimental studies established that the distribution of burrowing *Opisthophthalmus* in southern Africa is determined primarily by substratum hardness and, to a lesser degree, texture, each species being

restricted to substrata within a certain range of hardness, rather than to a particular type. Lamoral (1978a) maintained that the nature of the substratum is the most important factor that has and still determines the distribution of scorpions.

Newlands (1978) and Lamoral (1979) independently classified the southern African scorpions according to their habitat predilections. Both authors recognized the 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 sand or hard soil substrata (Table 3). Bradley (1988) and Polis (1990) redefined these ecomorphotypes for all scorpions (see also Tikader & Bastawade, 1983), and they can be categorized on the basis of substratum specialization into relatively stenotopic and eurytopic ecomorphotypes (Table 4).

Psammophilous (or arenicolous) and semi-psammophilous<sup>2</sup> species of the genera *Opisthophthalmus*, *Parabuthus*, *Hottentotta* Birula, 1908 and *Uroplectes* Peters, 1861 are adapted to life on soft sandy substrata (Lawrence, 1969; Newlands, 1972a; Eastwood, 1977; Lamoral, 1979; Fet *et al.*, 1998). They display several ecomorphological adaptations to increase locomotor and burrowing efficiency in loose sand: streamlined metasoma and telson, often lacking carinae; elongated telotarsal unguis; comb-like rows of long macrosetae ("sand combs") on the prolateral and retrolateral margins of the tibia, basitarsi and telotarsi of legs, especially the first and second pairs (Birula, 1917; Lawrence, 1969; Newlands, 1972a, 1978; Lamoral, 1979; Newlands & Martindale, 1980; Bradley, 1986; Polis, 1990; Fet *et al.*, 1998). These adaptations are exaggerated in ultra-psammophilous (thinophilous) species that occupy barren sand-dune environments in the Namib, e.g. *Opisthophthalmus flavescens* Purcell, 1898 and *O. holmi* (Lawrence, 1969).

The anterior two pairs of legs are used to scrape and rake soil out of the burrow by species of *Parabuthus* and *Opisthophthalmus* (Newlands, 1972a; Eastwood, 1977, 1978b; Lamoral, 1979). In addition, species of *Parabuthus* use the thickened metasoma for tail-scraping operations (Eastwood, 1977, 1978b). Similar tail-scraping behaviour has also been observed in some

**Australia** Smith (1966); Shorthouse (1971); Koch (1977, 1978, 1981); Shorthouse & Marples (1980); Locket (1990, 1993)

**Caribbean** Armas (1976)

**Central Asia** Fet (1980)

**India** Tilak (1970); Tikader & Bastawade (1983)

**Middle East** Rosin & Shulov (1963); Levy & Amitai (1980)

**North Africa** Cloudsley-Thompson (1961)

**North America** Williams (1966); Hadley (1974); Bradley & Brody (1984); Bradley (1986); Polis & McCormick (1986); Polis *et al.* (1986); Yamashita & Polis (1995a,b)

**South Africa** Lawrence (1969); Newlands (1972a,c, 1978, 1980); Eastwood (1977, 1978a,b); Harington (1978); Lamoral (1978a, b, 1979); Newlands & Martindale (1980)

**South America** San Martín (1961); Cekalovic (1965-1966); Maury (1968, 1978); Lourenço (1976)

**General** Cloudsley-Thompson (1975); Williams (1987); Bradley (1988); Polis (1990); Fet *et al.* (1998)

Table 2: Selected references to burrowing biology and substratum specialization in scorpions.

*Opisthophthalmus* (Newlands, 1972a). All psammophilous scorpions are stenotopes, maladapted to life outside their sandy environments, and are unable to burrow in harder soil (Polis, 1990). Such highly stenotopic species are predicted to experience limited vagility over harder substrata, and be prone to speciation by vicariance.

Pelophilous<sup>3</sup> species of *Opisthophthalmus*, *Cheloctonus* Pocock, 1892 and *Lisposoma* Lawrence, 1928 burrow in hard substrata such as sandy loam and clay soils (Newlands, 1972a,c, 1978; Eastwood, 1977; Lamoral, 1979). Ecomorphological adaptations of such species that facilitate burrowing in hard soil substrata include enlarged chelicerae (in cheliceral burrowers such as *Opisthophthalmus*); large, crab-like pedipalp chelae (in pedipalpal burrowers such as *Cheloctonus*); short, robust legs and telotarsal unguis; absence of basitarsal setal combs and, often, presence of stout, spiniform macrosetae distributed laterally and distally on the basitarsi (Newlands, 1972c, 1978; Harington, 1978; Lamoral, 1979; Bradley, 1986; Polis, 1990). Pelophilous *Opisthophthalmus* species use the chelicerae to loosen soil particles and the

Habitat	Newlands; Eastwood	Lamoral	Bradley, Polis
Under tree bark, in holes in trees	Arboreal	Epigeic: supra- and infracorticolous	Epigean: errant
Shallow scrapes under stones	Rock-dwelling: rupicolous	Hemiedaphic: infralapidicolous	Epigean: errant
Rock crevices and fissures	Rock-dwelling: lithophilous	Hemiedaphic: infrasaxicolous, lithoclasticolous	Epigean: lithophilous
Burrowing in soil	Burrowing: pelophilous	Hemiedaphic: fossorial	Epigean: fossorial
Burrowing in sand	Burrowing: psammophilous	Hemiedaphic: psammophilous	Epigean: psammophilous
Underground or in caves	Cavernicolous: troglodytic, troglophilous	Euedaphic: endogean	Hypogean: troglobitic, troglophilous, humicolous

Table 3: Ecomorphotypes of scorpions recognized by Newlands (1972a,c, 1973, 1978, 1987), Lamoral (1978a, 1979), Eastwood (1977, 1978b), Bradley (1988) and Polis (1990). Refer to **Appendix 1** for glossary of accepted definitions.

anterior two pairs of legs to scrape and rake soil out of the burrow (Lamoral, 1979), whereas pelophilous *Cheloctonus* species loosen soil with the chelae, and carry it out of the burrow (Harington, 1978).

Being equipped for burrowing in hard soil does not preclude these scorpions from inhabiting softer soils as “facultative psammophiles” (*sensu* Fet *et al.*, 1998). Hence, pelophilous scorpions are expected to be less stenotopic than psammophilous scorpions, a prediction supported by Lamoral’s (1979) observation that these species occupy a greater range of soil hardness than the latter. Pelophilous species should therefore be more vagile, and their propensity for speciation by vicariance lower, than predicted for psammophilous species.

Substratum hardness is carried to the extreme in the rock habitats occupied by lithophilous, lithoclasticolous (Lamoral, 1978a, 1979) or saxifragous scorpions such as species of *Hadogenes*, *Opisthacanthus* Peters, 1861 and some *Uroplectes*. Lithophiles are stenotopes, adapted to life in the narrow cracks and crevices of rocks, and are characterized by dorsoventral compression; some degree of elongation of the metasoma and pedipalps; stout, spiniform macrosetae on the telotarsi, operating in conjunction with highly curved telotarsal unguis to provide grip on rock surfaces (Newlands, 1972c, 1978, 1980;

Lamoral, 1979; Newlands & Martindale, 1980; Bradley, 1986; Polis, 1990). Many species also display raised superciliary carinae—to prevent the median ocelli from being scratched by the rock surface above—and the lateral ocelli may be unusually well developed for anterior light perception (Newlands, 1972b, c, 1980). Such adaptations are exaggerated in the southern African genus *Hadogenes*, all species of which are obligate lithophiles occupying the cracks and crevices of weathered rock outcrops, in regions of rugged, mountainous topography (Newlands & Prendini, 1997; Prendini, 2001b). The specialized telotarsal modifications that characterize these scorpions facilitate rapid locomotion in any spatial plane of their rock habitats, but hinder locomotion on other substrata. One would thus predict that they would experience limited vagility over soft substrata, and should be prone to speciation by vicariance.

Certain species of *Opisththalmus* that excavate shallow scrapes under rocks in areas of hard soil (e.g. *Opisththalmus austerus* Karsch, 1879, *O. karrooensis* Purcell, 1898 and *O. pattisoni* Purcell, 1899) display similar ecomorphological adaptations to *Hadogenes*, including dorsoventral compression and greatly elongated pedipalp chelae (Eastwood, 1978b). These characters are particularly exaggerated in the adult males, which in some species have abandoned burrow

Substratum affinities	Ecomorphological adaptations	Distributional range	Predicted relative vagility	Predicted relative speciation rate
Psammophilous <sup>1</sup>	Highly stenotopic	Restricted	Low	High
Lithophilous <sup>2</sup>	Highly stenotopic	Restricted	Low	High
Pelophilous <sup>3</sup>	Moderately stenotopic	Intermediate	Moderate	Moderate
Corticolous	Eurytopic	Widespread	High	Low
Lapidicolous <sup>4</sup>	Eurytopic	Widespread	High	Low

<sup>1</sup> "Arenicolous" or "psammophilic" (Fet *et al.*, 1998)

<sup>2</sup> "Infrasaxicolous and lithoclasticolous" (Lamoral, 1978a, 1979).

<sup>3</sup> "Fossorial" (*sensu* Lamoral, 1978a, 1979; Bradley, 1988; Polis, 1990).

<sup>4</sup> "Petrophilous" (Koch, 1961, 1962), "rupicolous" (Newlands, 1978) and "errant" (Bradley, 1988; Polis, 1990).

Table 4: Ecomorphotypes of southern African scorpion species, categorized according to substratum specialization, with distributional correlates, predicted relative vagility, and predicted relative speciation rates. Refer to **Appendix 1** for glossary of accepted definitions and **Appendix 2** for species list.

construction altogether in exchange for a semi-lithophilous existence under slabs of rock (Prendini, pers. obs.). Compared with pelophilous *Opisththalmus* species, such species have elongated telotarsi with higher numbers of spini-form macrosetae in the pro- and retrolateral rows, and markedly curved telotarsal ungues, which are thought to be scansorial adaptations. Species such as *Opisththalmus brevicauda* Lawrence, 1928, *O. haackei* Lawrence, 1966 and *O. ugabensis* Hewitt, 1934 are especially agile in their rocky scree-slope habitats, and even females appear to spend a considerable period outside of the burrow. Again, vagility across softer substrata is predicted to be limited in these semi-lithophilous species, hence they should also be prone to speciation by vicariance.

Obligate arboreal (epigeic *sensu* Lamoral, 1979), corticolous species, sheltering in holes or under the loose bark of old or dead trees, often several metres above the ground, occur in the genera *Uroplectes* and *Opisthacanthus* (Newlands, 1973, 1974, 1978; Lamoral, 1979; Newlands & Martindale, 1980). Corticolous species are eurytopic, exhibiting few ecomorphological adaptations except for moderate dorsoventral compression and well-developed telotarsal ungues (Polis, 1990), and are thus predicted to be less prone to speciation by vicariance.

The fifth<sup>4</sup> ecological category of scorpions recognized here, has been termed the "errant" ecomorphotype (*sensu* Bradley, 1988; Polis, 1990), to distinguish scorpions that move actively during nocturnal foraging, from those that are sit-and-wait foragers. By day, these errant scorpions

merely shelter under loose stones or other available debris, and display few ecomorphological adaptations for their generalist lifestyle. Such species have been variously termed rupicolous (Newlands, 1978), petrophilous (Koch, 1961, 1962), or infralapidicolous (Lamoral, 1978a, 1979). This last term, pertaining to life under stones (**Appendix 1**), is considered most appropriate, and is used hereafter. In southern Africa, this ecomorphotype includes most species of *Uroplectes*, *Pseudolychas* Kraepelin, 1911 and *Hottentotta*. Lapidicolous species are eurytopic and thus also predicted to be less prone to speciation by vicariance.

#### Median ocular displacement and the substratum hardness continuum

A distinctive morphological character of many pelophilous *Opisththalmus* species is the proximal position of the median ocelli, which in some species (e.g. *O. latimanus* C. L. Koch, 1841 and *O. pallipes* C. L. Koch, 1843) are situated near the posterior margin of the carapace. The median ocelli are more distally situated (i.e. closer to the anterior carapace margin) in many psammophilous species of *Opisththalmus* (e.g. *O. chrysites* Lawrence, 1967 and *O. holmi*).

Lawrence (1969) and Newlands (1972a) considered the proximal position of the ocelli to be apomorphic. Newlands (1972a) proposed an adaptationist hypothesis to account for the apomorphic proximal position of the ocelli, stating that, because substratum hardness increases with a reduction in particle size, the position of the

median ocelli is a function of the substratum particle size of the habitat.

Newlands (1972a) maintained that species occurring in areas of hard soil substrata require larger cheliceral muscles for burrowing operations, since greater mechanical effort is required to loosen the soil. Cheliceral muscles occupy the anterior cavity of the prosoma and the ventral muscles curve downward to their point of attachment on the sternal apodeme (segment VII). Accordingly, larger muscles require more space in the cephalothorax, leaving less space for the supra-oesophageal ganglion and its nerve connections to the median ocelli, which thus became displaced proximally over evolutionary time (Fig. 1). Larger cheliceral muscles could also induce anterior extension of the carapace, which would thus place the ocelli relatively far back on the carapace. Newlands (1972a) argued that ocular displacement did not occur in species inhabiting softer substrata where the large cheliceral muscles were not required. Hence, ocular displacement may be viewed as an effect of adaptation to hard substrata, derived in pelophilous species.

Newlands (1972a) tabulated evidence for his theory of median ocular displacement by arranging species according to their median ocular position on the carapace, and listing their substratum preferences alongside. This table reflected a general trend towards ocular displacement with increased substratum hardness. A single exception to this gradation—*O. flavescens*—was noted.

Unfortunately, the relationship between substratum hardness and ocular position on the carapace is less clear than portrayed by Newlands (1972a). In addition to *O. flavescens*, several other psammophilous species, e.g. *Opisthophthalmus capensis* (Herbst, 1800) and *O. schlechteri* Purcell, 1898, display proximally situated median ocelli, whereas in several pelophilous species, e.g. *Opisthophthalmus opinatus* (Simon, 1888) and *O. schultzei* Kraepelin, 1908, the ocelli are situated more distally.

Newlands (1972a) explained the *O. flavescens* anomaly with *ad hoc* dietary evidence: *O. flavescens* preys on *Onymacris* Allard, 1885 beetles in the Namib, and may require strong cheliceral musculature to break through the sclerotized elytra. However, mounting evidence suggests that Newlands's (1972a) putative ecological correlation is partial at best, and probably reflects a strong historical component.

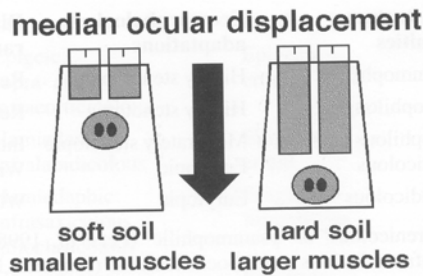


Fig. 1: Diagrammatic representation of a scorpion carapace, illustrating Newlands's (1972a) theory of median ocular displacement in southern African burrowing scorpions (Scorpionidae: *Opisthophthalmus*). Paired anterior structures represent chelicerae (external) and associated musculature (internal, shaded). Arrow indicates direction of displacement of the supra-oesophageal ganglion (also shaded) and associated median ocelli, caused by the enlarged cheliceral musculature.

Phylogenetic analysis of the species of *Opisthophthalmus* (Prendini, in prep.) suggests that proximal ocular displacement may have evolved on several independent occasions from the plesiomorphic distal position, perhaps in association with hard substrata, and was then retained in species that subsequently became psammophilous. Apomorphic reversals to the distal position have also occurred in certain psammophilous clades, in which the proximal position occurs among relatively plesiomorphic members.

In general, the substratum hardness continuum (Fig. 2) is a more useful concept for representing substratum specialist ecomorphotypes in a quantitative manner. When classified according to the hardness index of Lamoral (1978a, b, 1979), expressed as the force required to penetrate the substratum ( $\text{kg cm}^{-2}$ ), different scorpion species are seen to occupy different, overlapping regions, corresponding to Lamoral's (1978a, b, 1979) "soil hardness categories", along the continuum. Ultrapsammophilous species that inhabit unconsolidated sand dunes (e.g. *O. holmi*) are represented at one end, where almost zero force is required to penetrate the substratum. Lithophilous species (*Hadogenes* and *Opisthacanthus*) are represented at the opposite end, where great force is required for penetration. Other species, which inhabit substrata of intermediate hardness, are situated in between.



### Substratum specialization and vicariance

How might stenotopic substratum requirements promote speciation in scorpions? More than a century ago, Purcell (1899: 135) noted the propensity of *Opisthophthalmus* species to form "local races and varieties" in association with particular substrata. Purcell's (1899) observations can now be explained in accordance with the tenets of allopatric speciation. Species evolve from components of larger, more widespread populations, isolated in refugia, as a result of environmentally induced natural selection and/or genetic drift.

A prerequisite for the speciation of such spatially separated populations is the cessation of gene flow between them, without which incipient genetic differences would be swamped. Cessation of gene flow may result from dispersal or vicariance. The existence of a physical barrier to gene flow is implied by both potential scenarios for speciation, but vicariance and dispersal constitute alternative causes of distributional disjunction. Vicariance implies that the splitting of an ancestral population was caused by the appearance of a new barrier, whereas dispersal implies that the splitting occurred by movement across a pre-existing barrier (Platnick & Nelson, 1978).

Scorpion dispersal is effected by terrestrial vagility and, as noted by Birula (1917) and Harington (1984), scorpions are not particularly vagile. Because aquatic and aerial dispersal are improbable, barring unusual circumstances such as transoceanic rafting and synanthropy (Newlands, 1973, 1978), Lamoral (1978a) proposed that speciation in scorpions is best explained through a vicariance model. Any change in environmental conditions that caused the disruption of essential ecological requirements across the distributional range of a scorpion species would represent a new barrier, constitute a vicariance event, and could, in time, lead to speciation. What remains to be analysed is precisely how such disruption might arise.

### Vicariance and speciation in lithophilous species

As a mountain range erodes, its elevation reduces and results in the formation of peninsulas. Resistant rocks erode more slowly and

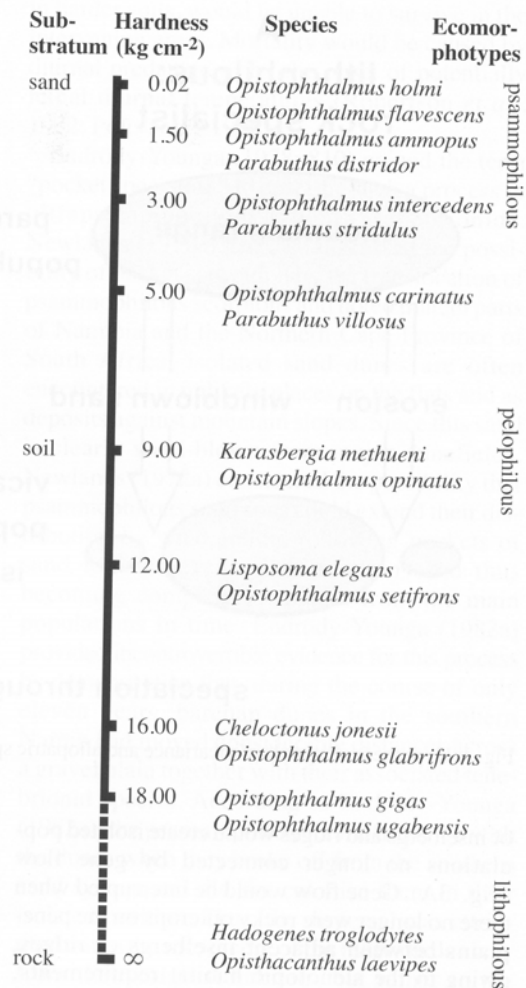


Fig. 2: The substratum hardness continuum for classifying substrata, and the organisms that inhabit them. Hardness is expressed as the force required to penetrate the substratum in kg cm<sup>-2</sup> (Lamoral 1978a, b, 1979). When classified according to the hardness of the substratum they inhabit, substratum specialist scorpion species occupy discrete, overlapping regions along the continuum. Ultrapammophilous species that inhabit unconsolidated sand dunes occur at one end, where almost zero force is required to penetrate the substratum, whereas lithophilous species occur at the opposite end, where great force is required for penetration. Various species, which inhabit substrata of intermediate hardness, are situated in between.

give rise to inselbergs and short ridges. If a mountain range were inhabited by a lithophilous species of scorpion, erosion causing the formation

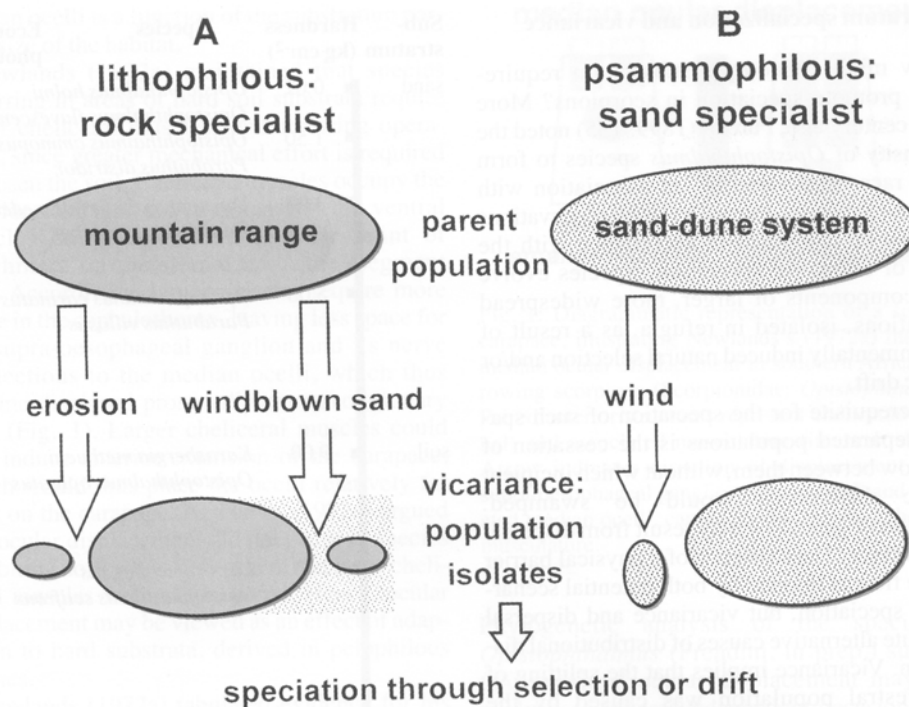


Fig. 3: Hypothetical models of vicariance and allopatric speciation in substratum specialist organisms.

of inselbergs and ridges would create isolated populations no longer connected by gene flow (Fig. 3A). Gene flow would be interrupted when there no longer were rocky outcrops on the penplains between adjacent inselbergs or ridges, owing to the stenotopic habitat requirements, i.e. the substratum specialization, of the scorpion species.

Williams (1980) provided evidence for morphological variation in geographically disjunct populations of *Syntropis macrura* Kraepelin, 1900, a lithophilous vaejovid scorpion from volcanic habitats of Baja California, Mexico. Similar observations for southern African *Hadogenes* species (Newlands, 1978, 1980; Newlands & Cantrell, 1985) suggest that very narrow valleys or plains may interrupt gene flow between adjacent populations. In the North West Province of South Africa, *Hadogenes gunningi* Purcell, 1899, inhabits the Magaliesberg and ridges to the south, whereas *H. gracilis* Hewitt, 1909 occurs on a series of ridges running parallel 2–3 km north. The narrow valley between them lacks rocky outcrops that would provide shelter,

without which these scorpions would succumb to diurnal temperatures (Robertson *et al.*, 1982; Polis *et al.*, 1986); it thus acts as a complete barrier to gene flow. The allopatric distributional ranges of *Hadogenes trichiurus* (Gervais, 1843) in the Tugela River Valley and its sister species, *H. zuluanus* Lawrence, 1937 in the Lebombo Mountains (both in the KwaZulu-Natal Province of South Africa), reveal evidence of a similar process. The geology of the hills in the area between is different; the boulders are composed of basaltic rock without cracks and crevices and therefore there are no suitable habitats for *Hadogenes* (Newlands, 1980).

In an analogous process, parts of mountain ranges may have become separated by the invasion of wind-blown sand, leading to speciation in the isolated scorpion populations (Fig. 3A). Wind action is believed to have transported vast quantities of sand across the western interior of southern Africa at various intervals of intensified aridity during the past 20–80 million years (Van Zinderen Bakker, 1975; Lancaster, 1981, 1984; Ward *et al.*, 1983). For example, the Uri-Hauchab

Mountains of the central Namib (Namibia) are separated from the western escarpment by a narrow belt of sand, connected to the central Namib dune system, which comprises aeolian deposits of littoral origin (Newlands, 1972b, 1978, 1980; Endrödy-Younga, 1982b). The process of isolation of these mountains is thought to have taken only a few million years, during which the isolated population of *Hadogenes* in the Uri-Hauchab Mountains evolved into a new species, *H. lawrencei* (Newlands, 1972, morphologically and genetically distinct from its sister species, *H. tityrus* (Simon, 1888), on the escarpment (Newlands & Cantrell, 1985). 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. The recency of this isolation event is attested by the lithophilous tenebrionid beetle fauna of these inselbergs, and the nearby Hauchab Mountains, which have not yet speciated from their conspecific populations on the escarpment (Endrödy-Younga, 1982b).

Such speciation by vicariance, as an effect of stenotopic substratum requirements, is suggested to account for the high species richness and restricted distributional ranges (Fig. 4A) of species in the lithophilous southern African scorpion genera, *Hadogenes* and *Opisthacanthus*, and semi-lithophilous species of *Opisththalmus*, as predicted by the EH.

#### Vicariance and speciation in psammophilous species

This process of speciation by vicariance may also be extended to fossorial (burrowing) scorpions. For example, populations of psammophilous and semi-psammophilous species, tracking deposits of a particular hardness, could have become isolated when pockets of suitable wind-blown sand were separated from major sand systems (Fig. 3B). Barchan sand dunes have been shown to move distances of 10–100 myr<sup>-1</sup> within historical time (Petrov, 1976). Accordingly, during past arid periods of increased wind velocity, e.g. the period from the Pliocene (Van Zinderen Bakker, 1975) to the Upper Pleistocene (Lancaster, 1981), sand movement must have been far greater. Any separation of sand dunes from a major sand system could constitute a vicariance event, as the stenotopic inhabitants, maladapted for burrowing

in harder soils, would be unable to survive in the intervening areas. Mortality would be caused by diurnal predators, or by the onset of potentially lethal diurnal temperatures (Robertson *et al.*, 1982; Polis *et al.*, 1986).

Endrödy-Younga (1978: 810) coined the term “pocket speciation” to describe such a process in ultrapsammophilous Namib tenebrionids. Newlands (1972a) had also discussed the possibility of pocket speciation by the translocation of psammophilous scorpions and noted that, in parts of Namibia and the Northern Cape Province of South Africa, isolated sand dunes are often encountered in unlikely places on the flats and as deposits against mountain slopes. Since this sand is clearly wind-blown from major dunefields, Newlands (1972a) considered the possibility that psammophilous scorpions could extend their distribution by wind action, following pockets of sand to their eventual destinations and thus becoming completely isolated from the main populations in time. Endrödy-Younga (1982a) provided incontrovertible evidence for this process by demonstrating that, during the course of only eleven years, barchan dunes in the southern Namib had moved considerable distances across a gravel plain together with their associated tenebrionid species. According to Endrödy-Younga (1982a), the psammophilous fauna travelled with the dunes when they broke off from the southern sand system and did not colonize them in their isolated position. Thus, the dispersal was attributed not to the movement of the individuals away from their original habitats, but rather to the translocation of their substratum and habitat, the dunes.

Endrödy-Younga (1982a, b) and Irish (1990) provided numerous examples of tenebrionids and lepismatids inhabiting isolated dunes in the southern and northern Namib, thereby adding further support to the physical evidence for northward migration of the dunes and their associated fauna. Irish (1990) discussed in detail the faunas of isolated inland dunefields, associated with river beds in the northern Namib, which contain the same, or sister species, of taxa inhabiting major sand systems closer to the coast. One such distributional pattern discussed by Irish (1990) is mirrored by the psammophilous burrowing scorpion, *Opisththalmus holmi* and its sister species, *O. jenseni* (Lamoral, 1972).

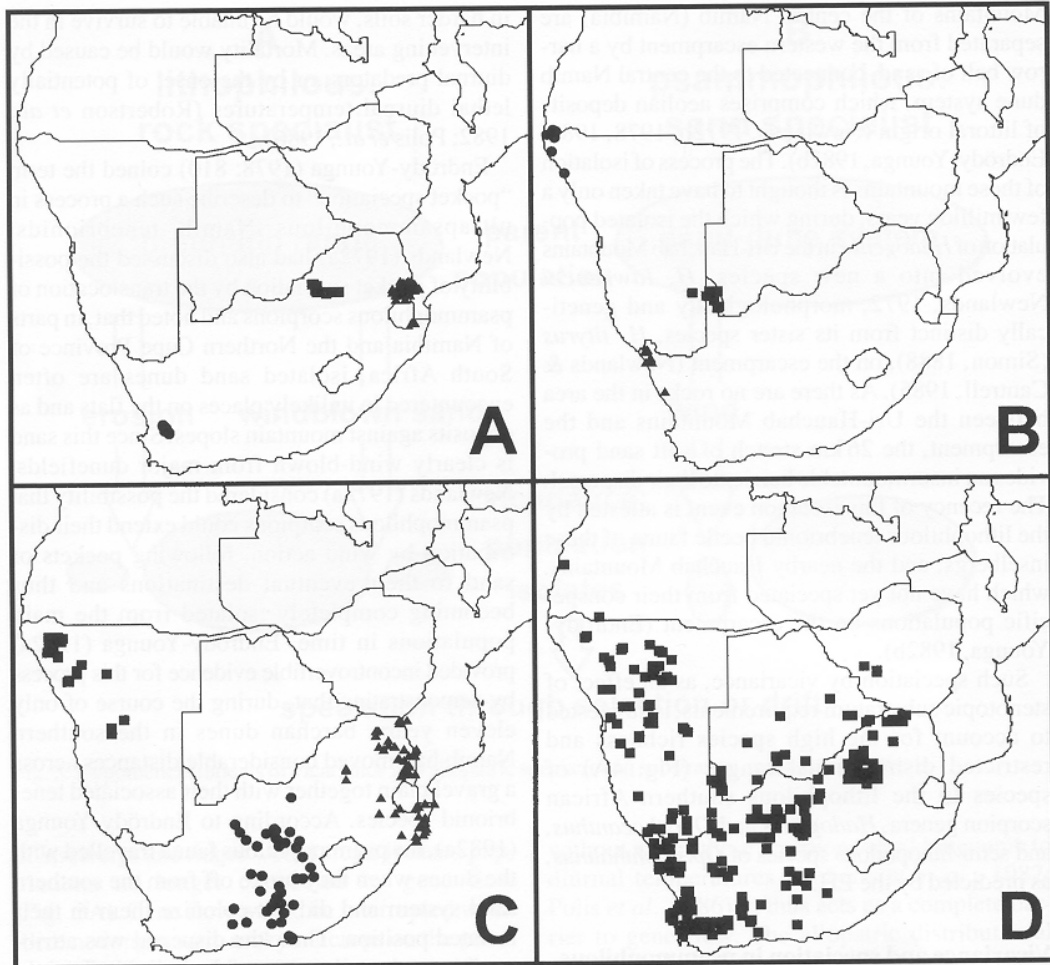


Fig. 4: Distributional ranges of selected stenotopic v. eurytopic scorpions in southern Africa (classified according to **Appendix 2**; distributional data from Prendini, 1995). **A** Lithophilous species: *Hadogenes gracilis* Hewitt, 1909 (squares); *Opisthacanthus laevipes* (Pocock, 1893) (triangles); *Opisthophthalmus pattisoni* Purcell, 1899 (circles). **B** Psammophilous species: *Parabuthus kalaharicus* Lamoral, 1977 (squares); *Opisthophthalmus ammpus* Lamoral, 1980 (triangles); *O. chrysites* Lawrence, 1967 (circles). **C** Pelophilous species: *Lisposoma elegans* Lawrence, 1928 (squares); *Cheloctonus jonesii* Pocock, 1892 (triangles); *Opisthophthalmus pictus* Kraepelin, 1894 (circles). **D** Lapidicolous species: *Uroplectes carinatus* (Pocock, 1890).

Isolated populations of psammophilous scorpion species in areas of wind-blown Kalahari sand further support Endrödy-Younga's (1982a) notions of translocation and pocket speciation. Three psammophilous scorpion species, characteristic of the Kalahari, occur in sandy areas north-west of the Soutpansberg, in the Northern Province of South Africa, several hundred kilometers east of the main Kalahari sand system, but not in the intervening calcrete areas (Newlands,

1969, 1974b; Prendini, 1995); these are *Parabuthus granulatus* (Ehrenberg, 1828), *P. kuanyamarum* Monard, 1937, and *Opisthophthalmus wahlbergii* (Thorell, 1876). Similarly, examples of allopatric or parapatric sister species of psammophilous *Parabuthus* and *Opisthophthalmus* occur in Namibia, especially the sandy regions of the south, and in northern and western Namaqualand (Northern Cape Province, South Africa). These observations of

scorpion distribution are, in turn, supported by other sympatric Kalahari arthropods, e.g. psammophilous lepismatids and tenebrionids (Penrith, 1982, 1984a, b, 1986a; Irish, 1987, 1990).

Throughout southern Namibia and the Northern Cape, numerous small dunes or dunefields, of Namib or Kalahari sand origins (Koch, 1962) are isolated from the main sand systems against mountains or on rocky plains. Such isolated dunefields are relatively recent and probably originated during the Upper Pleistocene (Tankard & Rogers, 1978) by reactivation and remodelling of older dune forms (Lancaster, 1981).

Phylogenetic analysis indicates that psammophilous and semi-psammophilous scorpion species in the genera *Parabuthus*, *Uroplectes* and *Opisthophthalmus* are the most derived (Lamoral, 1978a; Prendini, 2001a, in prep.). Psammophiles must, therefore, have evolved subsequent to establishment of these sand systems, speciating after initial dispersal events into an environment that had previously constituted a barrier.

Lamoral (1978a, 1979) proposed post-Pliocene adaptation to the sandy substrata to account for psammophilous scorpion species of the Kalahari, the Namib, and the sandy areas of southern Namibia and the Northern Cape. This hypothesis is supported by many south-western African arid endemic groups, e.g. *Comicus* Brunner v. Wattenwyl, 1888, dune crickets (Irish, 1986a) and the tenebrionids (Endrödy-Younga, 1978, 1982b; Penrith, 1979), in which the most plesiomorphic species inhabit the Karoo (arid interior of South Africa), the south-western parts of Namibia, and the Kaokoveld (north-western Namibia). Since these areas are characterized by rocky or hard soil substrata, it must be assumed that psammophilous taxa evolved from the more plesiomorphic pelophilous taxa whenever and wherever sandy substrata occurred (Irish, 1990). Nenilin & Fet (1992) and Fet *et al.* (1998) reached the same conclusion when they proposed that psammophilous scorpions in all deserts evolved *in situ* from the local available generalist stock.

The above observations, in turn, support the prediction by the EH of rapid, frequent speciation by stenotopes from eurytopic ancestors. The large number of psammophilous and semi-psammophilous scorpion species in genera such as *Opisthophthalmus* and *Parabuthus*, not to mention the tenebrionids, lepismatids, etc., cannot be

older than the late Tertiary to Quaternary sand deposits which they inhabit. Similarly, if the psammophilous *Vejovoides longiunguis* (Williams, 1969) from Baja California (Mexico), is assumed to have evolved *in situ*, then this species cannot be older than the sand dunes that it inhabits, which are thought to have formed no more than 20,000 years BP (Williams, 1969, 1980; Fet *et al.*, 1998).

The evidence for *in situ* evolution of psammophilous and semi-psammophilous lineages, after initial dispersal into sandy environments, is compelling. However, the subsequent speciation events that gave rise to most psammophilous species are more parsimoniously recognized as effects of vicariance promoted by stenotopic substratum requirements—i.e. translocation *sensu* Endrödy-Younga (1982a)—rather than dispersal *per se*. This is an important point, because it leads to the prediction of higher species richness for psammophiles, in accordance with the EH. If psammophily is viewed solely in terms of colonization and *in situ* adaptation, then other conclusions may be inferred. For example, Fet *et al.* (1998) proposed that the necessity of specific adaptations to sand restricts membership to relatively few species that are able to adapt, leading to the prediction that species diversity within sandy habitats is lower than in non-sandy habitats. Fet *et al.* (1998) quantified species richness and diversity of desert scorpions from California and Baja California and observed that each was significantly lower on sand compared to other habitats. However, the evidence for lower species richness in sandy habitats presented by Fet *et al.* (1998) must be viewed taking into account that these authors considered only strictly sand-adapted forms (ultrapsammophiles and psammophiles—their categories 1 and 2) to demonstrate ecological adaptations and patterns of evolution on sand. If semi-psammophilous species had been included in the analysis (as below), the pattern may have been different.

#### Vicariance and speciation in pelophilous species

Pelophilous species are capable of using a greater range of substratum hardness than other ecomorphotypes (Lamoral, 1978b). Accordingly, these less stenotopic species may be less easily isolated, and less prone to speciation by vicariance in evolutionary time. Indeed, the wide

<b>A Psammophilous</b>		<b>C Pelophilous</b>	
ARACHNIDA	INSECTA	ARACHNIDA	INSECTA
Araneae	Coleoptera	Araneae	Coleoptera
Ammoxenidae	Carabidae	Barychelidae	Carabidae
Eresidae	Anthiinae	Ctenidae	Anthiinae
Gnaphosidae	Graphipterinae	Ctenizidae	Graphipterinae
Heteropodidae	Scaritinae	Eresidae	Curculionidae
Loxoscelidae	Cicindelidae	Idiopidae	Brachycerinae
Lycosidae	Scarabaeidae	Lycosidae	Scarabaeidae
Nemesiidae	Scarabaeinae	Theraphosidae	Tenebrionidae
Palpimanidae	Tenebrionidae	Zodariidae	Tenebrioninae
Salticidae	Tentyriinae	Scorpiones	Scarabaeinae
Segestriidae	Trogidae	Bothriuridae	Tentyriinae
Sicariidae	Neuroptera	Buthidae	Trogidae
Zodariidae	Myrmeleontidae	Ischnuridae	Orthoptera
Scorpiones	Nemopteridae	Scorpionidae	Acrididae
Buthidae	Crocinae	Solifugae	Acridinae
Scorpionidae	Nemopterinae	Ceromidae	Calliptaminae
Solifugae	Orthoptera	Daesiidae	Coptacridinae
Daesiidae	Acrididae	Gylippidae	Euryphyminae
Hexisopodidae	Acridinae	Melanoblossiidae	Charilaidae
Melanoblossidae	Calliptaminae	Solpugidae	Gryllidae
Solpugidae	Euryphyminae		Lathiceridae
	Gryllidae		Pamphagidae
	Schizodactylidae		Pyrgomorphidae
	Stenopelmatidae		Stenopelmatidae
	Henicinae		Henicinae
	Stenopelmatinae		Tettigoniidae
	Thysanura		Hetrodinae
	Lepismatidae		Thysanura
			Lepismatidae
<b>B Lithophilous</b>			
ARACHNIDA	INSECTA		
Amblypygi	Blattodea		
Phrynichidae	Blaberidae		
Araneae	Coleoptera		
Eresidae	Curculionidae		
Migidae	Brachycerinae		
Selenopidae	Tenebrionidae		
Trochanteriidae	Tenebrioninae		
Scorpiones	Tentyriinae		
Ischnuridae	Orthoptera		
Scorpionidae	Acrididae		
	Lithidiinae		
	Pamphagidae		
	Pyrgomorphidae		

Table 5. Higher taxa of southern African arthropods that include substratum specialist species.

distributions of several pelophilous species, e.g. *Opisththalmus carinatus* (Peters, 1861), *O. pictus* Kraepelin, 1894 and *Cheloctonus jonesii* Pocock, 1892, contrast markedly with the often highly restricted distributions of many lithophilous and psammophilous<sup>5</sup> species (Fig. 4), suggesting that this may be the case.

Nevertheless, several pelophilous species of *Opisththalmus* also display markedly

restricted, allopatric distributions (Fig. 4A). Such species tend to be concentrated in the mountainous regions of Namibia, and the Western Cape and Northern Cape provinces of South Africa. Related species invariably occupy adjacent, but separate, mountain ranges or the intervening valleys. This is particularly clear among groups of semi-lithophilous species, and species in which the adults construct shallow burrows (scrapes) under rocks (Eastwood, 1978b). An example is provided by the *Opisththalmus chaperi* Simon, 1880 group, comprising five allopatric species in the Western Cape Province of South Africa (Prendini, 1995, in prep.). Two of these, *O. chaperi* and *O. intermedius* Kraepelin, 1894, occur at fairly low altitudes occupying discrete parts of the Breede River Valley. The remaining three species occur at higher altitudes, with *O. pattisoni* in the Cedarberg Mountains,

*O. fossor* Purcell, 1898 in the Hottentots-Holland Mountains and an undescribed species in the Kouebokkeveld (a montane plateau). Presumably the habitat requirement for rock cover promoted speciation by vicariance in this lineage, mountains acting as barriers promoting speciation of the first two species and valleys serving the same function for the other three. It is perhaps to be expected that they might speciate in a similar manner to that proposed for the lithophilous *Hadogenes*.

Finally, it must also be realized that an influx of aeolian deposits could provide a barrier to many pelophilous species just as it does for lithophilous species (albeit perhaps to a lesser extent). Thus the Kalahari sand system appears to have acted as a major agent of vicariance to pelophilous *Opisthophthalmus* and lithophilous *Hadogenes*, resulting in pairs of sister species inhabiting similar hard soil or rocky habitats on its eastern and western sides (Prendini, 1995). The plains-living Namib genus *Crypsicerus* Saussure, 1888, of the orthopteran family Lathiceridae, provides a similar example from the insects. *Crypsicerus* includes only two species, occurring north and south of the central Namib dune system (Irish, 1988b), which presumably acted as the agent of vicariance that ultimately promoted speciation in this pelophilous taxon.

### Substratum specialization and the Effect Hypothesis

It will be clear from the above discussion that stenotopic substratum requirements have promoted vicariance, and thereby allopatric speciation, in certain groups of arid-adapted southern African arthropods, including scorpions. Several of these taxa (e.g. tenebrionids and lepismatids) provide text-book examples of substratum specialization. However, many other taxa qualify as candidates for substratum specialization (Table 5).

These arthropods are all characterized by stenotopic substratum requirements (e.g. sand, rock) during the larval and/or adult stage, specialized ecomorphological adaptations (e.g. elongated tarsal unguis) for locomotion and/or burrowing in these substrata, and limited vagility across alternative substrata. Aerial or aquatic dispersal is also usually absent (e.g. many Orthoptera are apterous/brachypterous) or limited (e.g. Neuroptera are weak fliers). As would

be expected, most of these taxa occupy discrete, restricted distributional ranges, with closely related species being allopatric or parapatric. When sympatric, closely related species are allopatric, suggesting that niche divergence occurred secondarily in sympatry (for examples, see Endrödy-Younga, 1982a; Irish, 1990). Rapid, frequent speciation by vicariance in these arthropods may be viewed as an effect of substratum specialization.

Quantitative tests of the predictions of the EH reside in comparisons between the relative numbers of extant species of stenotopes and eurytopes and the extent of their distributional ranges. Two corollaries emerge from Vrba's (1980) prediction of faster rates of speciation among stenotopes, as applied to species richness in scorpions. First, substratum specialists (psammophiles, pelophiles and lithophiles) should outnumber substratum generalists (corticoles and lapidicoles). Second, the more stenotopic species (psammophiles and lithophiles, occupying the extremes of the substratum hardness continuum) should outnumber the less stenotopic species (pelophiles, occupying substrata of intermediate hardness).

If the southern African scorpions are classified into the five ecomorphotypes discussed above (see **Appendix 2**), substratum specialists account for 84% of the southern African scorpion species, compared with substratum generalists, confirming the first prediction (Fig. 5). In addition, the number of pelophilous species is approximately 29% of the number of psammophilous and lithophilous species, confirming the second prediction.

Similarly, the prediction by the EH that substratum specialists will be more range-restricted than substratum generalists can be tested by assessing the extent of the distributional ranges of the southern African scorpions. Extent of distributional range can be assayed by various indices, of which the number of quarter degree squares (QDS) containing point locality records, and the areas of the polygons created by joining the outermost point locality records are employed here (Table 6). Both indices reveal a common pattern, confirming the prediction of the EH. Although the variation in QDS for the various ecomorphotypes is not significant ( $P = 0.0584$ , Kruskal-Wallis Nonparametric ANOVA: 7.469), the mean and median values for the substratum generalists are considerably greater. In the area polygon, the mean and median values for the substratum

generalists are significantly greater ( $P = 0.0122$ , Kruskal-Wallis Nonparametric ANOVA: 10.908) than the values for substratum specialists.

### Conclusions

The combined effects of geomorphology and climatic change have acted as agents of vicariance determining the evolution of the southern African scorpions with their restricted substratum requirements, narrow ecological tolerances and limited vagility, and are primarily responsible for the high species richness and endemism in the subregion. In many cases, agents of vicariance are still in existence (e.g. mountain ranges and sand systems) and coincide with disjunct distributional patterns. Such patterns, in turn, support a vicariance mode of speciation on the whole. Substratum specialist taxa have experienced extensive speciation, giving rise to a high proportion of species, many of which are also endemic. *Opisthophthalmus*, in particular, has experienced what might be termed "adaptive radiation" in a similar manner to the burrowing scorpionoid genus *Urodacus* Peters, 1861 in Australia (Koch, 1977, 1978, 1981). Presumably specialization into psammophilous, pelophilous, and semi-lithophilous ecomorphotypes promoted rampant speciation by vicariance in both genera, in accordance with the EH.

Across the broader taxonomic spectrum, it seems that substratum specialization might have played an equally important role in the evolution of other arid-adapted southern African arthropod taxa (e.g. Coleoptera, Neuroptera, Orthoptera, Thysanura, Solifugae and fossorial Araneae) by

promoting vicariance and, hence, allopatric speciation. Ultimately, the complex geomorphology of the arid western half of southern Africa, with concomitant substratum diversity, provides the context without which the speciation of such substratum specialist taxa would not have occurred.

### Acknowledgements

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Substratum affinities	Ecomorphological adaptations	Number of species	Mean QDS	Median QDS	Mean area (km <sup>2</sup> )	Median area (km <sup>2</sup> )
Psammophilous	Highly stenotopic	46	37	11	281,984	19,790
Lithophilous	Highly stenotopic	39	24	12	87,847	15,157
Pelophilous	Moderately stenotopic	26	33	10	215,946	10,846
Corticolous + Lapidicolous <sup>†</sup>	Eurytopic	21	58	53	525,668 *	295,293 *

Table 6: Relationship between substratum specialization, ecomorphotype and extent of distributional range for southern African scorpion species. Distributional range is expressed as the number of quarter degree squares (QDS) containing point locality records and as the area (km<sup>2</sup>) of the polygon created by joining the outermost point locality records. Distributional data obtained from Prendini (1995, 2000b, c, 2001b, in prep.). Refer to **Appendix 1** for glossary of accepted definitions and **Appendix 2** for species list. <sup>†</sup>These ecomorphotypes were grouped for the statistical analysis because the observations for lapidicolous species do not represent a statistical sample ( $n = 4$ ). \* indicates a significant difference ( $P < 0.05$ , Kruskal-Wallis: 10.908).



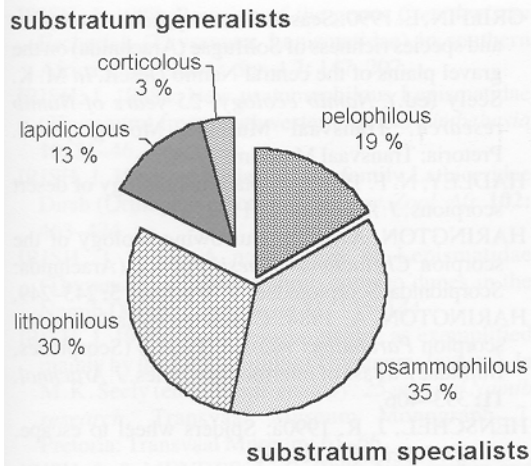


Fig. 5: Percentage species richness of stenotopic v. eurytopic scorpions in southern Africa (classified according to **Appendix 2**). Substratum specialist ecomorphotypes (lithophilous, psammophilous and pelophilous) are stenotopic, whereas substratum generalist ecomorphotypes (corticolous and lapidicolous) are eurytopic. Among the substratum specialist ecomorphotypes, lithophiles and psammophiles are relatively more stenotopic (occurring at opposite ends of the substratum hardness continuum) than pelophiles (inhabiting substrata of intermediate hardness).

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## Notes

<sup>1</sup>An adaptation is defined here *sensu* Gould & Vrba (1982), Coddington (1988) and Baum & Larson (1991) as an apomorphic function evolved after an historical change in environmental conditions.

<sup>2</sup>Fet *et al.* (1998: 611) used a “four point scale” for classifying psammophilous scorpions: (1) ultra-psammophiles: species found only in sand habitats with little vegetation; (2) psammophiles: species found in vegetated sandy areas; (3) fossorial psammophiles: species that spend almost all their time in burrows; these often lack the specialized adaptations of categories 1 and 2; (4) facultative psammophiles: species that inhabit sand and other substrates; generally these do not possess a highly modified morphology. These categories correspond to the following categories recognized in **Appendix 1**: ultra-psammophiles (1) and psammophiles (2) = psammophilous to ultra-psammophilous (1a); fossorial psammophiles (3) and facultative

psammophiles (4) = semipsammophilous (1b). These concepts are best represented by the substratum hardness continuum (Fig. 2).

<sup>3</sup>This term is synonymous with “fossorial” *sensu* Lamoral (1978a, 1979), Bradley (1988) and Polis (1990). However, since “fossorial” is taken to refer specifically to being adapted for digging or burrowing into the substratum (**Appendix 1**), use of this term to describe species that burrow in hard soil is considered misleading, for psammophilous species are also fossorial. Newlands’s (1972a) use of the term “pelophilous” is more appropriate for referring to such species. The term “fossorial psammophiles” proposed by Fet *et al.* (1998) is similarly misleading, because species that these authors regard as “ultra-psammophiles”, e.g. *Opisthophthalmus flavescens*, are also fossorial.

<sup>4</sup>Bradley (1988) and Polis (1990) only recognized four ecomorphotypes, placing corticolous species in their “errant” category. However, the paucity of species recorded with both epigaeic and hemiedaphic (*sensu* Lamoral, 1979: 773) habitat predilections suggests that the separation of these categories is ecologically meaningful.

<sup>5</sup>Penrith (1979) observed that to be widely distributed, a species must either have a wide substratum tolerance (i.e. substratum generalist), or a specific substratum available over a wide area at present or in the past (i.e. substratum specialist). *P. granulatus* and *O. wahlbergii* are notable exceptions to this trend in restricted distributions for psammophilous species (Prendini, 1995). However, because their widespread distributions (essentially delimited by the Kalahari sand system in the arid to semi-arid parts of southern Africa) are nonetheless defined almost entirely by the nature of the substratum, these exceptions prove the rule. Considerable geographic polymorphism is evident across the distributional range of both species, such that subspecies, now in synonymy, have been recognized in the past (Lamoral, 1979). Such variation is indicative of incipient speciation within locally isolated populations.

## Appendix 1

Glossary of terms applied to substratum specialization and ecomorphotypes in scorpions (adapted from Lincoln *et al.*, 1998)

**arboreal**: living predominantly in trees or large woody shrubs; adapted for life in trees; arboricolous; arboreicole; dendricole; dendricolous

**arenicolous**: living in sand; arenicole; psammobiontic; sabulicolous

**corticolous**: inhabiting bark (supra- above; infra-below); corticole; corticicole; corticicolous

**edaphic**: living in the soil (eu- entirely; hemi- partly)

**endogean:** living in the interstitial zone; pertaining to, or occurring within, the pore spaces (interstices) between sediment particles

**epigean:** living at or above the soil surface; epigaic; epigeal; epigeic; epigeous

**errant:** roaming

**eurytopic:** tolerant of a wide range of habitats; having a wide geographical distribution; eurytope; eurytopy; generalist

**facultative:** contingent; assuming a particular role or mode of life but not restricted to that condition; used of organisms having the facility to live, or living, under atypical conditions

**fossorial:** adapted for digging or burrowing into the substratum

**humicolous:** living on or in the soil; humicole

**hypogean:** living underground; hypogaeous; hypogeal; hypogeous

**lapidicolous:** living under or among stones (infra-below); lapidicole; saxicolous

**lithophilous:** thriving in rocky or stony habitats (semi-partly); lithoclasticolous; lithophile; lithophilus; lithophily

**pelophilous:** thriving in habitats rich in clay; pelophile; pelophilus; pelophily

**petrocolous:** living in rocky habitats; petrocole

**petrophilous:** thriving on rocks or in rocky habitats; petrophile; petrophilus; petrophily

**psammophilous:** thriving in sandy habitats (ultra-beyond; semi-partly); psammophile; psammophilic; psammophily

**rupicolous:** living on walls or rocks; rupestral; rupestrine; rupicole

**saxicolous:** living on or among rocks or stones (infra-below); lapidicolous; saxatile; saxigenous

**saxifragous:** living in rock crevices; saxifrage

**scansorial:** climbing or adapted for climbing; scandent

**specialization:** evolutionary adaptation to a particular mode of life or habitat; specialized; specialist

**stenotopic:** tolerant of a narrow range of habitats; having a narrow geographical distribution; specialized; specialist; stenotope; stenotopy

**substratum:** the sediment surface or medium inhabited by an organism

**thinophilous:** thriving on sand dunes; thinic; thinicole; thinicolous; thinophile; thinophily

**troglobite:** an obligate cavernicole; an organism found only in caves or subterranean passages; stygobie; troglobie; troglobitic; troglobiont

**troglo-dyte:** a subterranean organism; cave dweller; troglodytic

**troglophile:** an animal frequently found in underground caves or passages but not confined to them; eucaval; eutroglobiont

**troglophilous:** thriving in caves and subterranean passages; stygophilic; troglophile; troglophilic; troglophily

**tropism:** a directed reaction or orientation response of a motile organism towards (positive) or away from (negative) the source of the stimulus; tactic; tactism; taxes; taxis; taxy

## Appendix 2

List of southern African scorpion species classified into ecomorphotypes. Taxonomy follows most recent generic treatments: *Hadogenes* (Newlands, 1980; Newlands & Cantrell, 1985; Newlands & Prendini, 1997; Prendini, 2001b); *Opisthacanthus* (Lourenço, 1987); *Opisthophthalmus* (Lawrence, 1955; Lamoral, 1979; Prendini, 2000c, 2001c); remaining genera (Lamoral, 1979; Prendini, 2000b). The following taxonomically dubious species were excluded: *Cheloctonus anthracinus* Pocock, 1899, *C. intermedius* Hewitt, 1912; *Hadogenes angolensis* Lourenço, 1999, *H. austroafricanus* Penther, 1900, *H. bifossulatus* Roewer, 1943; *Pseudolychas ochraceus* (Hirst, 1911); *Uroplectes variegatus* (C. L. Koch, 1844). Ecological information was derived from Lawrence (1969), Newlands (1972a, b, 1974, 1978, 1980), Eastwood (1977, 1978a, b), Lamoral (1977, 1978a, 1979, 1980), Harington (1978), Newlands & Martindale (1980), and Prendini (unpublished data). Sibling species complexes (comprising more than one species) presently under revision are indicated with an asterisk.

### 1. *Psammophilous*

*a. Psammophilous and ultrapsammophilous.* Characteristics: construct burrows in unconsolidated sand (including sand dunes); burrow entrances situated in open ground; elongated legs; streamlined metasoma; greatly elongated, often unequal length telotarsal ungues; retrolateral row of telotarsal spiniform macrosetae may be missing on some legs in *Opisthophthalmus*; telotarsi with numerous long macrosetae ventrally and laterally; telotarsi and basitarsi may be laterally compressed; basitarsi with "sand combs", comprising a row of elongated setiform macrosetae (spiniform macrosetae absent); metasomal carinae often absent on some/all segments in *Opisthophthalmus* and *Parabuthus*.

*Taxa:* Buthidae: *Parabuthus distridor* Lamoral, 1980, *P. gracilis* Lamoral, 1979, *P. kalaharicus* Lamoral, 1977, *P. kuanyamarum* Monard, 1937, *P. raudus* (Simon, 1888). Scorpionidae: *Opisthophthalmus adustus* Kraepelin, 1908, *O. ammopus* Lamoral, 1980,



*O. chrysites* Lawrence, 1967, *O. concinnus* Newlands, 1972, *O. flavescens* Purcell, 1898, *O. holmi* (Lawrence, 1969), *O. jenseni* (Lamoral, 1972), *O. pygmaeus* Lamoral, 1979, *O. schlechteri* Purcell, 1898, *O. wahlbergii* (Thorell, 1876).

*b. semipsammophilous*. Characteristics: construct burrows in semi-consolidated sand to sandy-loam; burrow entrances usually situated in open ground, but under rocks in a few species; moderately elongated telotarsal unguis, may be of unequal length; retrolateral row of telotarsal spiniform macrosetae may be missing on some legs in *Opisthophthalmus*; telotarsi with a few long macrosetae ventrally and laterally; basitarsi with "sand combs", comprising some elongated setiform macrosetae and some short spiniform macrosetae; metasomal carinae may be absent on some/all segments in *Opisthophthalmus*.

*Taxa*: Buthidae: *Hottentotta arenaceus* (Purcell, 1901); *Parabuthus brevimanus* (Thorell, 1876), *P. calvus* Purcell, 1898, *P. capensis* (Ehrenberg, 1831), *P. granulatus* (Ehrenberg, 1831), *P. kraepelini* Werner, 1902, *P. laevifrons* (Simon, 1888), *P. mossambicensis* (Peters, 1861), *P. muelleri* Prendini, 2000, *P. namibensis* Lamoral, 1979, *P. nanus* Lamoral, 1979, *P. planicauda* (Pocock, 1889), *P. schlechteri* Purcell, 1899, *P. stridulus* Hewitt, 1913, *P. transvaalicus* Purcell, 1899, *P. villosus* (Peters, 1862); *Uroplectes pilosus* (Thorell, 1876), *U. teretipes* Lawrence, 1966. Scorpionidae: *Opisthophthalmus boehmi* (Kraepelin, 1896), *O. capensis* (Herbst, 1800), *O. crassimanus* Purcell, 1899, *O. fitzsimonsi* Hewitt, 1935, *O. gibbericauda* Lamoral, 1979, *O. granicauda* Purcell, 1898, *O. granifrons* Pocock, 1896, *O. intercedens* Kraepelin, 1908, *O. latro* Thorell, 1876, *O. lawrencei* Newlands, 1969, *O. leipoldti* Purcell, 1898, *O. litoralis* Lawrence, 1955, *O. lornae* Lamoral, 1979.

## 2. Lithophilous

*a. Lithophilous*. Characteristics: inhabit crevices in rocks or piles of loose rocks, or hide under flakes of exfoliating rock or flat rocks resting on bedrock surface; general dorsoventral compression; pedipalps, legs and metasoma dorsoventrally compressed, and often elongated; strongly curved telotarsal unguis; well-developed prolateral and retrolateral rows of spiniform macrosetae on telotarsi; well-developed superciliary ridges of median ocelli.

*Taxa*: Buthidae: *Uroplectes planimanus* (Karsch, 1879), *U. schlechteri* Purcell, 1901. Ischnuridae: *Hadogenes bicolor* Purcell, 1899, *H. gracilis* Hewitt, 1909, *H. granulatus* Purcell, 1901, *H. gunningi* Purcell, 1899, *H. lawrencei* Newlands, 1972, *H. longimanus* Prendini, 2001, *H. minor* Purcell, 1899, *H. newlandsi* Prendini, 2001, *H. phyllodes* (Thorell, 1876)\*, *H. taeniurus* (Thorell, 1876), *H. tityrus* (Simon, 1888)\*, *H. trichiurus* (Gervais, 1843)\*, *H. troglodytes* (Peters, 1861), *H. zuluanus*

Lawrence, 1937, *H. zumpti* Newlands & Cantrell, 1985; *Opisthacanthus basutus* Lawrence, 1955, *O. capensis* Thorell, 1876, *O. diremptus* (Karsch, 1879), *O. laevipes* (Pocock, 1893), *O. lamorali* Lourenço, 1981, *O. piscatorius* Lawrence, 1955, *O. validus* Thorell, 1876.

*b. semilithophilous*. Characteristics: construct shallow burrows or scrapes under rock, or hide in rock piles or under flat rocks resting on bedrock surface; general dorsoventral compression, especially of pedipalps; pedipalps elongated in adult male; strongly curved telotarsal unguis; well-developed prolateral and retrolateral rows of spiniform macrosetae on telotarsi; well-developed superciliary ridges of median ocelli.

*Taxa*: Scorpionidae: *Opisthophthalmus austerus* Karsch, 1879, *O. brevicauda* Lawrence, 1928, *O. cavimanus* Lawrence, 1928, *O. gigas* Purcell, 1898, *O. haackei* Lawrence, 1966, *O. intermedius* Kraepelin, 1894, *O. karrooensis* Purcell, 1898, *O. lamorali* Prendini, 2000, *O. longicauda* Purcell, 1899, *O. luciranus* Lawrence, 1959, *O. pallipes* C. L. Koch, 1843, *O. pattisoni* Purcell, 1899, *O. penrithorum* Lamoral, 1979, *O. peringueyi* Purcell, 1898, *O. ugabensis* Hewitt, 1934.

## 3. Pelophilous

Characteristics: construct burrows in hard soil; burrow entrances usually situated in open ground, but sometimes under stones; enlarged chelicerae (*Opisthophthalmus* only); large, crab-like pedipalp chelae (*Cheloctonus* and *Opisthophthalmus*); short, robust legs and telotarsal unguis; stout, spiniform macrosetae distributed laterally and distally on the basitarsi; spiniform macrosetae in both rows of the telotarsi (non-buthids only).

*Taxa*: Bothriuridae: *Lisposoma elegans* Lawrence, 1928\*, *L. josehermanorum* Lamoral, 1979. Buthidae: *Karasbergia methueni* Hewitt, 1913. Ischnuridae: *Cheloctonus crassimanus* (Pocock, 1896), *C. glaber* Kraepelin, 1896, *C. jonesii* Pocock, 1892. Scorpionidae: *Opisthophthalmus ater* Purcell, 1898, *O. carinatus* (Peters, 1861), *O. chaperi* Simon, 1880, *O. coetzeei* Lamoral, 1979, *O. fossor* Purcell, 1898, *O. fuscipes* Purcell, 1898, *O. glabrifrons* Peters, 1861, *O. keilandsi* Hewitt, 1914, *O. laticauda* Purcell, 1898, *O. latimanus* C. L. Koch, 1841\*, *O. macer* Thorell, 1876, *O. nitidiceps* Pocock, 1896, *O. opinatus* (Simon, 1888), *O. pictus* Kraepelin, 1894, *O. pluridens* Hewitt, 1918, *O. praedo* Thorell, 1876, *O. pugnax* Thorell, 1876, *O. scabrifrons* Hewitt, 1918\*, *O. schultzei* Kraepelin, 1908, *O. setifrons* Lawrence, 1961.

## 4. Corticolous

Characteristics: inhabit holes in tree trunks, or hide under peeling tree bark; strongly curved telotarsal unguis;

some elongation of pedipalps, legs and metasoma (buthids) or dorsoventral compression (non-buthids).

*Taxa:* Buthidae: *Lychas burdoi* (Simon, 1882); *Uroplectes otjimbinguensis* (Karsch, 1879), *U. vittatus* (Thorell, 1876). Ischnuridae: *Opisthacanthus asper* (Peters, 1861).

#### 5. *Lapidicolous*

Characteristics: hide under stones or other available debris on the ground; elongation of pedipalps in some species.

*Taxa:* Buthidae: *Afroisometrus minshullae* (FitzPatrick, 1994); *Hottentotta conspersus* (Thorell,

1876), *H. trilineatus* (Peters, 1861); *Pseudolychas pegleri* (Purcell, 1901), *P. transvaalicus* Lawrence, 1961; *Uroplectes carinatus* (Pocock, 1890), *U. chubbi* Hirst, 1911, *U. flavoviridis* Peters, 1861, *U. formosus* Pocock, 1890\*, *U. gracilior* Hewitt, 1913, *U. insignis* Pocock, 1890, *U. lineatus* (C. L. Koch, 1845), *U. longimanus* Werner, 1936, *U. marlothi* Purcell, 1901, *U. olivaceus* Pocock, 1896, *U. triangulifer* (Thorell, 1876), *U. tumidimanus* Lamoral, 1979. Note: *U. insignis* and *U. olivaceus* are facultative arboricoles, often being collected from under the peeling bark of dead trees.