Life in sandy deserts: the scorpion model

Victor Fet*, Gary A. Polis† & W. David Sissom‡

**Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755, U.S.A.*
†*Department of Biology, Vanderbilt University, Nashville, Tennessee 37235, U.S.A.*
‡*Department of Life, Earth, and Environmental Sciences, West Texas A &M University, Canyon, Texas 79016, U.S.A.*

The biology, ecology, biogeography, phylogeny, and evolution of sand-dwelling scorpions are reviewed. We present general features of sand that form the ecological theatre on which psammophiles have evolved. Sand scorpions, compared to those that live off sand, are not very diverse in any one local habitat, although they are often relatively abundant. Worldwide, they are represented by 29 genera, 11 of which exist exclusively in sand. Endemic genera belong to non-related families, suggesting that psammophilic adaptations evolved *in situ* in different sand deserts of the world.

©1998 Academic Press

Introduction

Deserts form 25–30% of the land's surface (Polis, 1991), and approximately 20% of desert surfaces are covered by sand (Seely, 1991). Widespread in many deserts (e.g. Namib, Sahara, Karakum), sandy substrates form 64% of the Sahara, 41% of the Libyan Desert, 52% of the Arabian Desert, but only 1% of North American deserts. Sand may either be relatively loose, forming dunes, or more consolidated, forming hills and flats.

Many taxa of plants and animals live in sandy deserts. Such species are often restricted to sand and typically express remarkable ecomorphological convergence that signifies the importance of sand as an evolutionary agent. In this paper we discuss the interplay between the physical features of sand and the biology of sand-dwelling species, with a particular emphasis on the ecology and evolution of desert scorpions.

Sand as a habitat for desert species

Sand presents several unique problems to 'psammophilic' or 'arenicolous' species (i.e. those that live in sand). First, sandy habitats are almost always formed when wind

© 1998 Academic Press

deposits sand. Individuals that live in windblown areas may suffer abrasion when hit by blowing particles (Bowers, 1982). This is a particular problem for plants (Seely, 1991). Second, the instability and movement of sand may bury plants and animal burrows and are major factors excluding non-adapted species. Third, mechanical difficulties make locomotion and burrowing more difficult than in other habitats. Mobile organisms usually require special adaptations to move in sand (see below); unless supported by an expanded surface area on the tips of legs, many species would sink in sand and thus cannot travel over it. Furthermore, the angle of repose (slope angle where sand cascades on itself) prevents burrows from being built in the energetically most efficient way (as a vertical tube) (Polis *et al.*, 1986). Fourth, sand is relatively impoverished, providing a low level of nutrients compared to non-sandy habitat soils (Bowers, 1982; Walter & Box, 1983; Seely, 1991; Danin, 1996). Total nitrogen content of sand typically is 1–2 orders of magnitude lower. Many psammophilic plants compensate for poor soil nutrients with a symbiosis with either vesicular-arbuscular mycorrhizae or nitrogen fixing bacteria.

However, many unique qualities make sand potentially beneficial to those taxa that can overcome these problems. Probably most important, sand can hold relatively more water than other desert substrates (Mayhew, 1968; Noy-Meir, 1973; Pavlik, 1980; Seely, 1991, and references therein; but see Petrov, 1976; Hennessy *et al.*, 1985). Sand holds water for several reasons: first, there is little or no runoff. Second, its high interstitial capillary pressure makes percolation rapid relative to other substrates; this dries the top surface forming a physical cap that inhibits evaporation to the air. Third, layering by wind creates a series of 'mini-aquifers' — laminar barriers that slow percolation and evaporative loss of water from deeper layers. Fourth, well sorted (homogeneous) and well rounded ('equant') grains exhibit maximum porosity to and permeability of water, thus increasing the capacity of sand to hold water relative to other substrates.

The overall effect is that sand holds more water. In many sandy areas worldwide, more water is translated eventually into a more productive biotic community (Hennessy *et al.*, 1985; Polis & McCormick, 1987). Plant biomass is high on many sandy substrates. For example in the Iranian and Afghanistan deserts, the height, cover and productivity of dune psammophytes are greater than in adjacent non-sandy habitats (Freitag, 1986). Such primary productivity is subsequently translated into higher levels of secondary productivity (herbivores, granivores, detritivores and predators of these groups) compared to adjacent non-sandy areas (Hennessy *et al.*, 1985; Polis & McCormick, 1987; Seely, 1991). For predators such as scorpions, both prey availability and feeding rates are significantly greater in sand compared to adjacent non-sandy areas (Polis & McCormick, 1987).

A second trait of sand is important to a subset of species that glean information from substrate vibrations. A number of unique physical qualities of sand slow the transmission of substrate-borne vibrations, thus making them readable to animals that can use such information (e.g. scorpions; Brownell, 1984). Sand is unique in this respect; substrate-borne vibrations travel too fast on non-sandy substrates to convey information usable to animals.

Thus, sand can be a relatively favourable ecological habitat in the desert if an organism possesses the suite of adaptations needed to surmount the problems inherently associated with sand.

Sand scorpions

Before ultraviolet (UV) lights came to be used widely to find scorpions in the field (by fluorescence of their cuticle), the difficulties of capturing burrowing scorpions restricted our knowledge of their diversity and biology (Polis, 1990). Most literature

was taxonomic, describing newly discovered species. Occasional specimens deposited in museums allowed the description of such unique psammophilic genera as *Liobuthus* from Central Asia, *Buthiscus* from North Africa and *Apistobuthus* from Arabia. The Old World sand scorpions were best described in regional studies from Africa (Vachon, 1952; Lawrence, 1969; Newlands, 1972; Lamoral, 1979, 1980), Asia (Fet, 1980, 1987, 1994; Levy & Amitai, 1980), and Australia (Koch, 1977). In the New World, little information existed before the use of UV light in the field in the late 1960s. Williams (1969, 1980), among the first to use black light in the field, catalogued and described the great diversity of desert scorpions from Baja California (Mexico) and south-western U.S.A., including several taxa restricted to sand.

Much of our knowledge of the biology of sand scorpions is based on the studies of an abundant North American species, *Paruroctonus mesaensis* Stahnke (Vaejovidae). Its ecology, evolution, biogeography, behaviour, life history, genetic population structure, sensory physiology, and pheromone biology were detailed by Farley, Brownell, Polis, and colleagues (Brownell & Farley, 1979; Polis, 1979, 1980*a,b*, 1990; Polis & Farley, 1979*a,b*, 1980; Brownell, 1984; Polis *et al.*, 1986; Polis & McCormick, 1987; Gaffin & Brownell, 1992; Yamashita & Polis, 1995*a,b*). The ecology, life history, and biology of an abundant Australian sand-dwelling scorpion, *Urodacus yaschenkoi* (Birula) (Scorpionidae), is also fairly well known (Shorthouse, 1971; Marples & Shorthouse, 1982).

With two notable exceptions, *Paruroctonus baergi* (Williams & Hadley) (Fox, 1975) and *P. utahensis* (Williams) (Bradley, 1988), knowledge of other sand scorpions is largely non-existent. One purpose of this paper is to collect the scattered literature on sand scorpions and to supplement this knowledge with our unpublished data.

What are 'sand scorpions'?

Scorpions live in sand deserts worldwide. Of 140 known scorpion genera (Fet *et al.*, in press), 29 are recorded from sand habitats. Of these, 11 genera exclusively inhabit sand. While some species live exclusively on sand, others have a broader niche that includes other substrates. A four-point scale can be adopted in considering scorpions found in sandy deserts (Koch, 1962; Newlands, 1972): (1) ultrapsammophiles: 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.

We will consider only the strictly sand-adapted forms (ultrapsammophiles and psammophiles, categories 1 and 2) to demonstrate ecological adaptations and patterns of evolution on sand.

Besides their strict habitat preference, psammophilic scorpions can be characterized by their specialized ecomorphological features. After reviewing the existing literature (Birula, 1917; Lawrence, 1969; Newlands, 1972; Lamoral, 1979, 1980), we concluded that only a few leg modifications are unequivocal psammophilic adaptations. Our analyses showed that many other proposed morphological traits did not qualify as adaptations to life in sand (e.g. size of unguicular spine or tibial spurs on legs; modified number of sensory organs such as trichobothria or teeth on pectinal organs; reduced morphosculpture and colouration). Among strictly psammophilic taxa we could find exceptions to most of those traits; conversely, some proposed traits were found in completely non-psammophilic scorpions.

Among the modifications of scorpion leg structure, the most well-known are so-called 'sand combs' (Figs 1, 2 and 4–7). These are very characteristic ('snowshoe'-like) mechanical devices to aid traction, locomotion, and burrowing in sand. Combs (or bristles) occur on the tarsomeres and tibiae of all sand-living scorpions. In most taxa, they tend to be best developed on the first three pairs of legs. Similar or analogous structures are well-known in many other animal groups (e.g. lizards, beetles, grasshoppers; Pravdin 1978). Other leg modifications in sand scorpions that act to increase the effective surface area of the tarsi are long ungues (claws) (Fig. 8 cf. Fig. 9) in some African *Opistophthalmus* (Newlands, 1972), the Mexican *Vejovoidus* (Williams, 1969) and Central Asian *Pectinibuthus* (Fet, 1987). Thus, all known ultrapsammophilic scorpions converge on this character. A similar character evolved in psammophilic cockroaches (e.g. *Mononychoblatta semenovi* Chop.; Pravdin, 1978) and some Gnaphosidae spiders (Fet, unpublished data), all from the Karakum Desert.

Other possible leg modifications include flattening of the distal leg segments (Figs 1, 5 and 7) and enlarged pedal spurs. In a number of sand taxa (e.g. *Apistobuthus, Liobuthus, Vejovoidus*), the tibiae and tarsi are dorsoventrally compressed. This would effectively increase the surface area of the leg for pushing against the sand during running and burrowing (much as oars are used to propel boats in water). Also, in *Anomalobuthus* (Fig. 6), *Apistobuthus* (Fig. 7), *Pectinibuthus* and *Plesiobuthus*, the pedal spurs are quite long and wide — in fact, they are almost as long as the tarsal claws. This may represent yet another adaptation to increase the surface area for effective locomotion and burrowing in sand.

Convergent evolution of the described features occurs repeatedly among taxonomically unrelated sand scorpions; thus the leg modifications represent a classical textbook example of a convergent morphological adaptation.

Diversity and abundance

We propose that the need for specific adaptations to sand restricts membership to relatively few species that are able to adapt to sand. This leads to two predictions: (1) species diversity within sandy habitats is lower than in non-sandy habitats, and (2) because sand is often relatively productive, the abundance of those few species that adapt to sand will be relatively much higher than that of non-sand species. What is the evidence for these speculations?

In general, species diversity on sand appears to be relatively low compared to non-adjacent habitats. This appears to be the case for many taxa, from plants (Freitag, 1986; Seely, 1991) to vertebrates (Table 1). Likewise, scorpion diversity on sand is often lower than in non-sand habitats. Table 2 quantifies species diversity and specifies richness of desert scorpions from California and Baja California; each is significantly lower on sand compared to other habitats. Although the number of scorpion species on sandy substrates is usually around five, most dune systems are dominated by one or two species of psammophiles. The one species that is numerically dominant in a habitat forms a mean of 78% of all individuals in sand but only 51% off sand (Table 2).

Many of these psammophiles are quite successful, with densities commonly ranging from 0·2–0·45 individuals m^{-2} (Table 3). Some of the most dense species in North American deserts occur on sand, e.g. *Paruroctonus mesaensis, P. baergi, P. utahensis, Vejovoidus longiunguis* (Williams, 1969).

Thus we conclude, for desert scorpions at least, that the few species that live on sand are quite successful, as suggested by their densities. Our observations and the literature (e.g. Polis, 1991; Seely, 1991) suggest that the same patterns hold true for other animal taxa: species diversity of rodents, reptiles (e.g. lizards or snakes), insects (e.g. beetles, Orthoptera) and arachnids (e.g. spiders and solpugids) is relatively low
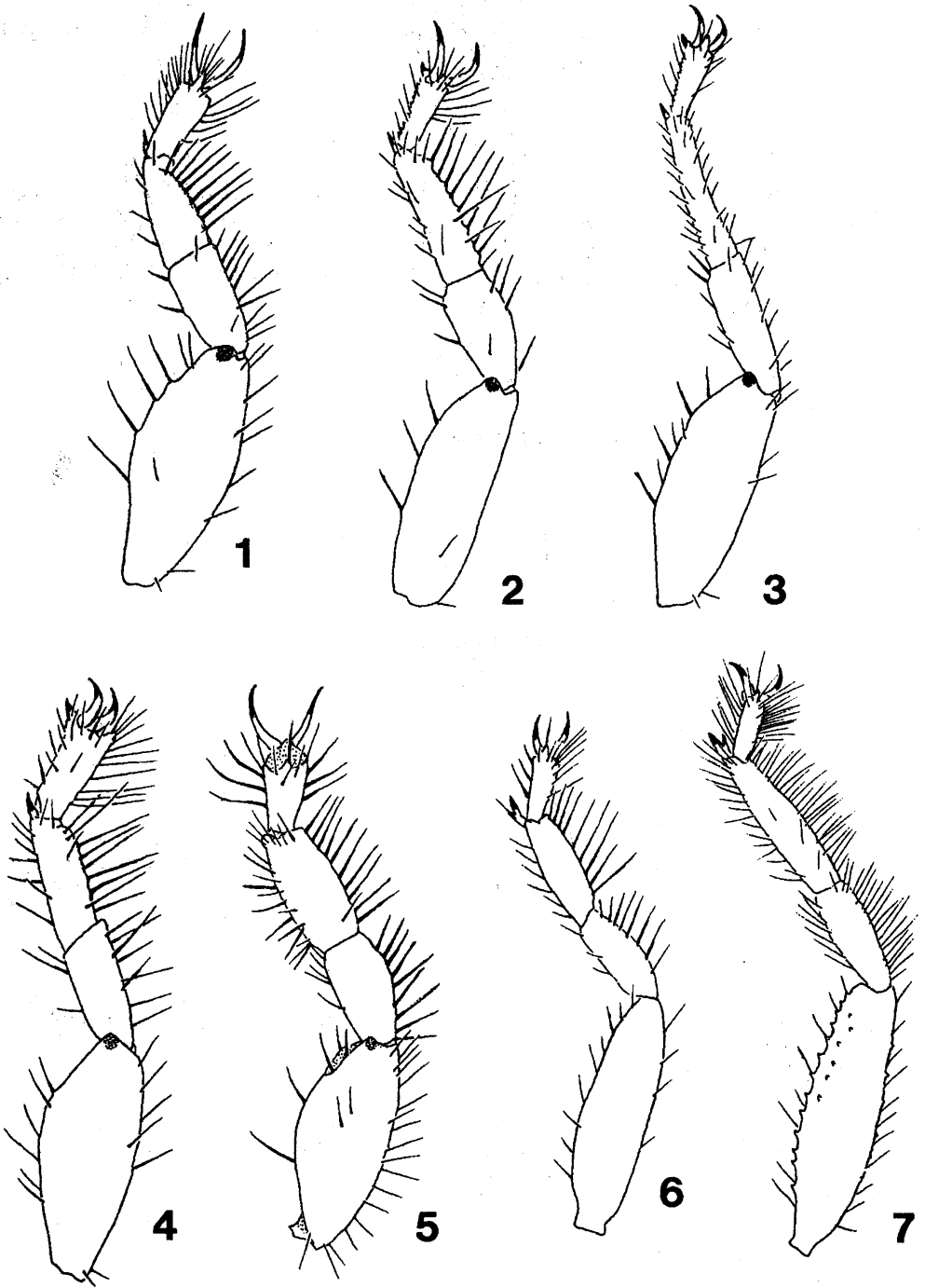
Figures 1–7. 'Sand combs' on scorpion legs. Dorso-prolateral view of right leg II (patella, tibia, tarsomere I and II) of representative psammophilic species (Figs 1, 2 and 4–7). The more generalized leg setation of *Vaejovis nitidulus* C. L. Koch (Fig. 3) is provided to facilitate comparison. Fig. 1. *Vejovoidus longiunguis*, Baja California, Mexico (Vaejovidae); Fig. 2. *Paruroctonus mesaensis*, SW U.S.A., NE Mexico (Vaejovidae); Fig. 3. *Vaejovis nitidulus*, central Mexico (Vaejovidae); Fig. 4. *Brachistosternus ehrenbergi*, Peru (Bothriuridae); Fig. 5. *Liobuthus kessleri*, Turkmenistan, Central Asia (Buthidae); Fig. 6. *Anomalobuthus rickmersi*, Turkmenistan, Central Aisa (Buthidae); Fig. 7. *Apistobuthus pterygocercus*, Arabian Peninsula (Buthidae).

compared to other habitats. However, these species are often highly adapted to sand and often occur in very high densities.

Geographic distribution

At the family level, different scorpion families dominate in different biogeographic regions. The family Buthidae includes all predominant psammophiles in the Middle East, Central Asia and North Africa; in South Africa and Australia it is the Scorpionidae; in North America, the Vaejovidae; and in South America, the Bothriuridae.
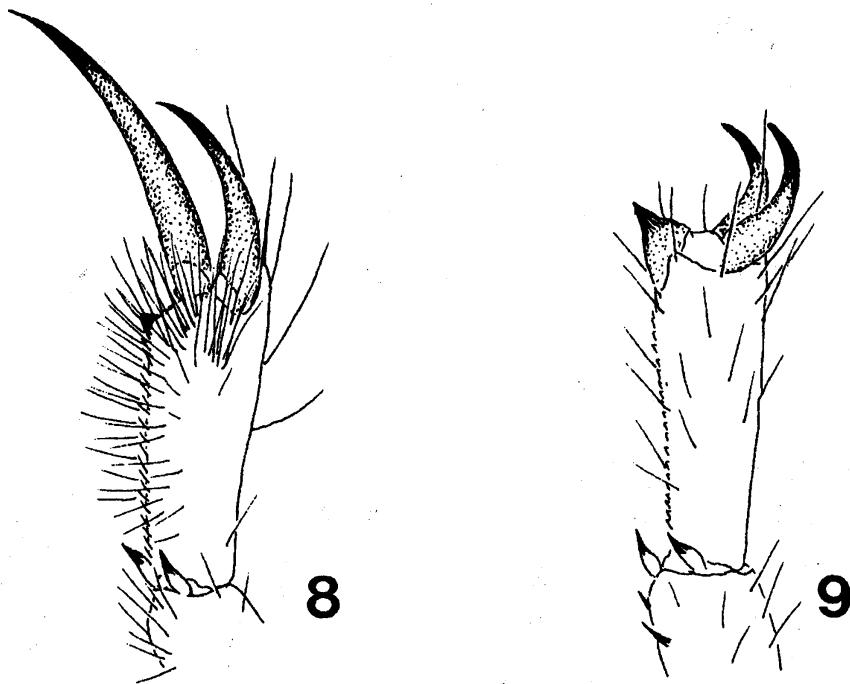
Figures 8–9. Prolateral view of tarsomere II of right leg IV. Fig. 8. Psammophilic species, *Vejovoidus longiunguis*; Fig. 9. Non-psammophilic species, *Vaejovis nitidulus*. Note relative development of ungues and median claw (dactyl).

Table 1. *Comparison of diversity of the Coachella Valley (California, U.S.A.) sand dunes/sand flats habitat vs. the rocky-sandy alluvial fan habitat (Wheeler & Wheeler, 1973; Mayhew, 1981)*

Taxon	Sand dunes and flats	Alluvial fan
Amphibians	0	3
Reptiles (lizards)	20 (11)	40 (20)
Birds	96	143
Mammals	21	35
(rodents)	8	10
Total vertebrates	137	221
Ants	8	28

At the genus level, endemic buthids are found only in the sand deserts of the Ancient Mediterranean region: these are *Anomalobuthus*, *Liobuthus*, *Pectinibuthus*, and *Psammobuthus* in Central Asia, *Apistobuthus* and *Vachoniolus* in Arabia, *Buthiscus* in North Africa, *Plesiobuthus* in Pakistan, and *Buthacus* in the Middle East, North Africa, and East Africa. Two psammophilic genera of Vaejovidae are endemic to North America: *Vejovoidus* and *Paruroctonus* (*Paruroctonus* is not strictly psammophilic but all of its members bear sand adaptations, i.e. bristle combs).

Local faunas are characterized by various levels of genus and species level diversity. Most species of psammophilic scorpions are endemic to certain sand deserts (e.g. species of *Opistophthalmus* in South Africa and *Urodacus* in Australia) or even small sand systems (e.g. *Buthacus yotvatensis* Levy et al. in Israel). Usually, only one or two psammophilic scorpions inhabit a certain sand system. For example, sandy substrates

Table 2. *Species richness, diversity and dominance of scorpions in sandy and non-sandy habitats*

| | Habitat | | | |
	Sandy	Non-sandy	t	p
Number of species	4·73±1·42	7·35±1·56	4·7	<0·0005
(range)	(3–7)	(4–11)		
Diversity	0·27±0·17	0·53±0·14	4·6	<0·0005
(range)	(0·09–0·50)	(0·31–0·76)		
Dominance	78·0±17·0	51·0±18·0	4·3	<0·0005
(range)	(50–99)	(25–80)		

The Shannon-Weaver Index is used to represent diversity. Dominance represents the per cent of the entire species assemblage formed by individuals from the single most numerous species. Data are taken from numerous sources but include Williams (1980; pers. comm.) and Polis (1990; unpublished data). In total, data from sandy habitats are taken from 11 North American sites and data from non-sandy habitats are from 23 sites in California (U.S.A.) and Baja California (Mexico).

Table 3. *Scorpion density in sandy and non-sandy habitats*

	Density (no. m^{-2})	Desert/locale	Reference
Psammophilic species			
Paruroctonus baergi	0·32	Sonoran	Fox, 1975
Paruroctonus mesaensis	0·15–0·40	Sonoran	Polis & McCormick, 1987
Paruroctonus utahensis	0·06–0·27	Chihuahuan	Bradley, 1988
Urodacus yaschenkoi	0·09–0·19	Australia	Shorthouse, 1971
Vejovoidus longiunguis	0·30–0·45	Vizcaino	Polis, unpublished
Five sympatric species	0·39	Sonoran	Fox, 1975
Four sympatric species	0·25–0·45	Sonoran	Polis & McCormick, 1987
Non-psammophilic species			
Centruroides exilicauda	0·20–0·40	Baja California	Polis, unpublished
Hadrurus spp.	0·50	Baja California	Polis, unpublished
Scorpio maurus	0·03–0·13	Negev	Shachak, 1980
Scorpio maurus	1·64	Tunisia	Krapf, 1986
Vaejovis confusus	0·02–0·06	Sonoran	Polis & McCormick, 1987
Serradigitus littoralis	8·0–12·0	Baja California	Due & Polis, 1985
Leiurus quinquestriatus	1·12	Israel	Shulov & Levy, 1978

in the Vizcaino Desert (Baja California) are dominated by *Vejovoidus longiunguis*; *Urodacus yaschenkoi* dominates most Australian sand deserts. Two strict psammophiles, *Opistophthalmus flavescens* Purcell and *O. holmi*, are sympatric in the Namib Desert (Lamoral, 1979). *Paruroctonus mesaensis* dominates many sandy habitats in western North American deserts where it is usually sympatric with one or more other species of *Paruroctonus* (e.g. *P. luteolus*). The highest known number of psammophilic scorpion taxa coexisting in the same area is found in the Eastern Karakum Desert in Central Asia (Fet, 1980); six species live in Repetek, four of which are specialized psammophiles. Three of those belong to monotypic psammophile genera (*Anomalobuthus, Liobuthus, Pectinibuthus*); the fourth is a sand-adapted subspecies, *Mesobuthus caucasicus parthorum* (Pocock) (Fet, 1980, 1994).

The scorpion fauna of the adjacent Turanian sand deserts is similar to that of the Karakum. A small area of isolated sands in the Ferghana Valley (between Uzbekistan and Tajikistan) has its own endemic psammophilic genus, *Psammobuthus* (Birula, 1911; Fet, 1980, 1989). This area is known for a number of endemic insect psammophilic species (although not endemic genera) (Kryzhanovsky, 1965). A similar psammophile was described from Northern Baluchistan (now Pakistan), *Plesiobuthus paradoxus* Pocock. Very little is known about the sand scorpion fauna of the Thal and Thar Deserts of India and Pakistan. No endemic, specialized psammophiles are yet reported from the deserts of Afghanistan, Mongolia, and China.

Sands of the Arabian Peninsula are inhabited by a huge, dominant psammophile scorpion, *Apistobuthus pterygocercus* Finnegan (G. Lowe, pers. comm.). Endemic psammophilic elements of Arabian deserts also include *Vachoniolus* (two species), *Microbuthus* (one species), and several species of *Buthacus*.

Of the well-studied desert scorpion fauna in Israel (19 desert species), most (13) avoid sandy habitats (Levy & Amitai, 1980). There are no endemic psammophilic genera in Israel. Species of the wide-ranging psammophilic genus *Buthacus* live in dunes and sandy soils. Local endemic forms include an endemic species, *Buthacus yotvatensis* from the inland sand dunes of the Arava Valley, and a subspecies, *B. leptochelys nitzani* Levy et al., in the Haluza sand dune system of the Negev Desert.

Sand deserts from North to East Africa are occupied predominantly by generalist desert species (*Androctonus, Buthus*, and *Parabuthus*). Specialized psammophiles are primarily represented by several species of *Buthacus*. The only known North African monotypic psammophilic genus, *Buthiscus*, inhabits sands of the Sahara (Algeria and Tunisia; Vachon, 1952).

In South Africa, the sand desert of Namib is characterized by many psammophilic species of the widespread desert genus *Opistophthalmus* (family Scorpionidae). Of 47 known species of this genus, one species (*O. flavescens*) is considered an ultrapsammophile, and at least 11 others are psammophilic (Newlands, 1972; Lamoral, 1979, 1980). Another scorpion taxon in South African sand deserts is the genus *Parabuthus* (Buthidae), among many xeric species of which only four are psammophiles: *P. granulatus* (Ehrenb.), *P. kuanyamarum* Monard, *P. stridulus* Hewitt, and *P. mossambicensis* (Peters) (Newlands, 1972; Lamoral, 1979, 1980).

In the deserts of Australia, a widespread xeric genus *Urodacus* (Scorpionidae) with its 19 fossorial species includes only two related species, *U. yaschenkoi* and *U. hartmeyeri* Kraepelin, which are psammophiles (Koch, 1977; A. Locket, pers. comm.).

In North America the dominant family Vaejovidae includes a prominent endemic ultrapsammophilic genus *Vejovoidus* with its only species, *V. longiunguis*, living in the sands of Vizcaino Desert in Baja California, Mexico (Williams, 1980). Other highly specialized psammophiles include many *Paruroctonus*; in this genus, of its 32 recognized species, most are considered psammophilic. Many occur on inland dunes and sand flats; many are found along sandy banks of river courses: e.g. *P. mesaensis* in the Sonoran and Mojave Deserts, *P. luteolus* (Gertsch & Soleglad), *P. hirsutipes*

Haradon, *P. borregoensis* Williams, *P. marksi* Haradon, and *P. baergi* in Arizona, California, and Sonora, *P. boreus* (Girard) in the Great Basin Desert, *P. utahensis* in the Great Basin and Chihuahuan Deserts, and many others. Some species occupy, either primarily or strictly, coastal dunes: e.g. *Paruroctonus arnaudi* and *P. ventosus* from Pacific coastal sand system in Baja California, *P. surensis* in Vizcaino sands, *P. xanthus* in river sands of the lower Colorado (Williams, 1980), and *P. maritimus* Williams in coastal dunes of California. The subgenus *Smeringurus* is striking because it contains one psammophilic species and three others that live in rocky desert habitats (Haradon, 1983). A single species of the genus *Paravaejovis*, *P. pumilis*, from Baja California Sur is also restricted to sandy habitats; taxonomic validity of this genus as compared to *Paruroctonus* has to be confirmed.

South American psammophile scorpions (all belonging to the family Bothriuridae) live in sandy deserts and coastal dunes of Peru, Chile, and Argentina; most are in the genus *Brachistosternus*. Several of these species are widespread throughout inland Argentina, Bolivia, Paraguay, and south-western Brazil (Maury, 1973; pers. comm.). The monotypic genus *Vachonia* may be also a psammophile.

Evolutionary patterns

In view of the specialized ecology, high taxonomic variety, and wide distribution of sand scorpions, a number of issues and observations in sand scorpion evolution can be discussed.

Repeated evolution of psammophilic scorpions at the family level

We suggest that specialized psammophilic forms of scorpions in all deserts evolved *in situ* from the local available generalist 'stock' (Nenilin & Fet, 1992). This hypothesis is easily tested at the family level.

The most prominent family in generic diversity of sand scorpions is the Buthidae, a family with a worldwide distribution due to pre-Gondwanaland dispersal (Sissom, 1990). However, no New World genera are psammophilic; it is strictly among the Buthidae of Africa and Asia where sand taxa (often monotypic genera) occur. Many other New World buthid genera are xeric and some occasionally occur on sand, although none dwell exclusively on sand.

All other (non-buthid) scorpion families form a monophyletic clade (Sissom, 1990); and among these, only Scorpionidae, Vaejovidae, and Bothriuridae have evolved (all independently) sand taxa. The Vaejovidae tend to be a xeric (North American) family, and Bothriuridae, a temperate (South American) one. The evolutionary pattern is striking in Scorpionidae, originally a tropical, Gondwanaland family (Couzijn, 1981). If we consider that the Australian, xeric *Urodacus* belongs to a separate subfamily (Urodacinae, a possible sister group to genera in Scorpioninae; L. Prendini, pers. comm.), psammophily evolved at least twice within the Scorpionidae clade: in Australia (Urodacinae) and South Africa (*Opistophthalmus*). Besides the desert genus *Opistophthalmus*, Scorpioninae include only the tropical, humid genera *Pandinus* (Africa) and *Heterometrus* (Asia) and a xeric Middle Eastern genus *Scorpio*. While generic diversity of Scorpionidae is very low (compared to Buthidae), the species diversity within this family can be quite high. The same can be said about the North American Vaejovidae.

Evolution at the species level and below

At the species level, often a polytypic arid scorpion genus includes one or several species exclusively confined and highly adapted to sand deserts. In such cases, a

common ancestral type is believed to have been a generalized xeric taxon. Examples include the genera *Parabuthus* (Buthidae, South Africa), *Opistophthalmus* (Scorpionidae, South Africa), and *Urodacus* (Scorpionidae, Australia). Of 11 scorpion genera known as exclusively psammophilic, eight are monotypic; all these genera, except *Vejovoidus*, belong to the Old World Buthidae.

The possible evolution of specialized sand taxa from non-psammophilic, generalized ancestors can be observed below the species level. For example, the large psammophile *Mesobuthus caucasicus parthorum* is widespread and dominant (300–500 per ha) in Central Asian deserts (Fet, 1980; Kuznetsov, 1984). Other geographic races of *M. caucasicus* (Nordmann) inhabit various xeric habitats from Ukraine to China; they only occasionally live on sand, including coastal dunes (e.g. the Black Sea coast; Fet, 1989). In this case, an autapomorphic development of psammophilic morphology strongly suggests that adaptation to sand life is derived in the genus *Mesobuthus*.

Evolution in coastal dunes and small sand systems

Some sand scorpions (as well as other psammophilic animals) could have evolved in coastal dunes, and subsequently expanded with aeolian sands. This is likely true for the Turanian fauna. Kaplin (1978) agrees with the opinion of many Russian botanists that the sand biota in the Turan region was formed in coastal dunes along water bodies (remnants of the Tethys Sea), and then expanded with the formation of large sand systems. Some scorpion species with evident psammophilic features occur today in the coastal dunes in areas where large sand deserts are absent (e.g. *Brachistosternus* in coastal dunes of Argentina). Alluvial (river banks) sands may also have been a habitat where some psammophilic scorpions initially evolved. For example, a small (c. 200 km^2) isolated system known as the Ferghana Valley sands in Central Asia is inhabited by an endemic monotype, *Psammobuthus*. These sands, far from any coast, were deposited in the Pleistocene by the ancient flow of the Sokh River (M. Golubev, pers. comm.).

In general, it appears that even small sand systems can provide enough opportunity for psammophile scorpions to evolve. Some of these sand systems likely resulted from fragmentation of formerly continuous areas, thus allowing for allopatric speciation. It is possible that the isolation of small sand areas facilitates the rapid evolution of specialized psammophilic forms from the available local stock. Thus we propose that, given a period of isolation, psammophiles are bound to emerge. The same trend is observed for psammophilic insects, lizards, and rodents (Kryzhanovsky, 1965).

Monotypic sand genera: recent origin or expanding habitat?

Is the formation of monotypic psammophilic genera a recent evolutionary event? Kaplin (1978) compared composition of endemic taxa of darkling beetles (Tenebrionidae) in the Karakum Desert. In sandy vegetation, 8% of the dominant species belong to endemic genera; in barchan (barren) dunes, 54% (with high numbers of monotypic genera). Kaplin (1978) suggested that the fauna of vegetated dunes in the Karakum is more ancient than that of barchans; thus monotypic sand genera are younger in age than polytypic as time was insufficient for them to radiate adaptively. However, non-differentiation of monotypic genera can be simply a byproduct of high gene flow because sand habitats may be homogeneous and mobile (Yamashita & Polis, 1995a,b). Sand dunes (barchans) can move c. 10 to 100 m year^{-1} (Petrov, 1976). Gene flow should follow historical connections among sand systems. For example, California sand fields were likely connected in the past (due to climatic fluctuations), and gene flow did not allow much differentiation (Yamashita & Polis, 1995a,b). Thus, evolution in sand — much as in aquatic or forest habitats — appears to be influenced by the

constant interaction of habitat fragmentation and coalescence, providing for differentiation and gene flow.

Highly adapted psammophiles would follow sand dune expansion in any direction, dispersing rapidly without significant differentiation. Ranges of such expanding sand scorpions may become enormous: *Liobuthus kessleri* Birula in Central Asia probably inhabits the entire sand area of both the Karakum and Kizylkum Deserts, from the Caspian Sea to the Syrdarya River, spanning *c.* 1200 km. Many other psammophiles in this area have extremely wide ranges, e.g. a gecko lizard, *Tetratoscincus scincus* (Schlegel) (Shcherbak & Golubev, 1997). Wide ranges are also characteristic for sand scorpions of the Arabian Peninsula (Vachon, 1979) and North Africa (Vachon, 1952).

Coexistence of psammophile scorpions

A unique case involves three scorpion species belonging to different monotypic genera that coexist in the sands of the Karakum (*Anomalobuthus, Liobuthus, Pectinibuthus*). Ecologically, these three genera partition their niches according to the degree of vegetative cover: the ultrapsammophilic *Pectinibuthus birulai* Fet is found only in the barren dunes while *Liobuthus* is most abundant under *Haloxylon* stands; *Anomalobuthus* takes an intermediate position (Fet, 1980, 1987, 1994). It is unclear how closely related these three genera are. If they are not close relatives, they may present a case of sympatric convergent evolution; conversely, if they are sister taxa, their common ancestor could have inhabited a larger dune system that became fragmented to produce allopatric speciation. There obviously were opportunities in the past for Turanian sand-adapted species to evolve in geographic isolation. For example, vicariant congeneric pairs of psammophilic beetle species exist in western Karakum and central/eastern Karakum (e.g. scarabaeids: *Achranoxia varentzovi* Semenov *vs. A. koenigi* Brske., or curculionids: *Mesostylus uzboicus* L. Arnoldi *vs. M. hauseri* Reitter). Differentiation possibly took place during the Pleistocene transfression of the Aralo-Caspian Sea which created several desert islands in the Karakum (Kryzhanovsky, 1965; Kryzhanovsky & Atamuradov, 1994). In this particular case, a vicariant pattern coinciding with a recent geological event could enable a reconstruction of a historical biogeographic scenario for psammophile scorpion species.

Sand scorpions and the age of sand deserts

The age of psammophilic taxa cannot be estimated directly since no fossils of desert scorpions exist. Some sand deserts, such as in the Namib Desert, are old, thus allowing enough time for endemics to form. On the other hand, geologically very young areas may possess endemic species or even genera. An example is the single species of its monotypic genus, *Vejovoidus longiunguis*, from the Vizcaino Desert in Baja California (Williams, 1969, 1980). A major portion of the Vizcaino sands was formed not earlier than 20,000 years ago. If we assume that *V. longiunguis* evolved *in situ* in these sands, its evolution was extremely rapid. Another plausible scenario would be more prolonged evolution in coastal sands.

Summary

Sand deserts represent a relatively harsh environment. Relatively few species are fully adapted to sand and diversities are typically lower than in non-sand habitats. However, the species that can live on sand do very well, often achieving very high densities. Scorpions exhibit intensive and extensive *in situ* evolution in all sand deserts of the world. Many species have converged upon a set of ecomorphological adaptations

related to life in sand. Representatives of 11 scorpion genera are found exclusively in sand; their distribution in the world's sand deserts qualifies for a textbook example of a vicariant biogeographic pattern. We suggest that sand scorpions can serve as a model group to study various aspects of the evolution and ecology of desert fauna, especially species that dwell in sand.

References

Birula, A.A. (1911). Skorpiologische Beiträge. 7–8. *Zoologischer Anzeiger*, **37**: 69–74.

Birula, A.A. (1917). Faune de la Russie et des pays limitrophes fondee principalement sur les collections du Musee zoologique de l'Academie des Sciences de Russie. Arachnides (Arachnoidea), Vol. 1, livr. 1, xx + 227 pp. (In Russian.) [English translation: Byalynitskii-Birulya, A. A. (1965). *Fauna of Russia and Adjacent Countries. Arachnoidea. Vol. I. Scorpions.* Jerusalem: Israel Program for Scientific Translations. xix, 154 pp.]

Bowers, J.E. (1982). The plant ecology of inland dunes in western North America. *Journal of Arid Environments*, **5**: 199–220.

Bradley, R. (1988). The influence of weather and biotic factors on the behaviour of the scorpion (*Paruroctonus utahensis*). *Journal of Animal Ecology*, **57**: 533–551.

Brownell, P.H. (1984). Prey detection in the sand scorpion. *Scientific American*, **251**: 94–105.

Brownell, P.H. & Farley, R.D. (1979). Detection of vibrations in sand by tarsal sense organs of the nocturnal scorpion, *Paruroctonus mesaensis. Journal of Comparative Physiology*, **131A**: 23–30.

Couzijn, H.W.C. (1981). Revision of the genus *Heterometrus* Hemprich and Ehrenberg (Scorpionidae, Arachnidea). *Zoologische Verhandelingen*, **184**: 1–196.

Danin, A. (1996). *Plants of Desert Dunes.* Berlin: Springer-Verlag. 177 pp.

Due, A.D. & Polis, G.A. (1985). Biology of the intertidal scorpion, *Vaejovis littoralis. Journal of Zoology (London)*, **207**: 563–580.

Fet, V. (1980). On the ecology of scorpions (Arachnida, Scorpiones) in South-East Karakum. *Revue Entomologique de l'USSR*, **59**: 223–228. (In Russian.)

Fet, V. (1987). A new genus and species of a scorpion from East Karakum: *Pectinibuthus birulai* Fet n.g. n.sp. (Scorpiones, Buthidae). *Revue Entomologique de l'USSR*, **66**: 443–446. (In Russian.)

Fet, V. (1989). A catalogue of scorpions (Chelicerata: Scorpiones) of the USSR. *Rivista di Museo di Scienzi Naturali E. Caffi (Bergamo), 1988*, **13**: 73–171.

Fet, V. (1994). Fauna and zoogeography of scorpions (Arachnida: Scorpiones) in Turkmenistan. In: Fet, V. & Atamuradov, K.I. (Eds), *Biogeography and Ecology of Turkmenistan*, pp. 525–534. Dordrecht: Kluwer Academic Publishers. 650 pp.

Fet, V., Sissom, W.D., Lowe, G. & Braunwalder, M.E. (in press). *The Catalog of Scorpions (Arachnida: Scorpiones) of the World.* New York: New York Entomological Society.

Fox, W.K. (1975). Bionomics of two sympatric scorpion populations (Scorpionida: Vaejovidae). Ph. D. dissertation, Arizona State University, Tempe. 85 pp.

Freitag, H. (1986). Notes on the distribution, climate and flora of the sand deserts of Iran and Afghanistan. *Proceedings of the Royal Society of Edinburgh*, **89B**: 135–146.

Gaffin, D.D. & Brownell, P.H. (1992). Evidence of chemical signalling in the sand scorpion, *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). *Ethology*, **91**: 59–69.

Haradon, R.M. (1983). *Smeringurus*, a new subgenus of *Paruroctonus* Werner (Scorpiones, Vaejovidae). *Journal of Arachnology*, **11**: 251–270.

Hennessy, J.T., Gibbens, R., Tromble, J. & Cardenas, M. (1985). Mesquite dunes and interdunes in southern New Mexico: a study of soil properties and soil water relations. *Journal of Arid Environments*, 9: 27–38.

Kaplin, V.G. (1978). *The Complexes of Soil Invertebrates in Sand Deserts of the Southern Subzone (East Karakum as an Example)*. Ashkhabad: Ylym. 161 pp. (In Russian.)

Koch, C. (1962). The Tenebrionidae of Southern Africa. XXXI. Comprehensive notes on the Tenebrionid fauna of the Namib Desert. *Annals of the Transvaal Museum*, 24: 61–106.

Koch, L.E. (1977). The taxonomy, geographic distribution and evolutionary radiation of Australo-Papuan scorpions. *Records of the Western Australian Museum*, 5: 83–367.

Krapf, D. (1986). Predator–prey relations in diurnal *Scorpio maurus* L. In: Barrientos, J.A. (Ed.), *Proceedings of the 10th International Congress of Arachnology*, Jaca, 1: 133.

Kryzhanovsky, O.L. (1965). *The Composition and Origin of the Terrestrial Fauna of Middle Asia (Based Primarily on Coleopteran Material)*. Moscow-Leningrad: USSR Academy of Sciences. 420 pp. (In Russian, English translation: New Delhi, India, 1980.)

Kryzhanovsky, O.L. & Atamuradov, K.I. (1994). Zoogeography of Coleoptera in Turkmenistan. In: Fet, V. & Atamuradov, K.I. (Eds), *Biogeography and Ecology of Turkmenistan*, pp. 403–418. Dordrecht: Kluwer Academic Publishers. 650 pp.

Kuznetsov, G.T. (1984). On the poisonous arthropods management in Turkmenia. In: *IX Congress of the All-Union Entomological Society*, Kiev, 1: 264–265. (In Russian.)

Lamoral, B.H. (1979). The scorpions of Namibia (Arachnida: Scorpionida). *Annals of the Natal Museum*, 23: 497–784.

Lamoral, B.H. (1980). Two new psammophile species and new records of scorpions from the northern Cape Province of South Africa (Arachnida: Scorpionida). *Annals of the Natal Museum*, 24: 201–210.

Lawrence, R.F. (1969). A new genus of psammophile scorpion and new species of *Opistophthalmus* from the Namib Desert. *Scientific Papers of the Namib Desert Research Station*, 48: 105–116.

Levy, G. & Amitai, P. (1980). *Scorpiones. (Fauna Palaestina. Arachnida I)*. Jerusalem: Israel Academy of Sciences and Humanities. 130 pp.

Marples, T.G. & Shorthouse, D.J. (1982). An energy and water budget for a population of arid zone scorpion *Urodacus yaschenkoi* (Birula, 1903). *Australian Journal of Ecology*, 7: 119–127.

Maury, E.A. (1973). Las tricobotrias y su importancia en la sistematica del género *Brachistosternus* Pocock 1894 (Scorpiones, Bothriuridae). *Physis*, 32: 247–254.

Mayhew, W.W. (1968). Biology of desert amphibians and reptiles. In: Brown, G.W. (Ed.), *Desert Biology*, pp. 195–356. New York: Academic Press. 635 pp.

Mayhew, W.W. (1981). *Vertebrates and their Habitats on the Deep Canyon Transect*. Riverside, CA: Deep Canyon Publications. 32 pp.

Nenilin, A.B. & Fet, V. (1992). Zoogeographical analysis of the world scorpion fauna (Arachnida: Scorpiones). *Arthropoda Selecta* (Moscow), 1: 3–31. (In Russian, with English summary.)

Newlands, G. (1972). Notes on psammophilic scorpions and a description of a new species (Arachnida: Scorpionides). *Annals of the Transvaal Museum*, 27: 241–253.

Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, 4: 25–41.

Pavlik, B.M. (1980). Patterns of water potential and photosynthesis of desert sand dune plants, Eureka Valley, California. *Oecologia*, 46: 147–154.

Petrov, M.P. (1976). *Deserts of the World*. New York: Wiley. 447 pp.

Polis, G.A. (1979). Diet and prey phenology of the desert scorpion, *Paruroctonus mesaensis* Stahnke. *Journal of Zoology (London)*, 188: 333–346.

Polis, G.A. (1980a). Seasonal and age specific variation in the surface activity of a population of desert scorpions in relation to environmental factors. *Journal of Animal Ecology*, 49: 1–18.

Polis, G.A. (1980b). The significance of cannibalism on the population dynamics and surface activity of a natural population of desert scorpions. *Behavioral Ecology and Sociobiology*, 7: 25–35.

Polis, G.A. (1990). *Biology of Scorpions*. Stanford, CA: Stanford University Press. 587 pp.

Polis, G.A. (1991). Desert communities: An overview of patterns and processes. In: Polis, G.A. (Ed.), *The Ecology of Desert Communities*, pp. 1–26. Tucson, AZ: University of Arizona Press. 456 pp.

Polis, G.A. & Farley, R.D. (1979*a*). Characteristics and environmental determinants of natality, growth and maturity in a natural population of the desert scorpion *Paruroctonus mesaensis*. *Journal of Zoology (London)*, 187: 517–542.

Polis, G.A. & Farley, R.D. (1979*b*). The ecology and behavior of mating in the cannibalistic scorpion, *Paruroctonus mesaensis* Stahnke. *Journal of Arachnology*, 7: 33–46.

Polis, G.A. & Farley, R.D. (1980). Population biology of a desert scorpion: survivorship, microhabitat and the evolution of life history strategy. *Ecology*, 61: 620–629.

Polis, G.A. & McCormick, S.J. (1987). Competition and predation among species of desert scorpions. *Ecology*, 68: 332–343.

Polis, G.A., Myers, C.A. & Quinlan, M.A. (1986). Burrowing biology and spatial distribution of desert scorpions. *Journal of Arid Environments*, 10: 137–146.

Pravdin, F.N. (1978). *Ecological Geography of Insects of Central Asia. Orthopteroids.* Moscow: Nauka. 271 pp. (In Russian.)

Seely, M.K. (1991). Sand dune communities. In: Polis, G.A. (Ed.), *The Ecology of Desert Communities*, pp. 348–382. Tucson, AZ: University of Arizona Press. 456 pp.

Shachak, M. (1980). Energy allocation and life history strategy of the desert isopod, *H. reaumuri*. *Oecologia*, 45: 404–413.

Shcherbak, N.N. & Golubev, M.L. (1997). *Gecko Fauna of the USSR and Contiguous Regions.* Ithaca: Society for the Study of Amphibians and Reptiles. 233 pp.

Shorthouse, D. (1971). Studies on the biology and energetics of the scorpion, *Urodacus yaschenkoi* (Birula, 1904). Ph.D. dissertation, Australian National University, Canberra. 163 pp.

Shulov, A. & Levy, G. (1978). Venoms of Buthidae. A. Systematics and biology of Buthinae. In: Bettini, S. (Ed.), *Arthropod Venoms. Handbook of experimental pharmacology*, Vol. 48, pp. 309–312. Berlin: Springer-Verlag. 977 pp.

Sissom, W.D. (1990). Systematics, biogeography and paleontology. In: Polis, G.A. (Ed.), *Biology of Scorpions*, pp. 64–160. Stanford, CA: Standford University Press. 587 pp.

Vachon, M. (1952). *Étude sur les Scorpions.* Alger: Institut Pasteur d'Algérie. 482 pp.

Vachon, M. (1979). Arachnids of Saudi Arabia. Scorpiones. *Fauna of Saudi Arabia*, 1: 30–66.

Walter, H. & Box, E. (1983). The Karakum desert, an example of a well-studied eubiome. In: West, N. (Ed.), *Ecosystems of the World, Vol 5. Temperate deserts and semi-deserts*, pp. 105–159. Amsterdam: Elsevier. 522 pp.

Wheeler, G. & Wheeler, J. (1973). *Ants of Deep Canyon.* Berkeley, CA: University of California Press. 192 pp.

Williams, S.C. (1969). A new species of *Syntropis* from Baja California Sur, Mexico with notes on its biology. *Pan-Pacific Entomologist*, 45: 285–291.

Williams, S.C. (1980). Scorpions of Baja California, Mexico and adjacent islands. *Occasional Papers of the California Academy of Sciences*, 135: 1–127.

Yamashita, T. & Polis, G.A. (1995*a*). A test of the central-marginal model using sand scorpion populations (*Paruroctonus mesaensis*, Vaejovidae). *Journal of Arachnology*, 2: 60–64.

Yamashita, T. & Polis, G.A. (1995*b*). Geographic analysis of scorpion populations on habitat islands. *Heredity*, 75: 495–505.