Ecological Zoogeography of the Saharo-Arabian, Saharan and Arabian Reptiles in the Sand Deserts of Southern Israel

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Abstract: Reptiles were surveyed in and around the sand areas in Israel, ha-ʿArava Valley (AV), Coastal Plain (CP), Rotem and Yamin Plains (MR) and Northern Negev (NN), from material in the Hebrew University and Tel Aviv University. Distributions of 28 species occurring in at least one sand area were mapped, and their ecological relationships studied zoocartographically. None is endemic. Three distribution patterns emerge: Saharo-Arabian reptiles are euryoecious psammophiles; they tend to occur in all sand areas and their northern limits tend to approximate the desert frontier defined by soils, climate and vegetation. Saharan species are mostly stenoecious psammophiles and tend to be restricted to NN and CP; Arabian species tend to be limited to AV. Species density is higher in NN and AV than in CP and MR. Relevant ecological aspects are treated briefly: adaptations to sand, community composition, vicariance among congeners, resource partitioning, etc. Among the biotic and abiotic factors considered as possibly limiting (or interacting to limit) the distributions of species, the major one appears to be soil ("islands of sand"), the second apparently humidity.

Keywords: Arabia, Israel, Sahara, Sinai, reptiles, sands, biogeography, zoocartography.

Introduction

The herpetofauna of Israel, in terms of taxa and of patterns of distribution, is reviewed elsewhere (WERNER in press). Here I discuss in greater detail the ecological zoogeography (HESSE et al. 1951) of the psammophile reptiles in the southern Israeli deserts. These were only briefly mentioned by HAAS (1952); meanwhile much more information has been gathered. I minimize redundancy with my above review and its bibliography by referring to it wherever this seems sufficient.

Biogeographical background

Israel was regarded as totally within Wallace's Mediterranean subregion (of the Palaearctic), a unit that rightly has been poorly received by global zoogeographers. Currently regional biogeographers agree that in this small country are represented four distinct biogeographical zones (fig. 1), originally based on phytogeographical research, hence in accord with Koeppen's climate classification (WERNER in press).

We find in Israel from north to south three regions of the Palaearctic: (a) the relatively mesic Mediterranean (sensu stricto) (Koeppen's Csa); (b) the steppic Irano-Turanian (Koeppen's BShs); and (c) the desertic Saharo-Arabian, earlier not split from the Saharo-Sindian (Koeppen's BWhs). Less clear-cut is (d) the Sudanian "penetration zone" (a region of the Pa-

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F. Krupp, W. Schneider & R. Kinzelbach eds. Beihefte zum TAVO A 28 (1987).

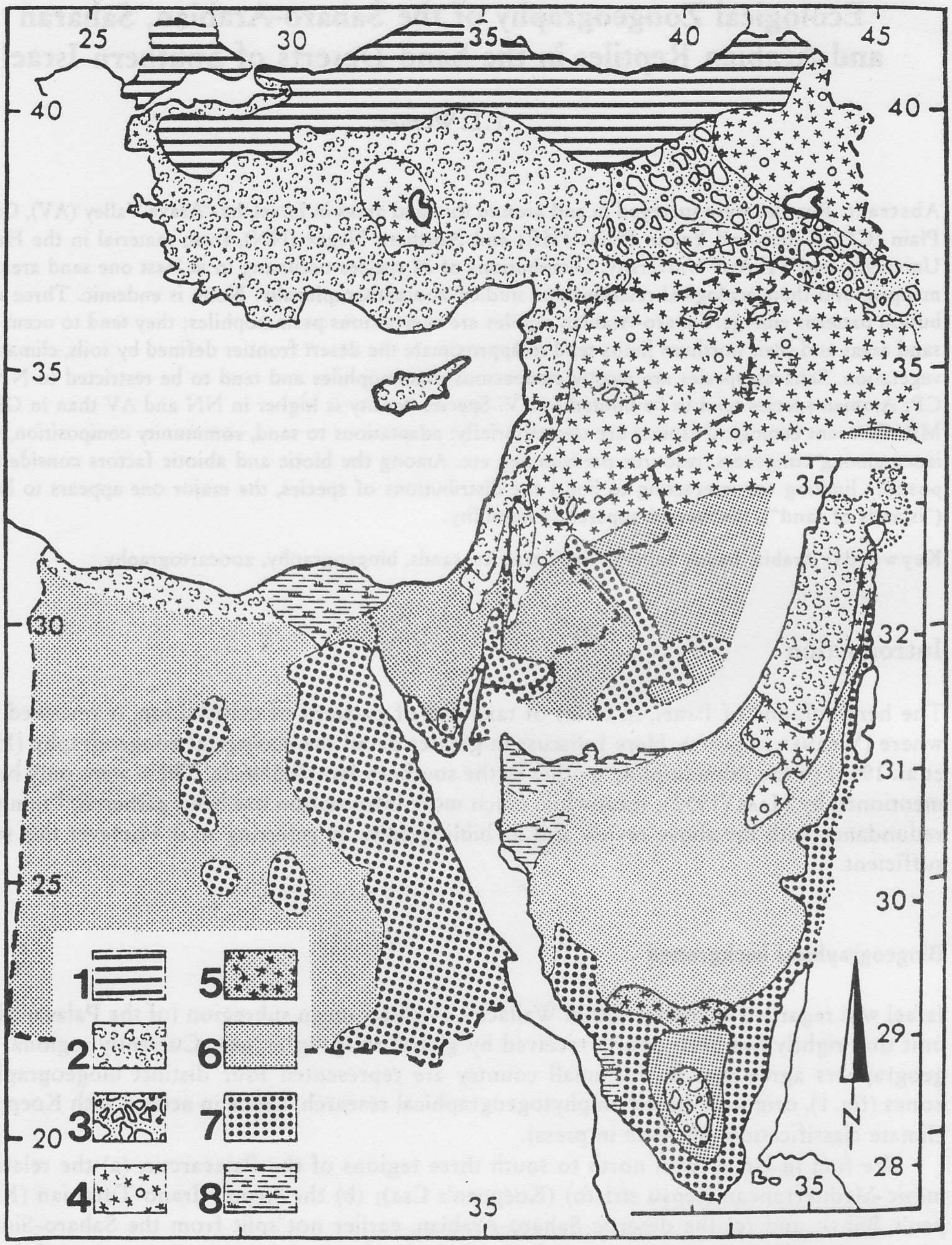

Fig. 1: Biogeography of the Levant with details for the survey area (fig. 2), based mainly on the geobotanical map of ZOHARY (1973) and partly on Werner (in press): 1, Euro-Siberian region with Euxinian and Sub-Euxinian forest; 2, Mediterranean region with woodland climax; 3, Irano-Turanian region with Kurdo-Zagrosian and other Iranian steppe-forest climaxes; 4, Irano-Turanian region with steppe and desert vegetation; 5, Irano-Turanian – Saharo-Arabian transition; 6, Saharo-Arabian region with desert vegetation (or none); 7, Sudanian region with tropical desert, savanna and forest vegetation; 8, halophytic and hydrophytic vegetation.

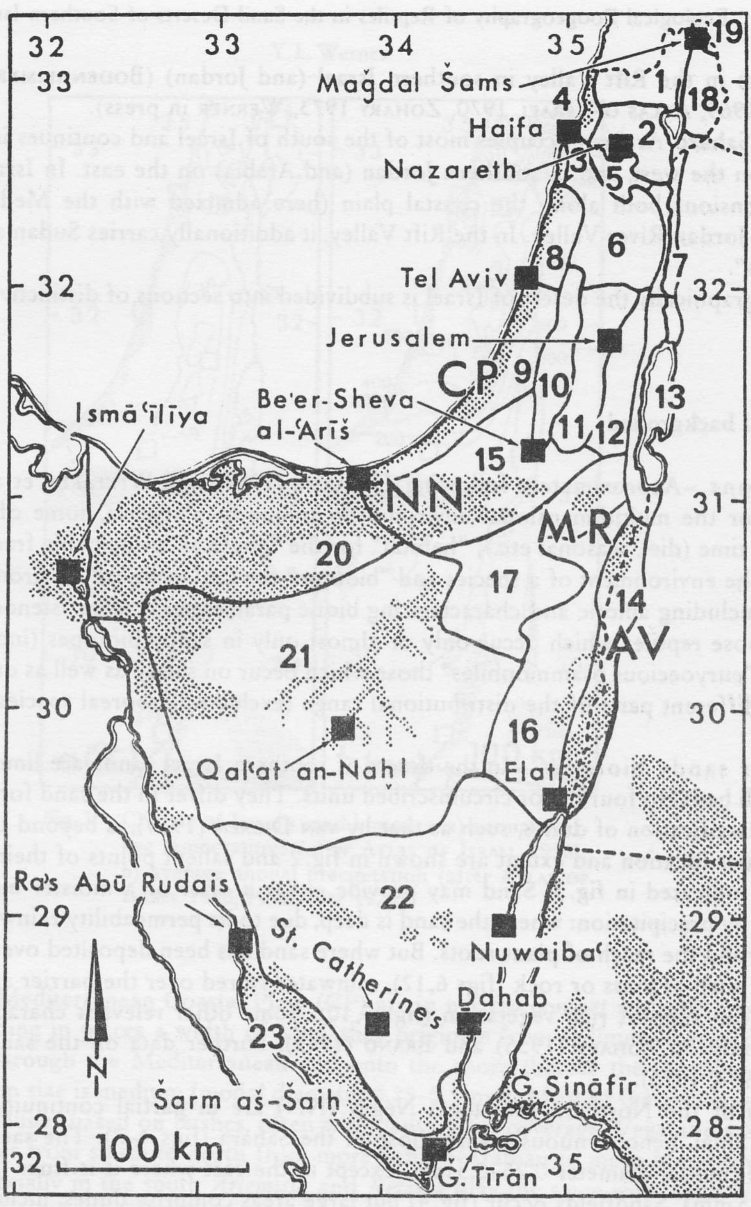

Fig. 2: The survey area. --- = limits of survey; -.-.- = frontiers. Major sand units (after Dan & Raz 1970, Horowitz 1979) stippled: AV, ha-ʿArava Valley; CP, Coastal Plain; MR, Mišor Rotem and Mišor Yamin plains; NN, Northern Negev. Relevant geographical divisions (adopted by the Fauna Palaestina Committee, Israel Academy of Sciences and Humanities) are: 4, Northern Coastal Plain; 7, Jordan Valley; 8 & 9, Central and Southern Coastal Plains; 12, Judean Desert; 13, Dead Sea Valley; 14, ha-ʿArava Valley; 15, Northern Negev; 16, Southern Negev; 17, Central Negev; 20, Northern Sinai; 21, Central Sinai Foothills; 22, Sinai Mountains; 23, Southwestern Sinai. Localities indicated here for orientation are repeated in subsequent maps without explanation.

laeotropic) in the Rift Valley in southern Israel (and Jordan) (Bodenheimer 1935, Haas & Werner 1969, Atlas of Israel 1970, Zohary 1973, Werner in press).

The Saharo-Arabian occupies most of the south of Israel and continues in Sinai (and the Sahara) on the west, and in southern Jordan (and Arabia) on the east. In Israel it has northward extensions both along the coastal plain (here admixed with the Mediterranean) and along the Jordan River Valley. In the Rift Valley, it additionally carries Sudanian "penetrants"[1] or "relicts".

Geographically the desert of Israel is subdivided into sections of distinctive characteristics (fig. 2).

Ecological background

Definitions. – Approximately following Udvardy (1959) and Wittaker et al. (1973) I use "niche" for the multidimensional environment unique to a species, some of its dimensions involving time (diel, seasonal etc.); "habitat" for the "physical" or palpable fraction (excluding time) of the environment of a species and "biotope" for the "physical" environment of a community (including abiotic and characterizing biotic parameters). I term "stenoecious psammophiles" those reptiles which occur only or almost only in sandy biotopes (including arboreal species); "euryoecious psammophiles" those which occur on sandy as well as other soils, sometimes in different parts of the distributional range (excluding arboreal species).

The four sandy biotopes. – In the desert of southern Israel sands are limited (apart from some wadi beds) to four major circumscribed units. They differ in the sand formations present but the classification of dunes, such as that by van Dieren (1934), is beyond the scope of this paper. Their location and extent are shown in fig. 2 and salient points of their climatic conditions are indicated in fig. 3. Sand may provide either a drier or a moister biotope than that indicated by precipitation: where the sand is deep, due to its permeability rainwater is lost in its depth beyond the reach of plant roots. But where sand has been deposited over less permeable substrate, such as loess or rock (figs 6, 12), rainwater stored over the barrier and protected by the sand can support rich vegetation (figs 5, 10). Some other relevant characteristics follow, based mainly on Zohary (1955) and Brand (1983). Further data on the sands are given by Tsoar (1974, 1976).

(a) Sands of the Northern (Western) Negev (NN) are in partial continuity with those of northern Sinai, hence tenuously with those of the Sahara (figs 4–7). The sand is of medium grain size (modal diameter 0.25–0.5 mm) except in the east where it is finer (modal diameter 0.125–0.25 mm). Sandfields occur (fig. 4) but large areas comprise dunes, including "Duni falcati" (barchans, van Dieren 1934) and parallel sand ridges (seif dunes) with semi-stabilized troughs (figs 4, 5). In the northern and eastern parts the dunes overlie a base of loess, and plant coverage is denser than in the southwest. Though the vegetation comprises a number of associations, the commonest dominant plants are *Stipagrostis scoparia* grass tussocks (mainly on mobile dunes), *Artemisia monosperma* shrubs (mainly in inter-dune troughs and on semi-stable dunes) and *Retama raetam* broom bushes (on stabilized sands).

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[1] In this paper "penetration" refers only to the geometrical pattern of the distribution and does not imply its causative process, usually unknown.

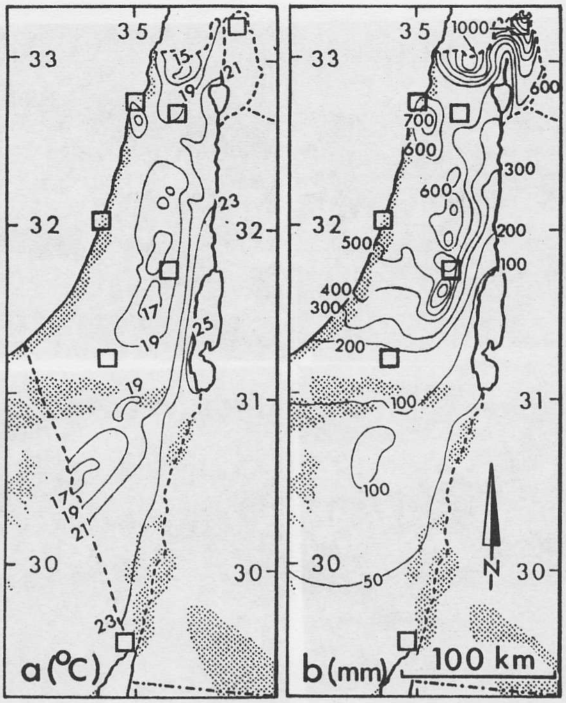
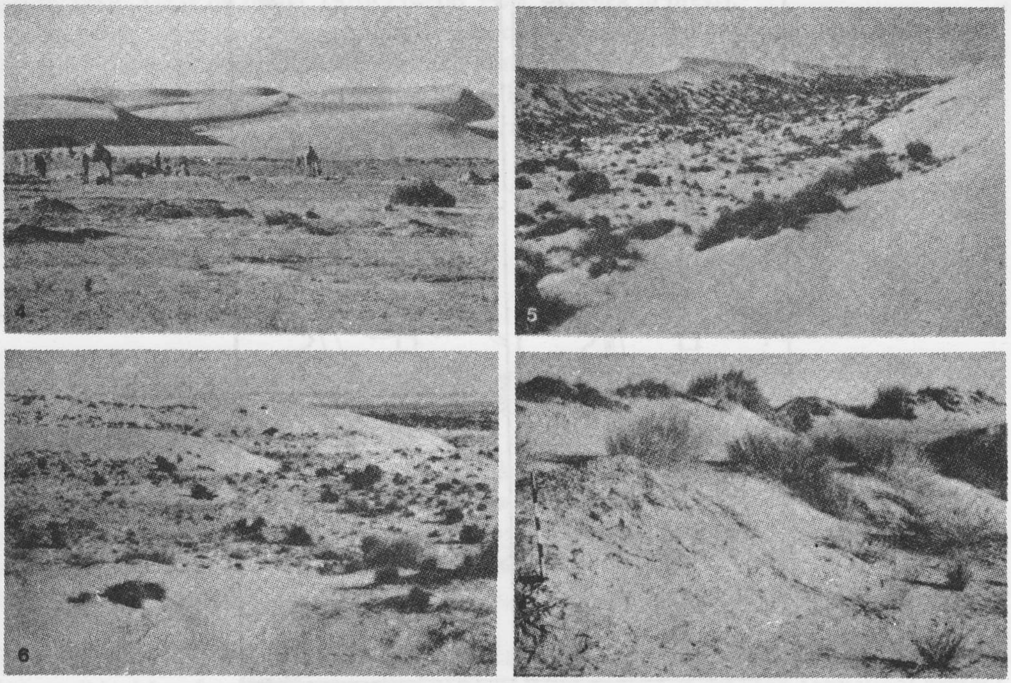


Fig. 3: Climate of Israel's sand biotopes: a) annual average temperatures (after Atlas of Israel 1956); b) average annual precipitation (after Atlas of Israel 1970, Horowitz 1979).

(b) Sands of the Mediterranean Coastal Plain (CP) are in narrow contact with the preceding (figs 8–9). Exceeding in places a width of 5 km, they originate from sediment carried by the Nile and swept through the Mediterranean and onto the shore (before the erection of the Aswān dam). Grain size is medium (modal diameter 0.25–0.5 mm). Most of the area comprises small to medium dunes based on bushes, often with dense plant coverage. Vegetation is quite varied and changes from south to north from more Saharo-Arabian to more Mediterranean. Basically and especially in the south *Artemisia* and *Retama* play the same roles as in NN but the grass tussocks on the mobile dunes are *Ammophila arenaria.*
(c) Inland sands of Mišor (plain) Rotem and Mišor Yamin (MR) are disjunct from any others (fig. 10). They originate from in-situ erosion of Neogenous sandstone and are the most coarse-grained in the area (modal diameter 0.25–0.5 mm). Much of the area comprises stabilized sand fields; dunes are small, shrub-based, and apparently of little mobility. The varying depht of the rock or compact soil under the sand results in varying water availability and varying richness and coverage of vegetation. The conspicuous dominant bushes, in order of frequency, are *Anabasis articulata, Retama raetam, Thymelaea hirsuta* and *Artemisia monosperma.*
(d) The inland sands of ha-ʿArava Valley (AV), the sector of the Syrian-African Rift Valley between the Dead Sea and the Gulf of Ẹilat (= Gulf of al-ʿAqaba), are in tenuous continuity

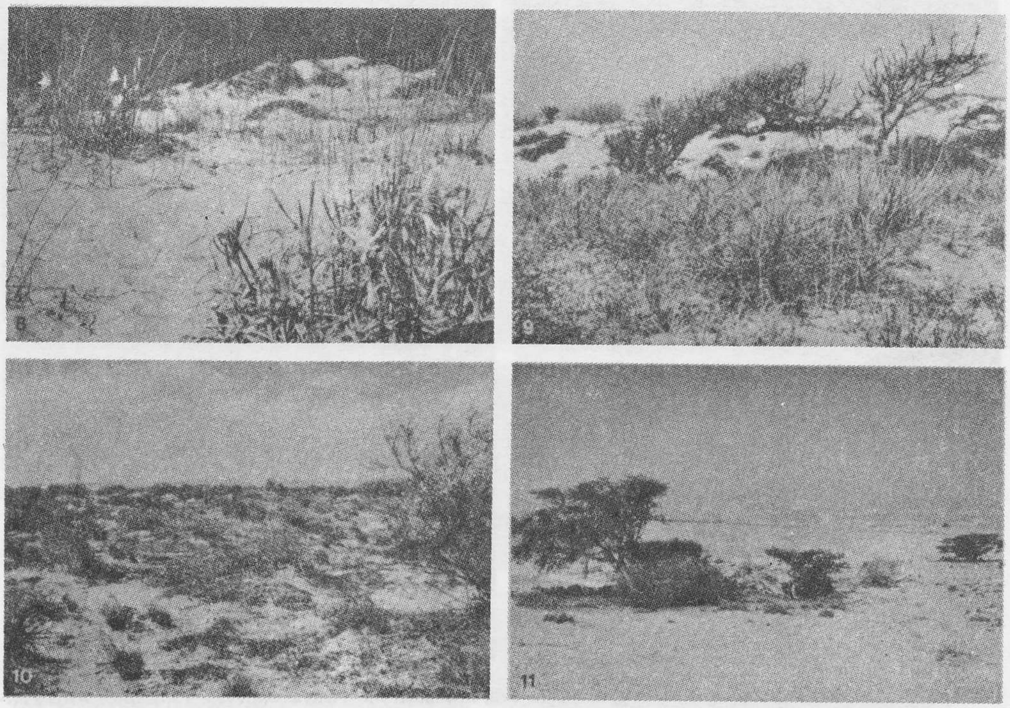


Figs 4–7: 4, Wandering Duni falcati with sand field in front in northeastern Sinai. – 5, Dune ridges (seifs) with semi-stabilized sand troughs, Ḥolot ʿAgur, Northern Negev. – 6, Wandering dunes encroaching upon loess plain, Ḥolot ʿAgur, Northern Negev. – 7, Small dunes with grass tussocks, Ḥolot ʿAgur, Northern Negev. (Black and white pattern on hoe handle, 50 cm).

with those of the Arabian desert (figs 11–13). They originate from local rocks, mostly Nubian sandstone, otherwise igneous. The sand is coarser in the north than in the south (but modal grain diameter is 0.25–0.5 mm in both). Areas of sand fields and sandy wadi beds alternate with areas of dunes with flowing sand, based on bushes. In the north the dominant plants are *Acacia tortilis* trees and *Nitraria retusa* bushes (fig. 11) but in the south – *Haloxylon persicum* and *Calligonum domosum* bushes (fig. 13).

It is of interest to what extent these sand units function zoogeographically as islands for psammophilous animals (Werner 1968, MacArthur 1972, Brand 1983). Sand in wadi beds may provide temporary bridges (figs 14, 15).

Adaptations of reptiles to sand as a habitat. – As habitats for animals, sand and other soil probably differ more than any other two substrates. The near-fluid texture of sand poses unique problems for the life of sand-inhabiting reptiles. Their corresponding morphological, physiological and behavioural adaptations have been discussed and sometimes investigated previously (Buxton 1923, Mosauer 1932, 1935, 1936, Stebbins 1943, 1948, Lawrence 1959, Mayhew 1968, Pough 1969, 1970, 1971, Pough et al. 1978, Louw & Holm 1972, Arnold 1984). Such adaptations enable their owners to live in the sands or endow them with a compet-

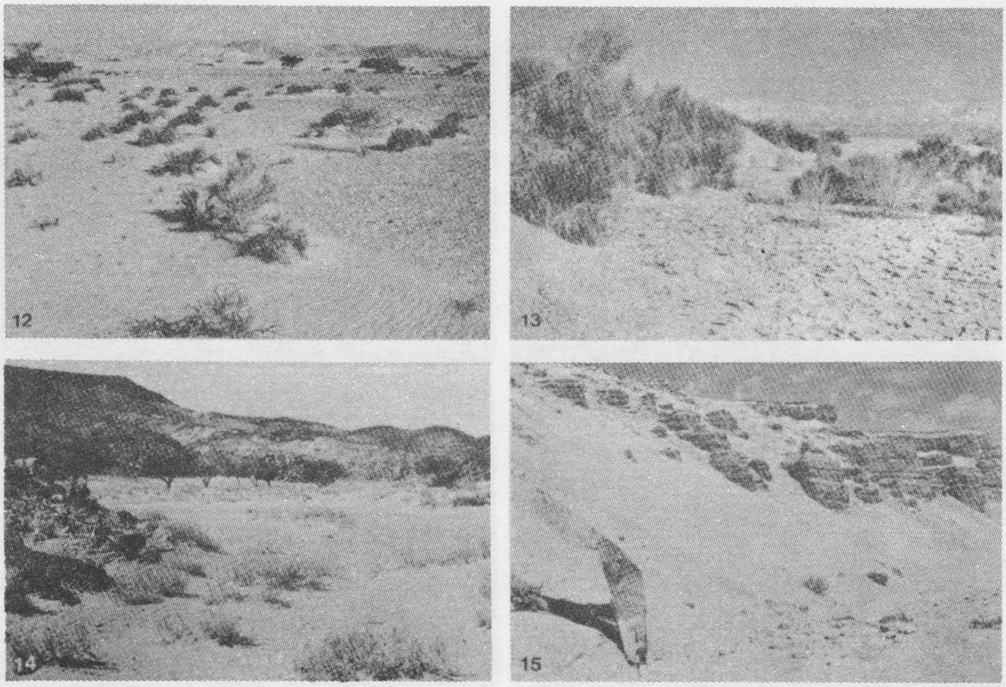


Figs 8–11: 8, Dunes with flowering *Pancratium maritimum* near Dor, Northern Coastal Plain. – 9, Stabilized sand field and dunes with small wind-stunted *Ficus sycomorus* trees, near Ziqim, Southern Coastal Plain. – 10, Typical view in Mišor Rotem (Rotem Plain) with blooming *Retama raetam,* front right. – 11, Sandy wadi bed with *Acacia tortilis* trees, near Ḥaṣeva, northern ha-ʿArava Valley.

itive advantage there; they also may constitute a disadvantage upon other ground. This zoogeographical role of psammophile adaptations warrants their following synopsis.

Locomotion over sand is facilitated in lizards by expansion of the feet. In *Acanthodactylus* the extent of fringing along the toes varies with the looseness of the substrate interspecifically and intraspecifically. It is well developed in *A. scutellatus* (fig. 16) but less so in population inhabiting arkose-admixed sand in western Sinai (pers. obs.). The toes of *Stenodactylus* ssp. are also fringed and those of *Scincus scincus* are flatly expanded (fig. 17). Psammophilous viperids locomote by sidewinding (Gans 1970) and so do here *Cerastes* spp. and *Pseudocerastes fieldi. Lytorhynchus diadema* employs a unique variety of serpentine locomotion wherein the loops push the sand down rather than sideways (pers. obs.).

Since on the one hand burrows tend to collapse, and on the other hand loose sand enables instantaneous submergence and sand-swimming, problems arise from submergence and locomotion within the sand medium. Wedge-shaped snouts, frequent in burrowing reptiles, are prominent in the sand-swimming *Scincus scincus* and *Sphenops sepsoides* (fig. 17). In these and in *Lytorhynchus* the mouth opening is protected from sand during submerged progression by its ventral position (countersunk jaw – Mosauer 1932; figs 17, 19). *Lytorhynchus* has an

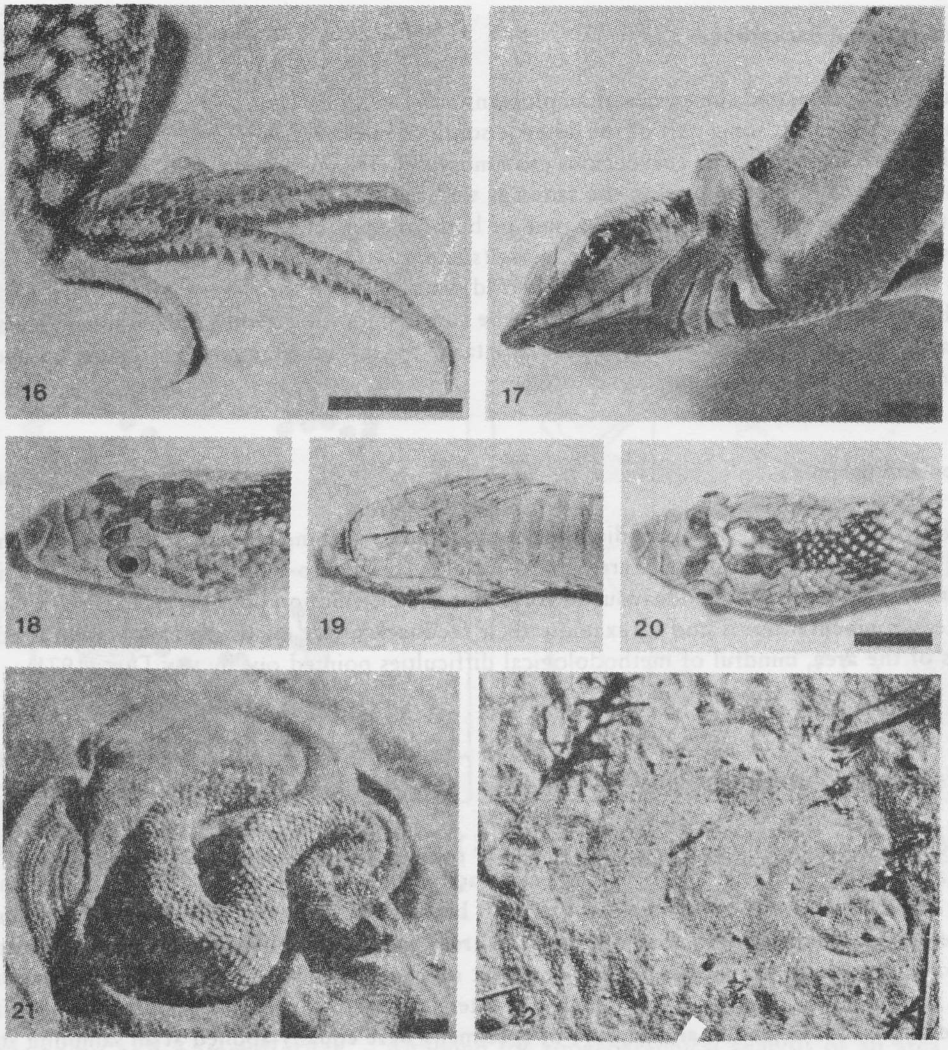


Figs 12–15: 12, Sand creeping onto reg, near Ḥaṣeva, northern ha-ʿArava Valley. – 13, Dunes with *Haloxylon persicum* bushes (left) and sandy loess in troughs drying up after rain, near Yòṭəvàtà, southern ha-ʿArava Valley. – 14, Sandy wadi with *Acacia* trees, among Sinai mountains. – 15, Windblown sand collecting along wadi cliffs, Wādī Isla, southwestern Sinai. (Black and white pattern on hoe, 50 cm).

expanded rostral, common in but not unique to psammophile snakes (fig. 18). *Cerastes* spp. can submerge stationarily by a sideways shuffling of the flattened body (figs 21–22). ARNOLD (1984) has suggested that the vertical flanks of *Scincus* (and *Sphenops*) improve the lateral thrust during sand-swimming.

The nasal passages, complexly adapted to sand in some iguanids (STEBBINS 1943, 1948), remain to be studied in Israeli psammophiles. Protection of eyes by fringed eyelids, eyelids with window (*Mesalina*) or spectacles (gekkonids, snakes) occurs also in non-psammophiles. But the relatively high species density of Gekkonidae on the sand (tab. 1) may reflect (besides their aptitude in exploiting the nocturnal time niche) the preadaptation of spectacled forms to sand. In parallel with the eyes of aquatic forms, those of *Cerastes* and *Pseudocerastes* are elevated (figs 21–22), those of *Lytorhynchus* view obliquely upwards (fig. 20). Ear openings are often small to obliterated as in other burrowers.

Under-sand breathing is problematical not only at the nasal passage level but also at the thoracal: upon exhalation the sand caves in and would stifle inhalation. *Scincus* and *Sphenops* are structured for breathing with the protected ventral surface, angularly set off from the lateral ones (Pough 1969, fig. 17).



Figs 16–22: Some adaptations of Israeli psammophilous reptiles to sand: 16, Foot of *Acanthodactylus scutellatus* showing fringe of spiny scales along 3rd and 4th toes. – 17, *Scincus scincus* showing shovel-shaped snout, countersunk jaw, angularly set-off venter and expanded toes. – 18–20, *Lytorhynchus diadema* showing expanded rostral (18), countersunk jaw (19) and eyes viewing upwards (20). – 21–22, *Cerastes vipera* in the act of digging in (21) and completely dug in with the elevated eyes exposed (22). Fig. 21 courtesy of the late Hermann Zinner. – (Scale bars: 16–20, 5 mm; 21–22, 10 mm).

Species showing such obvious morphological adaptations are usually stenoecious, restricted to the sand biotopes. Euryoecious species, lacking such adaptations, also occur in the sands.

Herpetofaunal background

Of the 101 species and subspecies of amphibians and reptiles in Israel, 47 are terrestrial reptiles occurring in at least some part of the desertic south of the country (Werner, in press). Only 28 of these are stenoecious or euryoecious psammophiles. This figure excludes species which are only occasionally encountered in the sands as well as those psammophiles which in Israel are limited to the north of the country. Some of both categories and even other species may be relevant as ecological vicariants. Thus, most (stenoecious or euryoecious) psammophile reptiles of Israel have the main part of their world distribution in the deserts of northern Africa, Arabia or both; zoogeographically they may be considered, respectively, Saharan, Arabian and Saharo-Arabian (sometimes Saharo-Sindian) taxa. So far no psammophile taxon has been defined as endemic within the survey area.

Scope and purpose

Here I deal specifically with the distribution boundaries within Israel of those psammophile reptiles which zoogeographically are Saharo-Arabian (or Saharo-Sindian), Saharan or Arabian (WERNER 1968, in press). I endeavour to formulate the distribution boundaries in geographical and environmental terms and to examine their feedback effect on the zoogeographical concepts of the area, mindful of methodological difficulties pointed out by VAN DIJK (1971).

Materials and methods

Material and sampling. - Data are from the National Collections (Hebrew University of Jerusalem, and Tel Aviv University). Collecting activities have been aimed for decades at sampling a maximum number of localities (fig. 23). In 1956-57 and especially 1967-82 sampling was extended over Sinai so that our "survey area" yielding relatively detailed information includes Israel with the Golan plateau and part of Mount Hermon, and the Sinai (WERNER 1982, in press). No rigid system of squares or inter-locality distances has been employed. Not all techniques for detection and capture of specimens were equally applied at all sampling stations; visual searching at night with lamps, useful on sand and critical for the discovery of certain psammophile geckos, has been employed in some sand areas but hardly or not in others. Hence some distribution maps utilized here are tentative.

Localities, mapping and interpretation. - Localities have been increasingly recorded in the catalogues with grid references (Israel Grid or UTM, usually to nearest 100 m) and with environmental comments. For older material grid references were reconstructed from maps but coded accordingly as a precaution.

Locality records were plotted by their coordinates to the nearest 1 km on 1 : 2,000,000 preprinted base maps (WERNER 1977). These maps were then compared to maps of environmental factors mainly from the ATLAS OF ISRAEL (1970). Further information on habitats in which species occurred, and on locations where they had been searched for in vain, was derived from personal field notes accumulated since 1948.

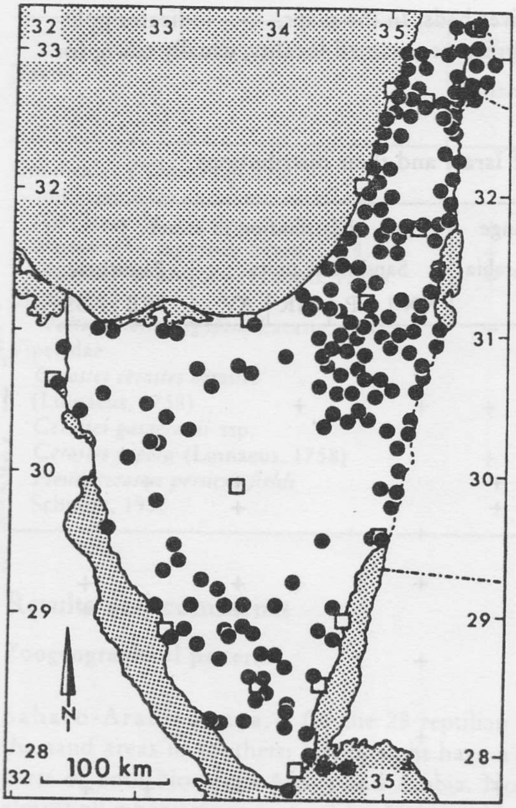


Fig. 23: Simplified plot of the main sampling localities for the herpetofaunal survey of Israel and Sinai (omitting points yielding a single species but also some yielding two or more species).

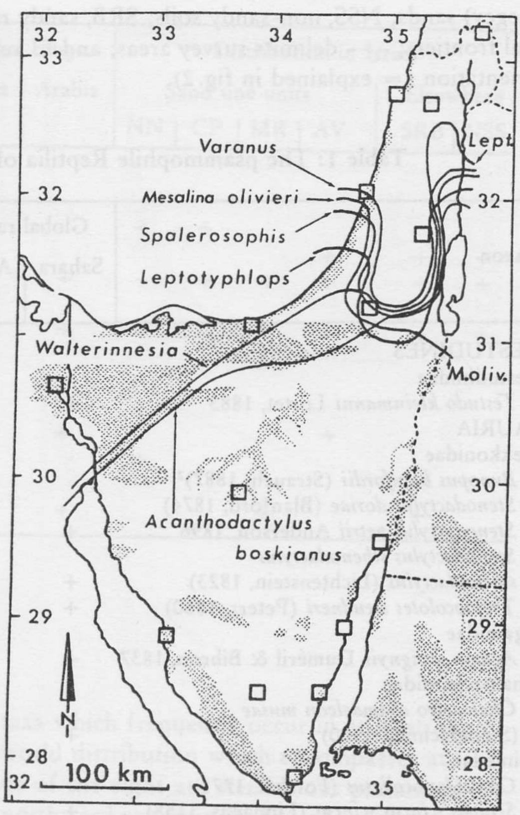


Fig. 24: Simplified representation of the northern distribution limits of six Saharo-Arabian psammophile reptiles in the survey area.

Taxonomy and nomenclature. – Although for zoogeographical analysis of an area one should generally count the animals at the standard taxonomic level of the species (Werner, in press), it seemed preferable in the present report to identify the animals as precisely as possible, i.e., to subspecies.

Full names of taxa treated are listed in tab. 1 with distributional data. Many names differ from those used by HAAS (1951 a, 1952), because the taxonomic interpretation or the nomenclature have changed. Authorities for such changes are tabulated elsewhere (WERNER in press, table 3). In the following text, species or subspecies are referred to by only the generic name whenever the genus includes only one relevant species or subspecies listed in tab. 1. Similarly, subspecies are only specified where necessary.

Abbreviations and symbols. – AV, ha-ʿArava Valley sands; CP, Coastal Plain sands; MR, Mišor (= plain) Rotem and Mišor Yamin sands; NN, Northern ha-Negev (= Western ha-

Negev) sands; NSS, non-sandy soils; SRB, sandy river beds. In the maps, -.-.- indicates political frontiers; --- delimits survey areas; and ☐ represents a named locality, usually town, for orientation (= explained in fig. 2).

Table 1: The psammophile Reptilia of Israel and their distributions.

Taxon	Global range		Distribution in Israel					
	Sahara	Arabia	Sand dune units				Elsewhere	
			NN	CP	MR	AV	SRB	NSS
TESTUDINES								
Testudinidae								
Testudo kleinmanni Lortet, 1883	+		+		+			
SAURIA								
Gekkonidae								
Bunopus blanfordii (Strauch, 1887)[2]		+				+	+	+
Stenodactylus doriae (Blanford, 1874)		+				+		
Stenodactylus petrii Anderson, 1896	+		+					
Stenodactylus sthenodactylus sthenodactylus (Lichtenstein, 1823)	+		+	+	+	+		+
Tropiocolotes steudneri (Peters, 1860)	+					+		+
Agamidae								
Agama savignyii Duméril & Bibron, 1837	+		+	?				
Chamaeleonidae								
Chamaeleo chamaeleon musae (Steindachner, 1900)	+		+					
Scincidae								
Chalcides ocellatus (Forskål, 1775)	+	+		+	+	+	+	+
Scincus scincus scincus (Linnaeus, 1758)	+		+					
Sphenops sepsoides (Audouin, 1829)	+		+	+		+	?	
Lacertidae								
Acanthodactylus boskianus (Daudin, 1802)	+	+			+	+	+	+
Acanthodactylus opheodurus (Arnold, 1980)		+			+	+	?	?
Acanthodactylus scutellatus scutellatus (Audouin, 1829)	+		+	+				
Mesalina olivieri schmidti (Haas, 1951)	+	+	+	+	+	+	+	+
Varanidae								
Varanus griseus griseus (Daudin, 1803)	+	+	+	+	+	+		
OPHIDIA								
Leptotyphlopidae								
Leptotyphlops macrorhynchus (Jan, 1864)	+	+	+	+	+			+
Colubridae ("Aglypha")								
Coluber elegantissimus (Guenther, 1878)		+				+	+	+
Lytorhynchus diadema (Duméril, Bibron & Duméril, 1854)	+		+	+	+	+		
Spalerosophis diadema cliffordi (Schlegel, 1837)	+	+	+	+	+	+		+

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[2] According to Arnold (1980), "it seems very likely that *B. blanfordii* should be placed in the synonymy of *B. tuberculatus* [Blanford, 1874]".

Taxon	Global range		Distribution in Israel					
			Sand une units				Elsewhere	
	Sahara	Arabia	NN	CP	MR	AV	SRB	NSS
Colubridae ("Opisthoglypha")								
Macroprotodon cucullatus cucullatus (Geoffroy-St. Hilaire, 1827)	+		+	+				
Psammophis aegyptius Marx, 1958	+					+	+	+
Psammophis schokari (Forskål, 1775)	+	+	+	+	+	+	+	+
Elapidae								
Walterinnesia aegyptia Lataste, 1887	+	+	+			+	+	+
Viperidae								
Cerastes cerastes cerastes (Linnaeus, 1758)	+		+					
Cerastes gasperettii ssp.		+				+		
Cerastes vipera (Linnaeus, 1758)	+		+					
Pseudocerastes persicus fieldi Schmidt, 1930		+			+		+	

Results and comments

Zoogeographical patterns

Saharo-Arabian taxa. – Of the 28 reptilian taxa which frequently occur in at least one of the sand areas in southern Israel, eight have a world distribution which encompasses at least parts of both Northern Africa and Arabia. None of the eight are stenoecious psammophiles almost all inhabit most parts of ha-Negev, with northward expansions of varying extent. *Chalcides ocellatus* occurs throughout the country, and so does *Psammophis schokari* except where replaced by *P. aegyptius* (near Eilat). The ranges of *Spalerosophis, Leptotyphlops, Varanus, Mesalina olivieri* and *Acanthodactylus boskianus* extend northwards along the Jordan valley or the CP or both, to varying extent (fig. 24).

The least sand-dependent of the eight is *Walterinnesia* which occurs mostly outside the sand areas but sometimes on them. It extends northwards in the Jordan valley quite a bit.

Saharan taxa. – The largest zoogeographical grouping is that of 14 North African reptiles unknown east of the Rift Valley.

Of these, 12 have in Israel a basically similar distribution, centered on the NN sands (fig. 25); most are stenoecious psammophiles, often with obvious morphological adaptations. A core of five, *Stenodactylus petrii, Agama, Scincus, Cerastes vipera* and also *Chamaeleo*, are confined to this area. The last spends most of its time in the shrubs and grass tussocks rather than on or in the sand itself. Extensions northwards along the CP sands are shown, in decreasing order, by *Stenodactylus sthenodactylus, Sphenops, Lytorhynchus, Acanthodactylus scutellatus* and *Macroprotodon. S. sthenodactylus* moreover occurs throughout ha-Negev and is the only Saharan psammophile (being euryoecious) extending northwards in the Jordan valley.

The northward extension of Saharan reptiles parallels that at the western extreme of the Sahara, into the Iberian peninsula (SALVADOR 1974). Only in *Macroprotodon* is the same nominal subspecies involved in both areas.

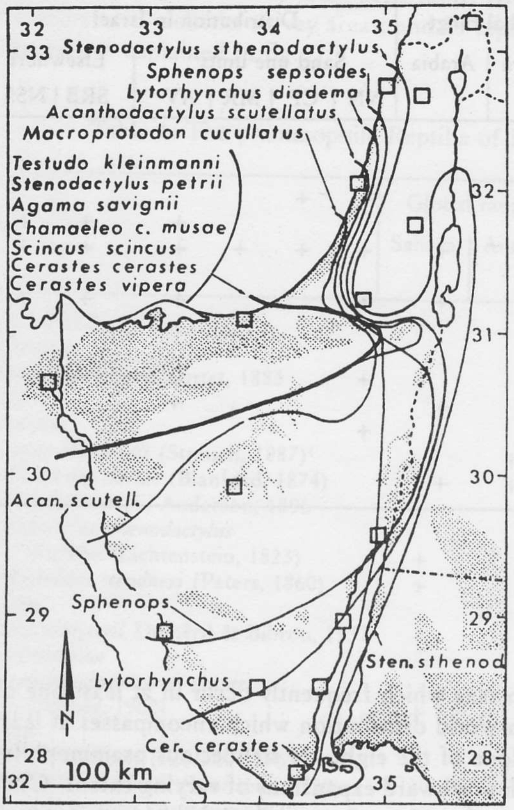

Fig. 25: Simplified representation of the eastern distribution limits of 12 Saharan psammophile reptiles in the survey area.

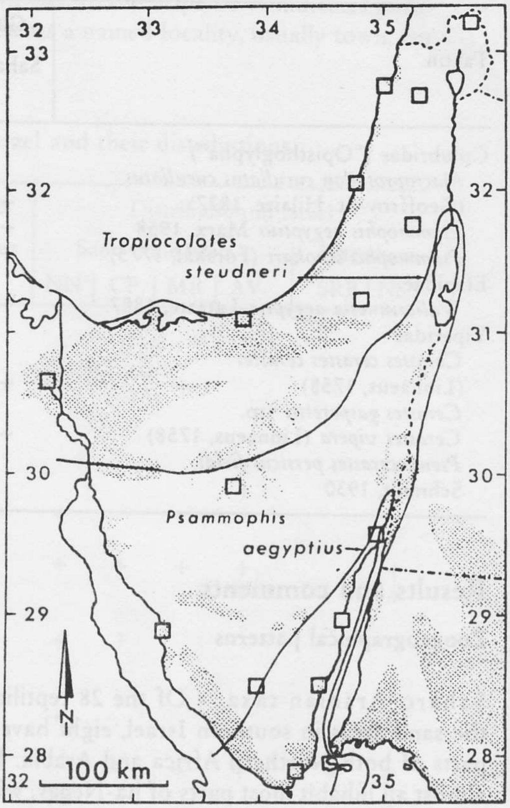

Fig. 26: Simplified representation of the eastern distribution limits of two African psammophile reptiles in the survey area. (Each has also been recorded from al-ʿArīš).

Three of the 12 species, in addition to *S. sthenodactylus*, range far to the southeast, in order of decreasing expansion: *Cerastes cerastes, Lytorhynchus* and *Sphenops*. Only the range of *Lytorhynchus* includes both the MR and AV; *Sphenops* reaches only the latter and *C. cerastes* – neither. *Testudo kleinmanni* extends eastwards to the MR area.

Two other African species apparently do not occur in NN and are only euryoecious psammophiles. *Tropiocolotes* ranges throughout the southern Negev, including AV; *Psammophis aegyptius* in Israel is limited to the southern AV (fig. 26).

Arabian taxa. – Finally, six taxa are known from Arabia (sensu lato) but do not occur in Africa (fig. 27). Four of these are limited, in Israel, to AV, with or without confluent wadis: *Bunopus, Stenodactylus doriae, Coluber elegantissimus* and *Cerastes gasperettii*[3]. *Acanthodactylus opheodurus* Arnold, 1980, as far as known by now, extends through the AV to MR in the north

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[3] Evidence on the specific status of *Cerastes gasperettii* will be published elsewhere.

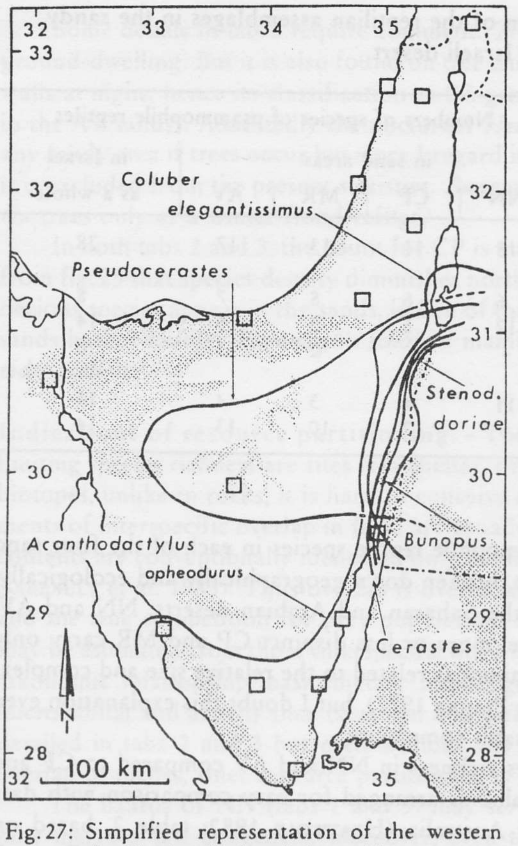

Fig. 27: Simplified representation of the western distribution limits of six Arabian psammophile reptiles in the survey area.

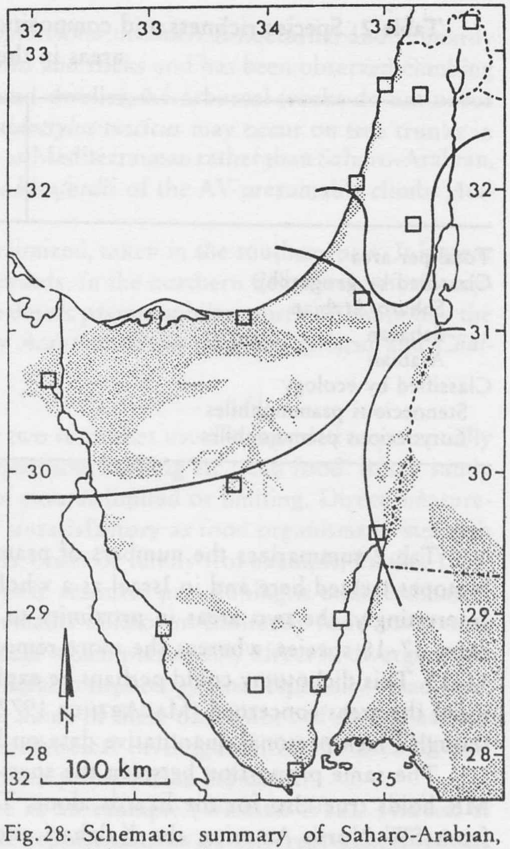

Fig. 28: Schematic summary of Saharo-Arabian, Saharan and Arabian distribution patterns of psammophile reptiles in the survey area.

and to at least southern Sinai in the south. *Pseudocerastes* does not occur in the AV (but see Mendelssohn 1965) but in the central Negev, including MR and sandy wadi beds (especially Naḥal Ramon); its range includes central Sinai but not African Egypt. Of the six, strict psammophiles are only *S. doriae* and *C. gasperettii*.

Ecological patterns

Community composition. – Although an ecological community comprises all organisms in a biotope, the question how many taxonomically related and ecologically similar species can coexist in a biotope is also of interest (Pianka 1969, Scott 1982, Huey et al. 1983). Ever since the 1960's increasing research has been addressed to the community ecology of herpetofaunal and especially saurian assemblages (Scott & Campbell 1982). Comparative data on species richness are now available for several desert areas in the world (Pianka 1971, 1977), although these have usually been discussed only in ecological, not zoogeographical, contexts.

Table 2: Species richness and composition of the reptilian assemblages in the sandy areas in the Israeli desert.

	Numbers of species of psammophile reptiles				
	in sand areas				in Israel as a whole
	NN	CP	MR	AV	
Total per area	18	11	13	17	28
Classified by geography					
Saharo-Arabian	6	6	8	7	8
Saharan	12	5	3	5	14
Arabian	–	–	2	5	6
Classified by ecology					
Stenoecious psammophiles	11	4	3	4	14
Euryoecious psammophiles	7	7	10	13	14

Tab. 2 summarizes the numbers of psammophile reptile species in each of the four sand biotopes treated here and in Israel as a whole, broken down geographically and ecologically. Interestingly, the two areas in proximity to the Saharan and Arabian deserts, NN and AV, carry 17–18 species, whereas the more remote, more or less disjunct CP and MR carry only 11–13. This dichotomy could perhaps be explained as related to the relative size and complexity of the areas concerned (MACARTHUR 1972, PIANKA 1977), but I doubt this explanation even though I lack personal quantitative data on habit complexity.

The same proportion between the species richness in NN and AV compared to CP and MR holds true also for the lizards alone. Tab. 3 is arranged for easy comparison with data from SW North America, the Kalahari and Australia (HEATWOLE 1982: table 2, based on PIANKA 1971: table 2). The species richness of NN and AV (9–10) equals that of PIANKA's (1967) North American site T, the only one branded as sandy through the presence of *Uma*. PIANKA's (1971) sandy study areas in the Kalahari (L, K, M, A, X & T) contained 14–16 lizard species, and his sandy study areas in Australia (1969: D, E) even 30 and 40 lizard species. Thus the lizard species density of CP and MR (6) appears extremely low.

Table 3: Species density of lizards with different habitats and time niches in the sandy areas of the Israeli desert.

Habitat and habits	number of lizard species				
	NN	CP	MR	AV	Mean
Diurnal, ground-dwelling	4	3	4	4	3.75
Diurnal, arboreal	1	0	0	0	0.25
Nocturnal, ground-dwelling	2	1	1	3.5	1.87
Nocturnal, arboreal	0	0	0	0.5	0.13
Fossorial	2	2	1	2	1.75
Total	9	6	6	10	7.75

Some details in tab. 3 require comment. *Tropiocolotes steudneri* is nocturnal and primarily ground-dwelling. But it is also found on tree trunks and rocks and has been observed climbing walls at night; hence its classification as 0.5 ground-dweller, 0.5 arboreal (rocks do not occur in the AV sands). Admittedly the nocturnal *Hemidactylus turcicus* may occur on tree trunks in any sandy area if trees occur but since I regard it as Mediterranean rather than Saharo-Arabian, it is excluded from the present statistics. *Bunopus blanfordii* of the AV presumably climbs *Acacia* trees only as a winter flood refuge.

In both tabs 2 and 3, the count for CP is maximized, taken in the southern part. It is clear from fig. 25 that species density diminishes northwards. In the northern CP two vicariant euryoecious species appear in the sands, in lieu of the desert psammophiles: north of Haifa bay the sands harbor besides *Psammophis schokari* mainly *Acanthodactylus schreiberi syriacus* and *Chalcides ocellatus.*

Indications of resource partitioning. – The two resources usually regarded as potentially limiting species richness are sites (for shelter, oviposition, basking etc.) and food. In the sandy biotopes, unlike in rocks, it is hard to conceive of sites as limited or limiting. Direct measurements of interspecific overlap in food are usually unsatisfactory as food organisms in stomach contents are conventionally identified only to class, order or family (for example, Pianka 1969, Barbault et al. 1985). Thus overlap is overestimated, resource partitioning is underestimated, and the true competition for prey populations remains unknown. Indirectly food partioning may be estimated from those interspecific differences which presumably affect it: divergence in taxonomic relationship, basic dietary habits, general morphology and especially head size, microhabitat and activity time (seasonal and diel). Some of these dimensions of divergence are detailed in tabs 2 and 3 but even without any methodical investigation of the breadth and overlap of niches, finer resource partitioning is often prima faciae indicated.

The lizards of NN (tabs 1 and 3) may serve as an example (Werner 1982). The list of nine includes few congeners; moreover, even the representatives of different genera of the same family tend to differ in size. Among the four diurnal ground-dwellers, *Varanus* is much larger than the rest, and carnivorous. *Agama,* much smaller, ranks next in size and is omnivorous, taking much plant material. Of the two lacertids, *Acanthodactylus scutellatus* is much larger than *Mesalina.* The nocturnal ground-dwellers are both gekkonids of the genus *Stenodactylus. S. petrii* is larger than *S. sthenodactylus,* with larger head and (relatively) larger eyes (Werner 1969); it is also a more strict psammophile. Unfortunately Frankenberg (1978) who demonstrated much divergence in precise activity times among Israeli nocturnal geckos had no *S. petrii* available; he found that the morphologically and ecologically similar *S. doriae* of AV differed significantly from *S. sthenodactylus* (the two coexist there). Of the two fossorial, sand-swimming, scincids, *Scincus* has a considerably larger (especially thicker) head than *Sphenops*; also, *Scincus* appears to locomote mainly in daytime, *Sphenops* at night.

Vicariance among congeners. – Conspicuous are three types of vicariance among congeneric species.

(a) Zoogeographically, among stenoecious psammophiles, congeners are sometimes divided among the sand areas. Thus besides the euryoecious *Stenodactylus sthenodactylus* which occurs on all sand areas, *S. petrii* occurs only on NN, and *S. doriae* only on AV (Haas 1956). Similarly NN has *Cerastes vipera* and more rarely *C. cerastes,* whereas AV has *C. gasperettii*; and if we expand the principle to cover similar genera, MR has *Pseudocerastes.*

(b) Adjacent ecologically different soils often carry different congeners. Thus on the NN sands we find *Acanthodactylus scutellatus,* on the adjoining brown desert soil – *A. boskianus* and on the adjacent loess – *A. pardalis* (Duvdevani & Borut 1974). Likewise, *Mesalina olivieri* of the NN sands is replaced on surrounding soils by *M. guttulata* (Haas 1951b) and *Sphenops* (formerly *Chalcides sepsoides*) by *C. ocellatus.* The last vicariance has been noted already by Mosauer (1932) in the Sahara.

(c) Presumably as a result of interacting zoogeographical and ecological factors, what appear to be the niche of one (stenoecious) psammophile species in one sand area, may be occupied in another sand area by another (euryoecious) psammophile species which also occurs outside the sand areas. *Acanthodactylus scutellatus* of the NN and southern CP is replaced in the northern CP by *A. schreiberi* and in MR and AV by *A. boskianus* and *A. opheodurus* (Duvdevani & Borut 1974, Werner 1986); whereas NN, CP and AV sands harbour *Sphenops sepsoides,* and only occasionally *Chalcides ocellatus*; the skink of MR is the latter.

Discussion of probable limitations for distribution

Possible biotic factors

The biotic determinants of distribution usually considered comprise food, predators and competitive exclusion. For most Israeli reptiles food habits are known only fragmentarily, anecdotally or from captivity but apparently none are so specialized that food availability could directly limit distribution. Conceivably in some areas and at certain times food scarcity sharpens interspecific competition.

Even less is known of the predators of reptiles. Some anecdotally known or reasonably suspected predators occur throughout the country, sometimes as vicariant representatives: notably large reptiles, *Falco* spp., *Circaetus gallicus, Lanius excubitor* sspp., Erinaceidae, Felidae, Vulpinae. Admittedly others occur only or mainly in the Mediterranean subregion (e.g., Ardeidae, Laridae, Alcedinidae, *Herpestes ichneumon*). On the other hand *Varanus* (predator – Stanner 1983) occurs only in the desert. Since there are no fewer reptile species in the Mediterranean subregion than in the deserts (Werner, in press), predation in itself is also no likely distributional factor.

Competitive exclusion is even more complex, and the verification of its presence or, especially, absence, more difficult than appears from much of the literature. Conventionally (and conveniently) it is investigated between closely related reptile species (Schoener 1977, Scott 1982, Huey et al. 1983) but unrelated animals may also compete for the same resource. Thus in a sparse-vegetation biotope lizards and nesting songbirds may compete for insects (Pianka 1967, 1971).

In Israel competitive exclusion is almost unresearched (exception: Avital 1981). Usually one considers that vicariance among related and similar taxa, without obvious physical zoogeographical barriers, indicates competitive exclusion. Presumably in vicariant pairs like *Chalcides ocellatus* (northern CP) and *Sphenops* (southern CP) or *Mesalina olivieri* (NN sands) and *M. guttulata* (adjoining other soils) it is competitive exclusion which draws a distributional line between the species. The precise location of this line would depend on the relative adaptedness of each species to sections of the environment and its fitness in them.

Where the range of a species terminates within a continuing biotope and with no obvious competitor beyond, one tends to suspect abiotic and especially climatic factors. Such cases are numerous among desert psammophiles in Israel, as discussed below.

Probable abiotic factors

The geographical distribution of a species is restricted by many interacting factors which should be analyzed by a direct search for correlations among the variables (van Dijk 1971, Disi 1987) and such a project is under way. Here I only examine the relative and general effectiveness of the major expected environmental limitations on species distributions.

Soil type. – I investigate here 28 reptiles which are more or less psammophilous. Of these, each of nine is limited to the sands of only one sand area (or part of it) or extends (far or little) into an adjoining sand area. Restricted to NN are *Stenodactylus petrii, Agama, Chamaeleo, Scincus* and *Cerastes vipera*; to NN and southern CP – *Acanthodactylus scutellatus* and *Macroprotodon*; to AV – *Stenodactylus doriae* and *Cerastes gasperettii*. The ranges of five others bridge stretches of non-sand so as to encompass additional major sand areas or minor sand patches (including wadi beds) but the animals occur only (or almost only) in the sand: the Saharan *Testudo kleinmanni, Sphenops, Lytorhynchus* and *Cerastes cerastes*, and the Arabian *Pseudocerastes*. These 14 make up the minimum list of stenoecious psammophiles.

At least 10 of the 14 show obvious adaptations to sand, if we only look at the most conspicuous characters: snout shape, eye position, flat abdomen, fringed toes, sidewinding (although sidewinding is practised, besides psammophilous viperids, also by *Echis coloratus* which inhabits rocky terrain [Mendelssohn 1965]).

Since no macroclimatic factors coincide with the sand areas, I conclude that for many of the 14 species the limiting factors lie in the substrate and substrate-inherent microclimatic parameters. The salient exception is *Chamaeleo* which should indeed be investigated.

Desert frontier. – Israel is divided into desert and non-desert, and this paper deals only with reptiles which occur in the desert sands. All eight Saharo-Arabian species are euryoecious psammophiles. Although two range countrywide (*Chalcides ocellatus* and *Psammophis schokari*), six (*Acanthodactylus boskianus, Mesalina olivieri, Varanus, Leptotyphlops, Spalerosophis* and *Walterinnesia*) and likewise the Saharan *Stenodactylus sthenodactylus*, occur only in the desert. All seven reach their northern limits within a belt of some 30 km width (figs 24, 25).

This belt coincides with Koeppen's region of steppe climate (= phytogeographical Irano-Turanian region), between the Mediterranean and desert climate regions (= phytogeographical Mediterranean and Saharo-Arabian regions). This is the northern limit (except in the west and east) of saline soils which occur spotwise (up to 40% of the area in places), containing up to 2% salts (mainly NaCl and $CaSO_4$). The collective boundary is centered on the 200 mm isohyete passing through Bəʾe̜r Ševaʿ, and, east of Bəʾe̜r Ševaʿ on annual isotherm 19° C. Further east, in the Rift Valley, the desert extends northwards in terms of soils, rainfall, temperature, overall climate and vegetation. Along the Rift Valley (N–S axis) temperature varies little but rainfall shows a more distinctive gradient (fig. 3).

Because of the coincidence of the various factors in the central section of the desert frontier, one cannot isolate here determinant factors. In this area the many-faceted desert's frontier constitutes the distributional boundary. But in the east along the Jordan Valley and especially in the west and along CP, zones of uniform soil are traversed by isotherms and further subdivided by isohyets.

Temperature and humidity. – Macrogeographically, the number of reptile species is correlated to latitude and summer temperature rather than humidity (TERENT'EV 1963); hence temperature probably limits the distribution of at least some species. In the Israeli climate temperature and humidity are broadly (inversely) correlated and interdependent microclimatically (WARBURG 1964). Nevertheless let us probe for their separate effects. Available microclimatic data (WARBURG 1964) being insufficient, I employ macroclimatic maps (ATLAS OF ISRAEL 1956, 1970) despite their limited relevance (HOLMES & DINGLE 1965).

The most conspicuous and consistent attribute of the Jordan Valley (apart from the saline soils) is its warmth. August temperatures average 30–32° C throughout up to Lake Kinneret in the north, and exceed this range in places. The annual average exceeds 23° C up to a northern limit halfway between the Dead Sea and Lake Kinneret. Around this point all six psammophiles which enter the Jordan Valley reach their limit. But *Acanthodactylus boskianus* and *Varanus* stop at about the 200 mm isohyet, whereas *Stenodactylus sthenodactylus, Leptotyphlops, Spalerosophis* and *Walterinnesia* extend further northwards. There are doubts about the northern limit of the last two because of reports undocumented by specimens. From distributions of non-psammophilous desert reptiles along the Jordan Valley it seems that as a rule the snakes range farther north than the lizards. Despite the moderation of the thermal gradient along the valley this may be an effect of temperature, since snakes as a group have lower thermal requirements than lizards do (BRATTSTROM 1965, MAYHEW 1968).

Along CP, too, temperatures are rather uniform but precipiation and the annual number of rainy days show N–S gradients. BYTINSKI-SALZ (1953) has noted that the northward penetration of Saharo-Sindian organisms in the coastal dunes is enabled by the relative dryness of the sand despite rain, due to its permeability. Still, sand moisture is proportional to local precipitation. It appears that humidity rather than temperature prevents several species from extending from NN into CP sands above approx. 200 mm isohyete or 25 rainy days (per year). Some of these have presumed vicariant competitors in CP but this is not so for *Stenodactylus petrii, Agama, Scincus, Cerastes vipera* and *C. cerastes.* Dealing with *C. vipera,* WARBURG (1964) reached the same conclusion.

Nine species do extend northwards in CP: *Leptotyphlops* and *Macroprotodon* to approx. 400 and 500 mm isohyets resp. (35–40 rainy days); *Mesalina olivieri, Varanus* and *Spalerosophis* to approx. 500 mm or 45 rainy days; and *Acanthodactylus scutellatus, Lytorhynchus, Sphenops* and *Stenodactylus sthenodactylus* extend respectively increasing distances northwards in the 500–600 mm (45–50 rainy days) rainfall zone, the last species even sustaining 50–55 rainy days. Of these nine, only *Leptotyphlops* and *A. scutellatus* have obvious northern vicariant competitors.

The particularly high temperatures in AV could be invoked to explain why Arabian species have not spread further west. On the other hand the AV hot zone is localized and most of the area to the east is again less warm. Unfortunately data on reptile distribution in northern Arabia are limited.

Historical aspects. – Alternatively the confinement of four out of six Arabian species to AV could be explained historically: "The species reached AV from the east, and being dependent on sand, failed to spread westwards for lack of a sand-bridge". The reciprocal explanation would apply to the Saharan species confined to NN or NN + CP. Or in other cases: "The species formerly occurred throughout the area but later geographical isolation resulted in speciation leading to vicariance". Three considerations counter the application of such historical explanations to given species. First, more collecting activity is necessary in some relevant areas, notably northwestern Arabia, before the occurrence of certain species in these areas can be excluded with confidence. Second, the current absence of a species from an area could be merely the outcome of ecological processes; the species could have lived there in the past and disappeared, with no fossils found or identified. Finally there persist too many doubts on the taxonomy of local reptiles, so that their distributions cannot be employed with confidence in historical calculations (Werner, in press).

Conclusions

1. Reptiles of the sands of southern Israel (28 ssp.) have distributions that group into three patterns (fig. 28): Saharo-Arabian species (8) tend to occur in all sandy as well as other biotopes, Saharan species (14) tend to be limited to the western sand biotopes (NN and CP) and Arabian species (6) tend to be limited to the easternmost sand biotope (AV).
2. Species density is higher in the biotopes proximate to the Sahara (NN; 18 spp.) or Arabian desert (AV; 17) than in more distal (CP; 11) and disjunct (MR; 13) biotopes.
3. Specific distribution boundaries show varying degrees of correlation to soil type, geobotanical zones, temperature and humidity; ecological intra-community effects on distribution are inferred from indications for resource partitioning on the one hand and various types of vicariance on the other hand. Sometimes different factors appear to dominate in different sectors of a given species boundary.
4. The distribution of the Saharo-Arabian euryoecious psammophiles in Israel tend to conform to the phytogeographical Saharo-Arabian and Irano-Turanian zones.
5. The distribution of several stenoecious psammophiles support the concept of "islands of sand".
6. It appears reasonable that the constellation of three principal patterns of distribution (conclusion 1) as well as the inter-biotope variation in species density (conclusion 2) have had historical reasons. Yet it is premature to apply the historical explanation to the boundary of any particular species.

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