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A Statistical Approach to Variation in *Cerastes* (Ophidia: Viperidae), with the Description of Two Endemic Subspecies

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Zusammenfassung

Bei 274 bzw. 301 Museumsexemplaren des *Cerastes cerastes* Komplexes (Viperidae) wurde die geographische Variation mittels statistischer Methoden analysiert. Die geographisch disjunkte südwestarabische Population von *Cerastes cerastes* wird gegenüber der in Nordafrika, im nördlichen Sinai und im südwestlichen Israel verbreiteten Nominatform als neue Unterart *C. c. hoofieni* Werner & Sivan abgegrenzt. Die durchweg hornlose Population von *Cerastes gasperettii* des 'Arava-Tals (im Großen Grabenbruch) unterscheidet sich von der auf der Arabischen Halbinsel vorkommenden Nominatform und wird als neue Unterart *C. g. mendelssohni* Werner & Sivan beschrieben. Diese taxonomische Hierarchie wird durch eine phänetische Clusteranalyse bestätigt. Der Unterschied zu *C. g. gasperettii* ist bei der sympatrisch vorkommenden *C. c. hoofieni* größer als bei der allopatrischen *C. c. cerastes*; hier wird ein Fall von Kontrastverschärfung vermutet. Die Variation der Ventraliazahlen bei den vier Populationen kann nicht durch Temperatureffekte erklärt werden.

Abstract

Morphological geographical variation was examined on museum specimens of snakes formerly assigned to *Cerastes cerastes* (Viperidae) using cluster analysis (274 specimens) and univariate statistics (301 specimens). The *Cerastes cerastes* population of southwestern Arabia, geographically disjunct from the nominate population of North Africa, northern Sinai and southwestern Israel, is described as a new subspecies, *C. c. hoofieni* Werner & Sivan. The consistently hornless *C. gasperettii* population of the 'Arava Valley (in the Great Rift Valley) differs from the nominate population in the Arabian Peninsula and is described as a new subspecies, *C. g. mendelssohni* Werner & Sivan. This taxonomical hierarchy is confirmed by phenetic cluster analysis. Difference from *C. g. gasperettii* is greater in the sympatric *C. c. hoofieni* than in the allopatric *C. c. cerastes*; this is a suspected case of character displacement. Variation in the number of ventrals among these four populations cannot be explained as a temperature effect.

Introduction

The history, geographical variation and taxonomy of the genus *Cerastes* (Ophidia: Viperidae) in the Levant were reviewed by Werner et al. (1991) and Werner & Sivan (1992): earlier the larger species, the horned or sand viper, had been regarded as one species, "*Cerastes cerastes*", distributed widely over North Africa and southwestern Asia. This view was still held, for example, by Welch (1983: 83). But morphological examination revealed that two species are involved: *C. cerastes* Linnaeus in Africa, extending through Sinai into the Western Negev of Israel, and *C. gasperettii* Leviton & Anderson (formerly a subspecies) in Asia, extending from Arabia into the 'Arava Valley of Jordan and Israel (in the Great Rift Valley). The two species are depicted in Werner (1995: 74). In the southwestern corner of the Arabian Peninsula, the African *C. cerastes* occurs in addition to *C. gasperettii* (confirmed by Schätti & Gasperetti 1994) and in sympatry with it. This is further proof of their status as distinct species.

These two species share polymorphism in the presence or absence of supraocular horns (Sterer 1992). Similar polymorphism is known in another viperid genus, *Bitis* of South Africa: the supraocular horns of *B. caudalis* and the supranasal horns of *B. gabonica* are absent in some individuals (FitzSimons 1962, Branch 1988). Perhaps this conspicuous polymorphism, occurring in varying proportions throughout the range of *Cerastes* in Africa and Arabia, had created a misleading impression of geographical uniformity, diverting attention from morphological geographical variation of taxonomical significance (Werner et al. 1991, Werner & Sivan 1992). Herein we address two particular geographically localised populations.

The *Cerastes cerastes* population in southwestern Arabia is disjunct from all other populations of the species, separated by about 1500 km of terrestrial route from the nearest one in Sinai. If measured across the Bab-el-Mandeb, bridging Yemen and Ethiopia, the distance to the nearest Sudanese populations (Joger 1984, Mahmoud et al. 1997) is somewhat smaller.

The *Cerastes gasperettii* population in the 'Arava Valley of Israel is exceptional in that all individuals examined (n = 104) and all those observed (hundreds) lack the pair of supraocular horns. Disi (1983) and Disi et al. (1988) confirmed the same from specimens (n >33) from the 'Arava Valley within Jordan. But horned individuals occur in close proximity outside the 'Arava Valley – not only *C. cerastes* in Wadi Huwara, northern Sinai, 15 km west of Elat (Werner et al. 1991: Fig. 4) but also *C. gasperettii* in Jordan in Wadi Rum, about 40 km east of the 'Arava Valley (Disi et al. 1988; see also Werner & Sivan 1992: Fig. 5). This situation led to the suspicion that the 'Arava population may in some ways be unique and isolated in terms of reproduction from the adjacent populations of not only *C. cerastes* but also *C. gasperettii*.

Our aim in this paper is to evaluate the taxonomic status of the populations of *Cerastes cerastes* in southwestern Arabia and of *Cerastes gasperettii* in the 'Arava Valley, using multiple statistical analyses of the morphological variation in museum material of the two species.

Material and methods

Material

The material initially examined (350 specimens) and listed by Werner et al. (1991) comprised samples as follows: North Africa W of Egypt (36); Egypt and Sudan (54); Sinai and Western Negev of Israel (71); 'Arava Valley (104); Jordan (1); Arabian Peninsula (73); Iraq and Kuwait (11). Following the exclusion of juveniles (see below) and specimens lacking data on some characters, we used 128 males and 146 females for cluster analysis, and 140 males and 161 females for univariate statistics (after the addition explained below).

Museum abbreviations follow Leviton et al. (1985).

Many of the specimens had been kept alive for a long time, especially at TAU, up to 18 years and possibly longer (Werner 1983). This should not have affected the validity of their biometrical data (Arnold & Peterson 1989).

Upon completion of all statistical analyses and this text, we were enabled by the kindness of Dr. B. Schätti (Museum d'histoire naturelle, Genève) to augment the sample of five *Cerastes cerastes* from the southwestern Arabian Peninsula with eight more specimens from coastal Yemen. As explained below, not all statistical tests could be repeated after this last-minute addition.

Characters and abbreviations

ra	Rostrum-anus length (Werner 1971).
percra	Percents of ra (Werner 1971).

We used the morphological characters defined earlier (Werner et al. 1991, Werner & Sivan 1992) in accordance with conventional classification (Anderson 1898, Leviton & Anderson 1967), so as to facilitate comparisons. Below is the annotated list of mensural, meristic and qualitative characters which we employed in statistics and clustering, after excluding redundant characters. From these we later computed characters in terms of percra or other proportions.

Mensural characters

- Rostrum-anus length (ra): Distance from tip of snout to cloaca (to nearest mm).
- Tail length: Distance from cloaca to tip of tail, if complete (mm).
- Head length: Distance from tip of snout to line joining posterior tips of mandibulae, measured parallel to long axis of body with special callipers (Goren & Werner 1987, 1993) (to nearest 0.1 mm).
- Head width: Greatest width of head (to nearest 0.1 mm).
- Head depth: Depth of head, behind the eyes (to nearest 0.1 mm).
- Dorsal scale length: The joint length (in tenths of millimetres) of a sequence of five scales of the mid-dorsal scale row, measured halfway between tip of snout and tip of tail, divided by five.
- Eye diameter: Longest diameter of visible part of eye (to nearest 0.1 mm).

Meristic characters

- Supralabials: Number of supralabial shields, total of left plus right sides.
- Dorsals at midbody: Number of dorsal scales across back at half length between tip of snout and tip of tail (approximately the thickest part of the body).
- Ventrals: Number of ventral scales from the first scale that is distinctly wider than long, to (but excluding) anal plate.
- Subcaudals: Number of subcaudal scale pairs from first pair behind the cloaca to (and including) tip of tail.

Qualitative characters

- Tubercles on occiput: Presence or absence of a pair of enlarged, tubercular, scales on occiput (Werner et al. 1991: Fig. 1; Fig. 3 herein).
- Horns: Presence or absence of supraocular "horns" (Werner et al. 1991: Fig. 2; Fig. 2 herein).
- Colour pattern on head: All specimens have a dark postocular stripe (Werner 1890), its upper margin usually counter-shaded whitish or grey-

ish, along the upper margin of the cheek, sloping posterio-ventrad from the eye (WERNER et al. 1991: Fig. 2 E; Fig. 5 herein). An index from 1 to 3 describes its relative width. On the "cheek", below the eye and the postocular stripe, there may be up to three dark spots (WERNER et al. 1991: Figs. 2 A-C; Fig. 2 herein). An index from 1 to 8 describes their extent (number; darkness relative to that of the postocular stripe).

- Colour pattern on back: The dorsal pattern of dark blotches varies within and between specimens in complex ways (WERNER & SIVAN 1992: Fig. 4). Although we classified types and shall briefly discuss them, we did not quantify this character.

Photography

We photographed many individuals, alive or preserved, mainly for the dorsal colour pattern. We used a Leica Visoflex System (bellows and 135 mm lens) and Kodak's Panatomic-X (32 ASA), T-max (100 ASA) or Kodachrome 64 ASA film. With the last-named, the millimetre ruler photographed with the specimen carried a colour scale made of Ostwald standard colour papers.

Statistics

Because of the sexual dimorphism in *Cerastes* (WERNER et al. 1991: Tabs. 1-2), we treated each sex separately. Loath to exclude the juveniles, we tried to sex them by the character "number of ventrals minus subcaudals". Although males and females differed in this character, some overlap remained and the sex of juveniles could not be determined with confidence, which meant they had to be excluded from statistics. Our analysis comprised three stages.

(1) To test whether specimens would cluster in accordance with their conventional classification, we performed hierarchical cluster analysis (ABBOTT et al. 1985) on the whole initial adult material of both species. We selected the minimum variance clustering method (or WARD's method), which uses the squared Euclidean distances, thus emphasising the greater inter-group distances. Only individuals providing a substantial amount of data were included in this analysis. For these, the few missing data points, if any, were substituted with values estimated by the multiple linear regression method for missing data. But the individuals supplying too few data and thus excluded from cluster analysis did contribute to the estimation of means and standard deviations of those characters for which they provided data.

(2) For each character we tested the significance of differences between the means of the four groups defined by this cluster analysis. We have reduced the presentation of the biometrical data (Tab. 1) to averages ± standard deviations, without ranges, because ranges depend on sample size, which is heterogeneous in this material. Between every two relevant taxa the means were compared using the two-tailed t-test, for equal variances or for unequal variances according to the case.

(3) To better estimate the relations among the four validated taxa, we performed the cluster analysis represented in the dendrograms of Fig. 7 in the following way: First, the distance between any two individuals was calculated, using GOWER's mixed data coefficient of distance (ABBOTT et al. 1985). Next, the distance between any two taxonomic groups, e.g. A and B, was defined as the unweighted average of the distances (calculated in the previous stage) over all relevant pairs, i.e. pairs in which one individual belongs to group A and the other to group B. The between-groups distances thus obtained, were used to construct the dendrograms, using the unweighted pair group average method.

Since the various characters involved are perceivably inter-correlated, our method of calculating the between-group distance as the mean of the between-pair distances has an obvious advantage over the commonly used method of calculating the between-group distance as the distance between the vectors of the group means.

In the cluster analyses (stages 1 and 3) we could only include the initial 128 male and 146 female specimens. But the biometrical data and t-tests in Tab. 1 (stage 2) include specimens with missing data and the additional 3 male and 5 female paratypes from Yemen (with MNHG numbers).

Results and comments

Distinction between *C. cerastes* and *C. gasperettii*

The WARD dendrograms explained under Statistics as Stage 1, which show all individuals examined, are not reproduced here. Instead, we summarise their content here, while copies of the original dendrograms are available from the Curator of Amphibians and Reptiles, National Museum of Natural History, Hebrew University of Jerusalem, 91904 Jerusalem, Israel.

The primary bifurcation of the WARD dendrograms for males and females, based on the full character set, largely confirmed the previous taxonomic identification of the specimens (WERNER et al. 1991, WERNER & SIVAN 1992). Comments on the few exceptions follow this section.

The dendrogram for males comprised two major clusters: (A) contained 73 specimens: 70 from North Africa and Sinai, and two from southwestern Arabia (BMNH 51.7.17.88, BMNH 1937.11.1.15), all previously recognised as *C. cerastes*; and exceptionally one specimen from the 'Arava Valley (TAU 10413).

Table 1: Quantitative characters in four taxa of *Cerastes*. The main columns give mean ± standard deviation (SD) for the respective species and sex with the number of specimens (n) in parentheses. The small columns headed "Sig." show the significance of the difference between data to their left and right: * = $0.01 < p < 0.05$; ** = $p < 0.01$.

		C. cerastes cerastes		*C. cerastes hoofieni*		*C. gasperettii gasperettii*		*C. gasperettii mendelssohni*
Character	Sex	Mean ± SD (n)	Sig.	Mean ± SD (n)	Sig.	Mean ± SD (n)	Sig.	Mean ± SD (n)
ra, maximum (mm)	♂♂	798	—	449	—	640	—	725
	♀♀	709	—	517	—	785	—	760
Tail length, percra	♂♂	13.2 ± 1.6 (72)	**	14.0 ± 0.4 (5)	*	13.3 ± 0.1 (24)	**	11.3 ± 1.8 (34)
	♀♀	10.9 ± 1.5 (58)		11.8 ± 1.1 (8)		10.9 ± 1.2 (29)	**	9.3 ± 1.0 (58)
Head length, percra	♂♂	5.8 ± 0.6 (72)		6.2 ± 0.5 (5)		5.9 ± 0.5 (24)	**	5.5 ± 0.5 (33)
	♀♀	5.6 ± 0.5 (58)	**	6.2 ± 0.2 (8)	**	5.6 ± 0.5 (30)	**	5.2 ± 0.4 (59)
Head length as % of head width	♂♂	119.2 ± 14.3 (71)		119.6 ± 13.2 (5)		125.8 ± 11.0 (22)		125.9 ± 12.3 (35)
	♀♀	119.3 ± 10.9 (56)		126.3 ± 11.2 (7)		125.9 ± 11.3 (31)		122.2 ± 9.9 (60)
Head length as % of head depth	♂♂	253.9 ± 28.7 (70)		266.1 ± 22.5 (4)		274.2 ± 35.9 (20)		290.0 ± 26.7 (35)
	♀♀	263.6 ± 23.7 (24)		259.4 ± 33.0 (7)		266.5 ± 19.7 (31)	**	291.7 ± 19.4 (61)
Eye diameter as % of head length	♂♂	17.3 ± 1.7 (72)		16.6 ± 0.6 (5)		16.9 ± 1.7 (24)		16.8 ± 1.7 (34)
	♀♀	16.9 ± 1.9 (57)		15.7 ± 1.6 (8)	*	17.6 ± 2.3 (32)		16.8 ± 1.7 (60)
Dorsal scale length, percra	♂♂	0.78 ± 0.10 (76)		0.81 ± 0.05 (5)		0.76 ± 0.11 (25)		0.73 ± 0.12 (33)
	♀♀	0.75 ± 0.10 (60)	*	0.85 ± 0.08 (8)	**	0.67 ± 0.07 (29)		0.68 ± 0.07 (59)
Supralabials, right + left	♂♂	25.0 ± 1.4 (73)		24.0 ± 1.2 (5)	**	28.6 ± 1.5 (23)	*	27.5 ± 1.6 (31)
	♀♀	25.0 ± 1.5 (57)		25.8 ± 1.8 (8)	**	29.8 ± 2.0 (31)	**	26.7 ± 1.4 (59)
Dorsals at midbody	♂♂	33.7 ± 1.4 (75)	**	31.3 ± 2.6 (4)		32.5 ± 1.7 (23)	**	34.0 ± 1.3 (34)
	♀♀	34.7 ± 1.5 (55)	**	30.8 ± 1.3 (8)	**	33.9 ± 1.6 (29)	**	35.5 ± 1.4 (58)
Ventrals	♂♂	140.9 ± 4.0 (76)	**	134.0 ± 3.4 (4)	**	155.2 ± 2.6 (22)	**	149.7 ± 4.1 (35)
	♀♀	145.7 ± 4.7 (58)	**	137.8 ± 2.5 (8)	**	159.9 ± 5.0 (29)	**	157.2 ± 2.1 (61)
Caudals	♂♂	35.7 ± 3.9 (70)		34.2 ± 1.8 (5)		36.3 ± 2.4 (24)	**	31.4 ± 3.0 (32)
	♀♀	32.4 ± 3.3 (57)		31.1 ± 2.4 (8)	**	34.4 ± 1.9 (31)	**	30.2 ± 2.2 (61)

Cluster (B) contained 55 specimens: 54 from Arabia and the 'Arava Valley, all previously recognised as *C. gasperettii*, but also one from Sinai (TAU 10603).

The dendrogram for females comprised two similar major clusters: (A) contained 58 specimens: 54 from North Africa and Sinai, and three from southwestern Arabia (BMNH 1985.721, BMNH 1903.6.26.51, CAS 134142), all previously recognised as *C. cerastes*, and one from the 'Arava Valley (TAU 10586). Cluster (B) contained 88 specimens: 86 from Arabia with Iraq and the 'Arava Valley, all previously recognised as *C. gasperettii*, and exceptionally one specimen from Sinai (TAU 10652) and one from the Western Negev (TAU 10409).

Exceptional specimens

The five specimens (out of 274) which originated from southwestern Arabia but clustered in the dendrograms with the African *C. cerastes* material had already been recognised as *C. cerastes*, and will be discussed in the next section.

The other five specimens that clustered in unusual positions in the two primary branches (A for *C. cerastes*, B for *C. gasperettii*) of both male and female dendrograms, warrant the following comments:

TAU 10409: The morphology of this hornless female agrees with its dendrogram placement (Arabia etc.) rather than with its catalogued locality ("Western Negev"). It is catalogued as having been collected on 27.VIII.1973 by Shimshon Niv, a resident of the 'Arava Valley, who, when asked, only remembered having brought several *Cerastes* from the 'Arava and one horned individual from Sinai.

TAU 10413: This specimens' morphology accords with its recorded place of origin, 'Arava Valley. We can offer no explanation, but we note that the position on the dendrogram is marginal and adjacent to the opposite major branch.

TAU 10586

TAU 10603

TAU 10652: These three specimens had been kept alive in captivity for 2-6 years, a well-known source of errors in data. Their morphology agrees with their dendrogram placement rather than with their catalogued locality.

Hence in four cases the catalogued locality seems erroneous. We have no explanation for TAU 10413, which may just be a single, random, extreme case.

Distinction between *C. cerastes* of southwestern Arabia and of Egypt

In the major (A) branches of the dendrograms, neither the two males nor the three females of Arabian *C. cerastes* clustered in exclusive end-branches. Nevertheless, the two males in the male dendrogram were close to each other and the three females in the female dendrogram were also in close proximity.

Because the collecting localities of these five *C. cerastes*, as well as those of the eight additional specimens, were geographically disjunct from the main range of *C. cerastes*, we tested each character for the significance of the difference of this group (13 specimens) from the *C. cerastes* sample from Egypt (the terra typica restricta – FLOWER 1933: 830) and from the *C. gasperettii* sample from Arabia (excluding the 'Arava Valley). The results are presented in Tab. 1 for males and females.

Distinction between *C. gasperettii* of the 'Arava Valley and of Arabia

For males, cluster (B) comprised two main secondary clusters: (B1) contained 21 specimens, all from Arabia and Iraq; (B2) contained 34 specimens: 32 from the 'Arava Valley, but also the one from Sinai (TAU 10603) and one from Kuwait (BMNH 1972.372).

For females, cluster (B) comprised two main secondary clusters: (B1) contained 35 specimens: 25 from Arabia and Iraq and 10 from the 'Arava Valley; (B2) contained 53 specimens: 48 from the 'Arava Valley, three from Arabia and Iraq (BMNH 1938.2.18.7, BMNH 1947.3.23.4, BMNH 1985.728), one from Sinai (TAU 10652) and one allegedly from the "Western Negev" (TAU 10409). In view of the tendency towards segregation shown by the 'Arava Valley specimens, we tested each character for the significance of the difference between this group and the remaining *C. gasperettii* material (mainly from all over Arabia). The results are presented in Tab. 1 for males and females.

Taxonomic interpretation

General

MAYR et al. (1953) regarded subspecies as geographically defined subunits of species that are not fully reproductively isolated from adjacent subspecies. MAYR & ASHLOCK (1991) extended the discussion to cover various problems, opinions and precedents. They advised that if the samples clearly differ in one or several respects, or if there are pronounced steps in a cline (and depending on additional obvious conditions), then widespread species should be split into subspecies. They commented that "subspecies that are isolates are incipient species" (loc. cit.: 97) and concluded that "It is preferable to treat allopatric populations of doubtful rank as subspecies" (loc. cit.: 105).

Both the southwestern Arabian population of *C. cerastes* and the 'Arava Valley population of *C. gasperettii* comply with the quoted and implied conditions. We thus interpret our results as indicating the existence of two hitherto undescribed subspecies.

The descriptions below are preceded by synonymies which only document, from the most useful sources, the most frequently encountered names that have been explicitly applied (or clearly implied) to the two actual populations discussed here.

Cerastes cerastes hoofieni n. ssp. WERNER & SIVAN (Figs. 1-4)

Cerastes cornutus, BOULENGER 1896, Vol. 3: 502-503 [according to GASPERETTI (1988: 435), BOULENGER'S specimen "v" would be identical with BMNH 51.7.17.88, ♂]; ANDERSON 1901: 151.

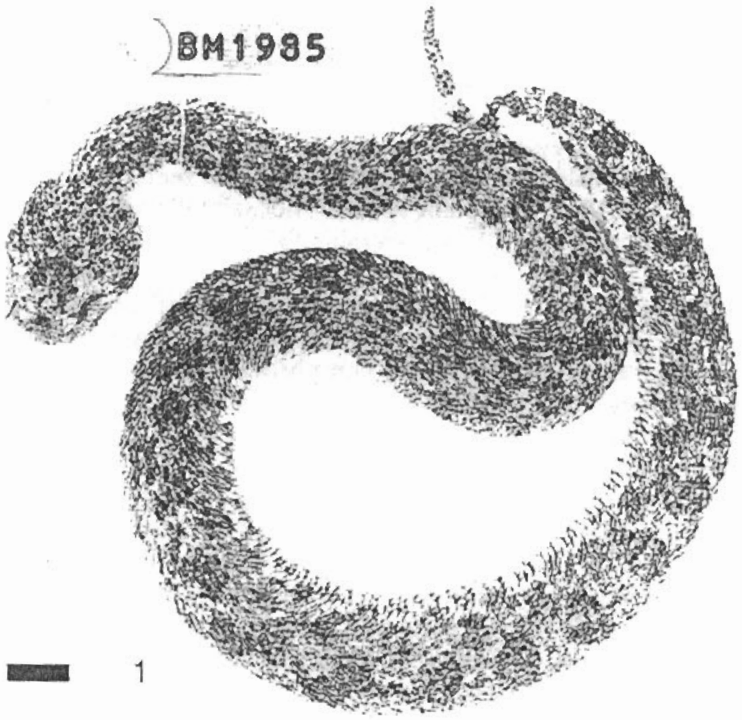
Aspis cerastes, MERTENS 1944: 33-35 (part, by implication).

Cerastes cerastes, LEVITON & ANDERSON 1967: 187 (Tab. 6: footnote 8); WERNER et al. 1991 (part); WERNER & SIVAN 1992 (part).

Cerastes cerastes gasperettii, ARNOLD 1980: 319 (part); JOGER 1984: 40-42 (part); GASPERETTI 1988: 334-341, 435-438, 450 (part, including Fig. 24, from near Khasawiyah).

Type material: Holotype: BMNH 1985.721, ♀, 1982, coll. W. BÜTTIKER, pres. J. GASPERETTI. Type locality: King Khalid Airbase, Saudi Arabia (18°18'N 42°44'E). Paratypes (13): BMNH 51.7.17.88, ♂, Arabia; BMNH 1903.6.26.51, ♀, El Kubar, S. Arabia [13°48'N 44°45'E], approx. 1900, Wyman BURY; BMNH 1937.11.1.15, ♂, Robat nr. Sheikh Othman, Arabia [12°52'N 44°59'E], n.d., B.F. HAYTHORNTHWAITE; BMNH 1982.1167, juv., Org 30 km N of Hudaydah, N. Yemen, 15°05'N 42°58'E, 9.IV.1980, M. AL-SAFADI; CAS 134142, ♀, Saudi Arabia, between Khasawiyah (16°56'N 42°37'E), Gos (16°58'N 42°27'E), Wadi Baysh (17°30'N 42°30'E), XII.1971, J. GASPERETTI; MHNG 2427.28, ♀, MHNG 2479.35, ♂, MHNG 2536.78, ♂, MHNG 2542.12, ♀, and MHNG 2554.26, ♀, Khawkha; MHNG 2549.89, ♂, MHNG 2549.90, ♀, Ja'ar; MHNG 2582.11, ♀, km 44 Al Hudaydah – Az Zaydiyah.

Differential diagnosis: *Cerastes cerastes hoofieni* differs from other *C. cerastes*, and from *C. gasperettii*,



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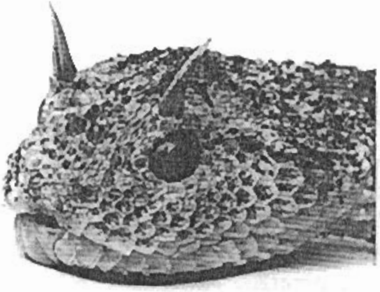

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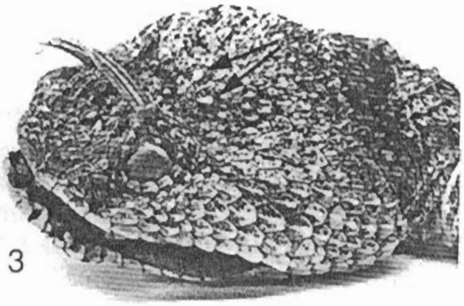

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Figs. 1–3: *Cerastes cerastes hoofieni* n. ssp. WERNER & SIVAN.
Fig. 1: Holotype BMNH 1985.721, female, dorsal view (scale bar = 10 mm).
Fig. 2: Same, head.
Fig. 3: Head of paratype BMNH 1937.11.1.15, male, to show occipital tubercles (arrows).

in its low numbers of body scales: Dorsals across the middle of the body average about 31 (compared to population averages of 32-34 for males and 34-36 for females in the other *Cerastes*); ventrals average 134 for males and 138 for females (compared to population averages of 141-155 for males and 146-160 for females in the other *Cerastes*). The tail is relatively long, averaging 14 percra in males (compared to population averages of 11-13 percra in other *Cerastes*) and 12 percra in females (compared to 9-11 in others). As in other *C. cerastes* and in *C. gasperettii*, supraocular horns may be present or absent.

Description: Descriptions of the genus *Cerastes* were provided by BOULENGER (1896), ANDERSON (1898) and GASPERETTI (1988). The species *C. cerastes* sensu stricto was described by WERNER & SIVAN (1992). Here we describe the female holotype of *C. c. hoofieni*.

Measurements (in mm): Head and body: 373; tail: 46; head length: 24.7; head width: 20.0; head depth: 12.5; eye: 4.3; length of sequence of five mid-dorsal scales: 16.1.

Pholidosis: Nasal shield large, its length 164.7% of the height of the first supralabial. Occipital tubercles inconspicuous. Supraocular horns present, keeled. Eye separated from supralabials by a minimum of four scales, the number increasing rostrad and caudad; supralabials: 12 left, 11 right; 29 dorsals at the middle of the total length; 139 ventrals; 30 subcaudals.

Head pattern faint: dorsally, on posterior half, three transverse rows of alternating small dark spots, 4-6 per row, each covering up to seven of the small scales; laterally a darkish postocular line present, slanting caudad and ventrad from dorsocaudal aspect of eye. Between eye and supralabials a row of three indistinct dark spots present.

Dorsal coloration: pattern relatively regular on posterior part of body and anterior part of tail, with distinct dark mid-dorsal blotches of broadly elliptical shape, about 7 scales broad and 3 scales long, separated by spaces of 2-3 times the scale

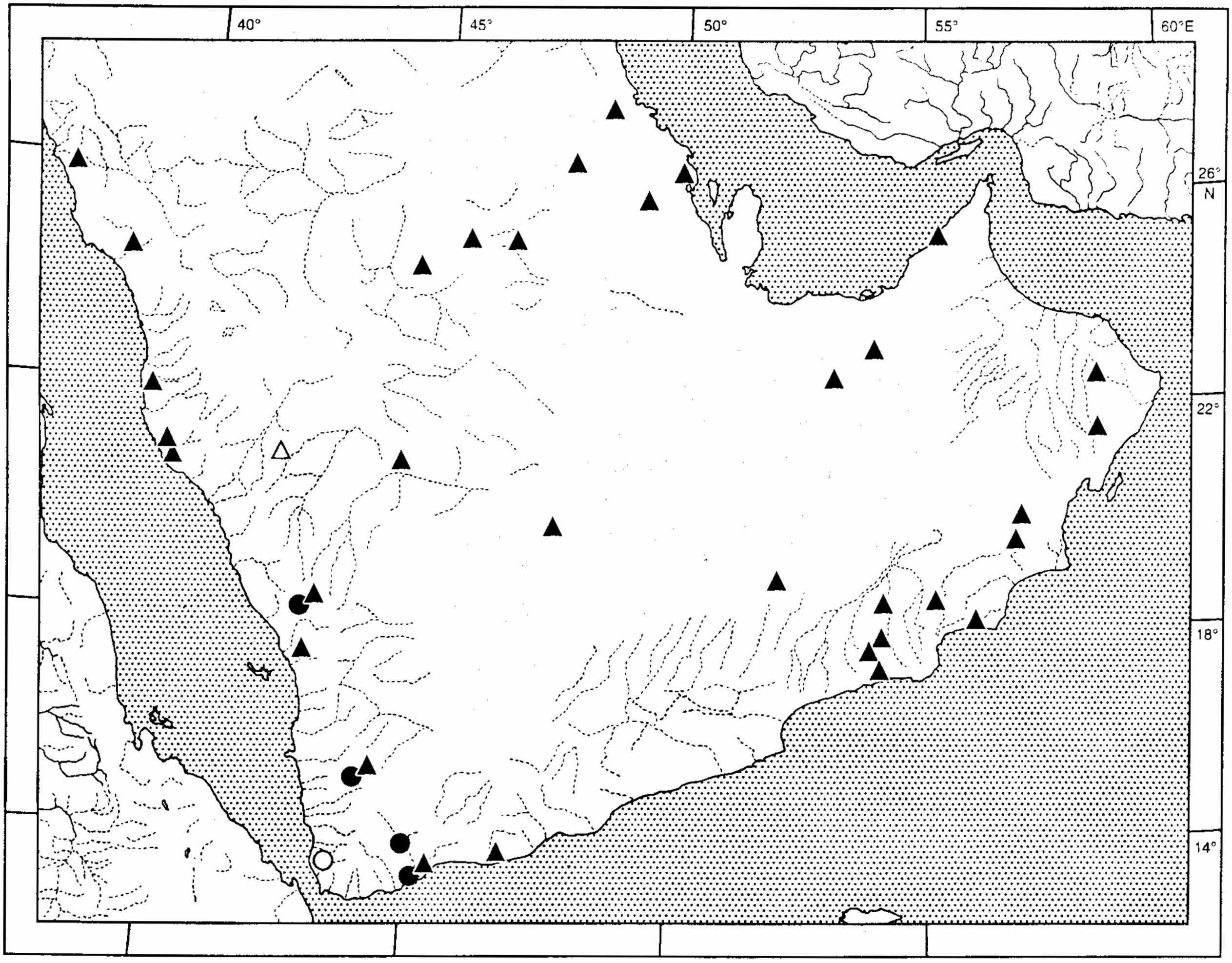


Fig. 4: Map of the southern Arabian Peninsula with locality records of *Cerastes c. hoofieni* (circles, all examined) and *C. g. gasperettii* (triangles). Solid symbols refer to data from WERNER et al. (1991), open symbols refer to additional data from SCHÄTTI & GASPERETTI (1994). Each symbol represents one or more museum specimens.

length. Smaller roundish dark blotches laterally on the flanks, in alternation with the mid-dorsal blotches and almost touching them. Pattern variable and irregular on central and anterior parts of dorsum, with a tendency to form cross-bands on the neck (Fig. 1).

Variation: Nasal shield moderate, its length in the 13 paratypes averages 119.8% of the height of the first supralabial (93.3-146.7%). Occipital tubercles usually moderately conspicuous (Fig. 3). Supraocular horns present in seven paratypes (3 ♂♂, 4 ♀♀), absent in six (2 ♂♂, 3 ♀♀, 1 juv.). Variation of quantitative characters summarised in Tab. 1. Dorsal coloration is as variable within and among individuals as in other *C. cerastes* (WERNER & SIVAN 1992: Fig. 4 A-D). For example, in BMNH 1982.1167 the blotches of the mid-dorsal series are of the same size as in the holotype, but they are almost square throughout most of the body while on the neck they form cross-bands. Conversely, in CAS 134142 regular elliptical transverse blotches are restricted to short body sections and represented by oblique blotch-pairs over the first and third quarters of the snake.

Distribution: All available evidence points to *C. c. hoofieni* being endemic to the southwestern corner of the Arabian Peninsula (Fig. 4).

Comments: ANDERSON (1901: 151) seems to have been the first who commented on the heterogeneity of *Cerastes* in southwestern Arabia: "The two extremes, or nearly so, of the range of variation in the ventrals are met with in Southeast Arabia, as this individual [female from Abian country] possesses 139 ventrals, whereas in the Hadramut the highest number of ventrals (164) hitherto recorded of the species is met with. An Aden specimen obtained by Colonel YERBURY in 1895 had as many as 159 ventrals." The occasional occurrence of individuals with extraordinarily low ventral counts in southwestern Arabia was also noted by LEVITON & ANDERSON (1967) and ARNOLD (1980).

The zoogeographical aspects of this population, now named *Cerastes cerastes hoofieni*, have already been discussed (Werner & Sivan 1992).

Etymology: The subspecies endemic to southwestern Arabia is named after Mr. Jacob Haim Hoofien (born Tel Aviv 21.X.1913, deceased Kefar Shemaryahu 11.VI.1997), in recognition of his leadership in the study of Middle Eastern reptiles and especially their systematics and nomenclature.

Cerastes gasperettii mendelssohni **n. ssp. Werner & Sivan (Figs. 5-7)**

Vipera cerastes, Strauch 1869: 112-113 [according to Anderson 1896: 71, 83; Leviton & Anderson 1967 and Gasperetti 1988: 435; Strauch reports a specimen from "Arabah, Arabia Petraea" in the Munich Museum].

Cerastes cornutus, Anderson 1896: 71, 83, 87 (part), 89 (part).

Aspis cerastes, Mertens 1944: 33-35 (part, by implication); Barash & Hoofien 1956: 159; Mendelssohn 1963: 143-148; Warburg 1964: 1017-1041.

Cerastes cerastes, Haas 1951: 92 (part); Haas & Werner 1969: 367 (part); Dor 1987: 486.

Cerastes cerastes cerastes, Leviton & Anderson 1967: 185 [formulated as a possibility]; Joger 1984: 40-42 (part).

Cerastes cerastes gasperettii, Gasperetti 1988 (part, by implication): 334-341, 435-438, 450; Leviton et al. 1992: 112-113 (part, and Pl. 20: D-F from Yotvata, 'Arava Valley).

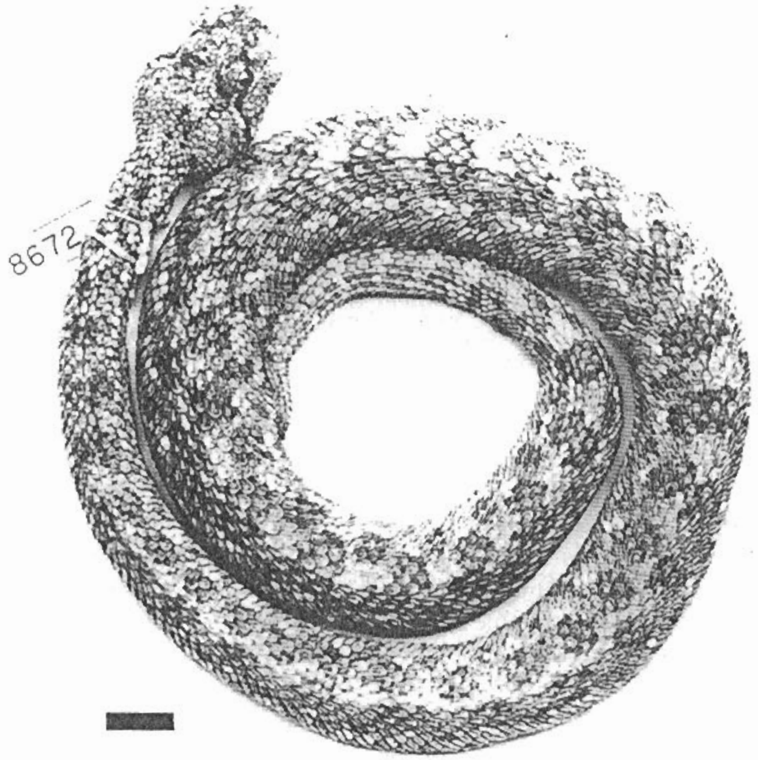
Cerastes gasperettii, Werner 1988: 362; Werner et al. 1991 (part); Werner & Sivan 1992 (part).

Type material: Holotype: HUJ-R 8672, ♂, VI.1976, Esther Moskowitch (Don.). Type locality: 'En Yahav, 'Arava Valley, Israel. Paratypes from the type locality (21): HUJ-R 8555, ♀, XI.1972, Micha Atidia; TAU-R: 4735, ♀, 17.VIII.1961, Y. Refael; 4738, ♂, 4740, ♀, 20.VIII.1961, Y. Refael; 4813, ♀, 4814, ♂, 29.IX.1963, Y. Refael; 5442, ♀, 2.XI.1963; 5688, ♀, IV.1963, M. Licht; 6833, ♂, 30.VI.1966; 6836, ♂, 13.X.1966; 8139, ♂, 27.X.1966; 8165, ♀, IX.1962; 8176, ♂, 30.VI.1966, Ben-Arie; 9203, ♀, 14.IX.1970, Navon; 10102, ♂, 5.V.1972; 10291, ♀, 19.XII.1971; 10413, ♂; 10458, ♀; 10602, ♂; 10675, ♂; 11235, ♂, 20.XII.1974, Gideon Canani. Other paratypes (79): HUJ-R: 4252, ♀, Yotvata, IX.1953; 4379, ♀, Yotvata, VI.1958, S. Alpert (Don.); 8229, ♀, Hazeva, VI.1966, Y. Cohen (Don.); 8673, ♂, Hazeva, 15.VI.1976, Werner; 8999, ♂, 9000, ♀, Hazeva area ('Arava), Spring 1980, A. Bouskila; 16201, ♀, Hazeva area ('Arava), Summer 1981, A. Bouskila; 16243, ♂, 'Idan, 12.IV.1982, A. Bouskila (Don.); TAU-R: 1230, Wadi Girafi, 29.VII.1953; 2033, ♀, Yotvata, 23.IX.1955; 2230, ♂, Wadi Menaye, 15.IV.1955; 2245, ♀, Yotvata, X.1955; 2259, ♂, Wadi Menaye, 1952; 2498, ♀, Yotvata, 24.II.1957; 3127, ♀, Yotvata, X.1956; 3148, ♂, 3149, ♀, Yotvata; 4416, ♀, Yotvata, 9.IX.1960; 4452, ♀, Yotvata, 21.VIII.1960; 4802, juv., 15 km S of Sedom, 1.I.1962, Horesh; 4820, ♂, Yotvata, 1.X.1960, Giora; 4919, ♀, Yotvata, 28.VIII.1961; 5343, ♂, Yotvata, 27.II.1962, R. Zur; 5441, ♀, Yotvata, 19.IX.1963, Mazad; 5553, ♂, 12.XI.1963, Mazad; 5561, ♀, 5574, ♀, Yotvata, 18.XII.1963, Mazad; 5642, ♀, Yotvata, 28.X.1963, Mazad; 5655, ♀, Yotvata, 6.VII.1964, Mazad; 5659, ♀, Yotvata, 12.IX.1963, Mazad; 5754, ♀, Yotvata, 29.V.1964, Mazad; 5839, ♀, Yotvata, 29.V.1964; 5879, ♂, 6138, ♀, 6139, ♀, Yotvata, 1.X.1964, Mazad; 6144, ♀, Yotvata, 1962, Mazad; 6164, juv., Yotvata, 19.VII.1965, G. Ilani; 6216, ♂, Yotvata, 9.VII.1964, Mazad; 6217, ♀, Grofit, 6.VIII.1965, S. Ron; 6222, ♀, Yotvata, 18.XII.1963, Mazad; 6729, ♂, Yotvata, 25.IV.1965, G. Moed; 8137, ♀, Yotvata, Maded; 8177, ♀, Yotvata, 9.XII.1966; 8178, ♂, Hazeva, 27.VIII.1968, Dromi; 8192, ♀, 8201, ♂, 8220, ♀, Yotvata, 6.VII.1976, Maded; 8869, ♂, Hazeva, 27.VIII.1968, Droman; 8971, ♀, Hazeva, 10.IX.1969, S. Niv; 9036, ♀, Yotvata, 4.IX.1963, Horesh; 9159, ♀, W of Hazeva, 2.IV.1970, Korot; 9167, Hazeva, Niv; 9301, ♀, Hazeva, 27.X.1969, Niv; 9309, ♀, Hazeva, 5.VI.1970, Petel; 9373, ♀, Hazeva, 8.X.1969, Niv; 9778, ♀, Hazeva, 5.IV.1970, Niv; 9902, ♀, Hazeva, 8.VIII.1971, Niv; 10026, ♀, 10027, ♀, Hazeva, 26.V.1972, Nodelman; 10032, ♀, Hazeva, 8.VIII.1973, Niv; 10036, ♂, 6.VI.1972, Nodelman; 10051, ♂, 'En Hazeva, 26.III.1972, Amitai; 10138, juv., 10139, ♂, Hazeva, X.1972, Philip; 10184, ♀, Elat, 27.XI.1972, Zibrin; 10318, ♂, Hazeva; 10465, Hazeva, 21.IX.1972, Niv; 10586, ♀, Katura, 21.IX.1972; 10604, ♀, Hazeva; 10809, ♂, Hazeva, 21.IX.1972, Niv; 11024, ♀, Hazeva, 30.VIII.1975; 11138, ♀, Hazeva, 30.VIII.1975; 11259, ♂, Zofar; 11584, ♂, Hazeva, 21.IX.1972, Niv; 12336, ♀, Hazeva; 12342, ♀, Beer Zofar, 15.IX.1976, R. Portugali; 12464, ♂, Isamar (10 km S of Yotvata); 12668, ♀, Hazeva, 21.IX.1968, Niv; 12732, ♂, 'En Ziq.

Differential diagnosis: *Cerastes gasperettii mendelssohni* differs from other large *Cerastes* (i.e. excluding *C. vipera*) in the complete absence of horned individuals and in its extremely short tail: Tail length averages 11 percra in males (compared to population averages of 13-14 in other large *Cerastes*) and 9 percra in females (compared to population averages of 11-12 in other large *Cerastes*). Accordingly, the number of subcaudals averages 31 in males (compared to population averages of 34-36 in other large *Cerastes*) and 30 in females (compared to population averages of 31-34 in other large *Cerastes*). Other differences from *C. gasperettii gasperettii* are included in Tab. 1.

Description: The species *C. gasperettii* was described by Werner & Sivan (1992). Here we describe the male holotype of *C. g. mendelssohni*.

Figs. 5–7: *Cerastes gasperettii mendelssohni* n. ssp. Werner & Sivan.
Fig. 5: Holotype HUJ-R 8672, male, dorsal view (scale bar = 10 mm).
Fig. 6: Same, head, showing lack of occipital tubercles.
Fig. 7: Live specimen photographed at Hazeva, 'Arava Valley, in October 1966 by D. Senn, dorsal pattern showing shift between median blotches and zigzag design.



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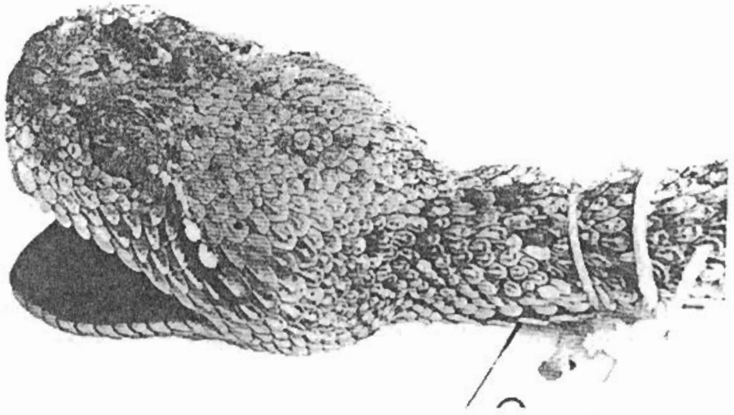

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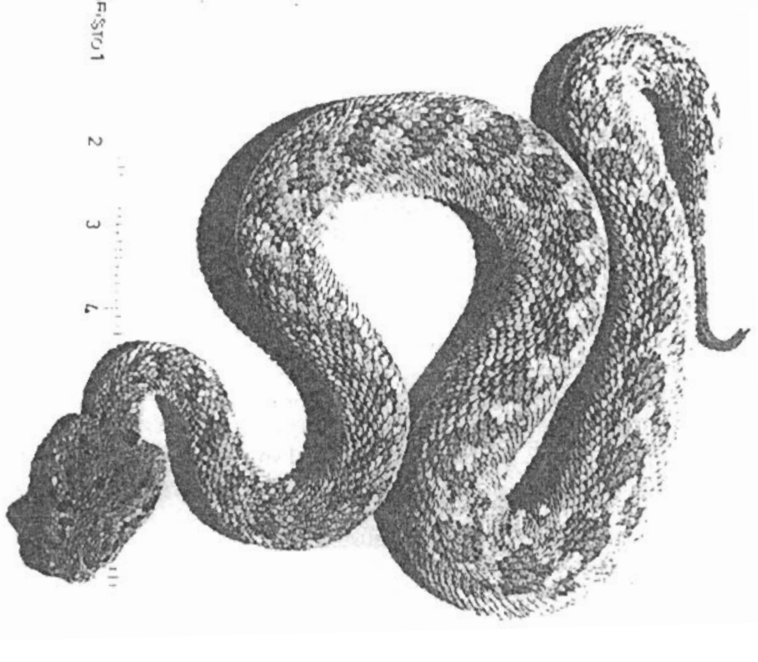

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Measurements (in mm): Head and body: 499; tail: 57; head length: 26.0; head width: 19.2; head depth: could not be measured because of the mouth being open; eye: 4.2; length of sequence of five mid-dorsal scales: 15.2.

Pholidosis: Nasal shield large, its length 176.9% of the height of the first supralabial. Occipital tubercles absent. Supraocular horns absent. Eye separated from supralabials by a minimum of four scales (and some interstitial granules), the number increasing rostrad and caudad; supralabials: 13 left, 12 right; 34 dorsals at the middle of the total length; 148 ventrals; 34 subcaudals.

Head pattern distinct: dorsally irregularly scattered small dark dots of irregular shape; laterally conspicuous dark postocular line slanting caudad and ventrad from dorso-caudal aspect of eye, accentuated by whitish upper margin. No dark blotches between eye and supralabials.

Dorsal coloration: variable along body. Distinct dark mid-dorsal transverse blotches on neck and on middle third of body, about 8 scales broad and 2.5 scales long, separated by spaces of 2 times the scale length. On anterior parts of the dorsum the mid-dorsal series is represented by two dorsolateral series of smaller roundish blotches, alternately positioned on left and right side (Fig. 5). Smaller roundish dark blotches laterally on the flanks, in alternation with the dorsal blotches, the separation from them accentuated by an incomplete row of whitish scales.

Variation: Nasal shield length averages 141.7% of the height of the first labial (100-200%, n = 40). Occipital tubercles always absent. Supraocular horns always absent. Variation of quantitative characters is summarised in Tab. 1. Dorsal pattern varies within and among individuals; it usually comprises mid-dorsal blotches on some part of the body, and oblique pairs of blotches, sometimes forming a zigzag pattern, on other parts (Fig. 7). Sometimes the pattern is chequered throughout (Werner & Sivan 1992: Fig. 4 F). Very rarely are there regular discrete blotches along the whole body; a single specimen (photographed and released) had blotches with light centres, almost ring-like. So far, the range of variation of the pattern has included no specimen with rhomb-like blotches as in *C. g. gasperettii* CAS 136472 from Arabia (Werner & Sivan 1992: Fig. 4 E).

Distribution: All available evidence points to *C. g. mendelssohni* being endemic to the sand areas within the 'Arava Valley of Israel and Jordan (within the Great Rift Valley, between Sedom in the north and Elat in the south). Nothing can be added with certainty to the published map (Werner et al. 1991: Fig. 4), in which all triangles refer to this subspecies, including the one east of the Dead Sea, at El Karak. MCZ 9692 from "El Karak, Dead Sea Plateau" was presumably not collected at El Karak (where the habitat is unsuitable) but on the plateau below.

Comments: The 'Arava Valley has repeatedly been invoked somewhat loosely as a general distribution barrier between Saharan and Arabian desert herpetofaunas (Werner 1971, 1987; Arnold 1987; Joger 1987), but a closer examination of the data reveals that its role as a barrier for arenicolous reptiles comprises three discrete functions:

First, its sands provide a westernmost outpost habitat for four Arabian arenicolous species, which occur here but apparently cannot disperse further westwards: *Bunopus tuberculatus* and *Stenodactylus doriae* (Werner 1987), *Coluber elegantissimus* (Werner & Sivan 1991) and *Cerastes gasperettii* (Werner et al. 1991; Werner & Sivan 1992). Indeed, we cannot confirm the statement of Arnold (1987: 249) that *Bunopus tuberculatus* and *Coluber elegantissimus* extend to the west of the 'Arava; nor that of Spawls & Branch (1995: 123) that *Cerastes gasperettii* occurs west of the head of the Gulf of Elat, within Sinai.

Second, the 'Arava Valley sands provide an easternmost outpost habitat for three Saharan arenicolous species, which managed to reach these sands but failed to climb and cross the steep rocks bounding the 'Arava on the east, and are unknown in Jordan: *Sphenops sepsoides* (Werner 1968, 1987), *Stenodactylus sthenodactylus* and *Lytorhynchus diadema* (Werner 1987).[1] In our experience this zoogeographic group is smaller than it would seem from the information given by Arnold (1987: 249), who included some Saharan arenicolous reptiles whose ranges fail to extend as far east as the 'Arava (and thus cannot encounter it, or its eastern rocks, as barrier): *Stenodactylus petrii*, *Agama savignyi*, *Acanthodactylus s. scutellatus*, *Scincus s. scincus*, *Macroprotodon* and *Cerastes vipera*.

Third, the rocky eastern rim of the 'Arava apparently also acts as a barrier for some arenicolous species of southern Jordan which fail to descend the rim and to pass westwards into the 'Arava sands. We lack detailed data on the distribution of arenicolous reptiles just east of the 'Arava Valley but Amr et al. (1994) list *Stenodactylus grandiceps*, *Acanthodactylus grandis*, *A. tristrami*, *Scincus scincus meccensisis* for southern Jordan and also *Phrynocephalus arabicus* which was only recently dis-

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[1] A record of *Lytorhynchus diadema* from Petra (Disi 1988) seems to indicate that this (and probably other) species also occur in the Jordanian part of 'Arava valley as well as in the lower valleys of its eastern affluents. The editor.

covered about 60 km east of the southern 'Arava (Wittenberg 1992). None of these species occurs in the 'Arava Valley.

Presumably, the rocky eastern rim of the 'Arava Valley serves to isolate *Cerastes gasperettii mendelssohni*, inhabiting the 'Arava sands, from the conspecific populations to the east. The absence of supraocular horns, for example, may be a founder effect in the 'Arava, and the "horns" character apparently did not invade the 'Arava Valley at a later time. Horned individuals occur not far to the east of the 'Arava (see Introduction). The subspecies *Cerastes gasperettii mendelssohni* is thus endemic to the sands of the 'Arava Valley, in Israel and by implication also in Jordan. Within Israel its potential environment comprises only a few hundred square kilometres, an area in heavy demand for agriculture and development; by the time of writing the natural habitat has already been considerably reduced and includes a nature reserve of only a few tens of square kilometres. Although all reptiles are protected by law in Israel, this is clearly a case of a taxon whose survival depends on the conservation of a sufficient part of its habitat.

Etymology: The endemic 'Arava Valley subspecies is named for Professor Emeritus Heinrich Mendelssohn, Tel Aviv University, in recognition of his leadership in the study of the biology of Israel's vertebrates in general and venomous snakes in particular, and in the conservation of animal species.

Key to *Cerastes* in the Middle East

1 Ventrals fewer than 120; eye diameter at most as large as a mid-dorsal scale; 3-4 rows of scales between eye and supralabials; no supraocular horns .... ***Cerastes vipera***

– Ventrals at least 130; eye diameter at least as large as a mid-dorsal scale; about 5 rows of scales between eye and supralabials; with or without supraocular horns 2

2 Ventrals in males usually <147, in females usually <154; a pair of enlarged tubercles near the midline in the occipital area (may be inconspicuous) (*Cerastes cerastes*) 3

– Ventrals in males usually >147, in females usually >154; no pair of enlarged tubercles near the midline in the occipital area (*Cerastes gasperettii*) 4

3 Ventrals usually >138; with or without supraocular horns (N Africa, N Sinai and SW Israel) .... ***Cerastes cerastes cerastes***

– Ventrals usually <140; with or without supraocular horns (SW Arabian Peninsula) .... ***Cerastes cerastes hoofieni***

4 Subcaudals in males usually >33, in females usually >31; with or without supraocular horns (Arabian Peninsula, Iran and Iraq) ...... ***Cerastes gasperettii gasperettii***

– Subcaudals in males usually <33, in females usually <31; no supraocular horns ('Arava Valley of Israel and Jordan) .... ***Cerastes gasperettii mendelssohni***

Discussion

Pholidosis and climate

Pholidosis is used in snake systematics, although, within genotypic ranges, it is phenotypically affected by temperature during embryogenesis (Fox et al. 1961, Osgood 1978). The effect is especially conspicuous in the numbers of ventrals and subcaudals (Fox 1948, Fox et al. 1961, Osgood 1978) which reflect the number of body segments (Alexander & Gans 1966). The pattern of the temperature effect on segment number is that at medium temperature the number of segments is minimal, and at both lower and higher temperatures the number of segments increases. In reptiles as in fish this principle is seen only when a sufficient range of temperatures is applied (Werner 1961, Fowler 1970, Osgood 1978).

The geographical variation in the number of segments sometimes accords in the same pattern with the geographical variation in climate, in snakes (Klauber 1941, 1956; Ehrlich 1992; Ehrlich & Werner 1993), serpentiform lizards (Parker 1956, as interpreted in Werner 1961) and the tails of other lizards (Werner 1964).

The temperature effect on the number of segments may often be too small to confound or simulate taxonomic differences (Osgood 1978) but may sometimes be reinforced by a correlation of the number of ventrals with body size (Klauber 1956: 178). It seems prudent to explore the possibility of temperature effects in all studies of snake taxonomy that involve numbers of ventrals and subcaudals.

In the present study we have no data for testing the relations among ventral counts of individuals and environmental temperatures at their collection sites, but two facts indicate that the differences in ventral counts observed here among populations of *Cerastes* are unlikely to merely represent temperature effects:

(a) In broad terms, summer temperatures in the Arabian Peninsula are a little above those of Egypt and below those of the Rift Valley (Karmon & Brawer 1967). If the variation in ventral count were mainly a temperature effect, one would expect the lowest numbers where the climate is intermediate, in Arabia, but the ventral count in specimens from Arabia exceeds those of specimens from both Egypt and the Rift Valley.

(b) In the southwestern corner of the Arabian Peninsula, *C. c. hoofieni*, having low ventral counts, occurs in sympatry with *C. g. gasperettii*, having high counts.

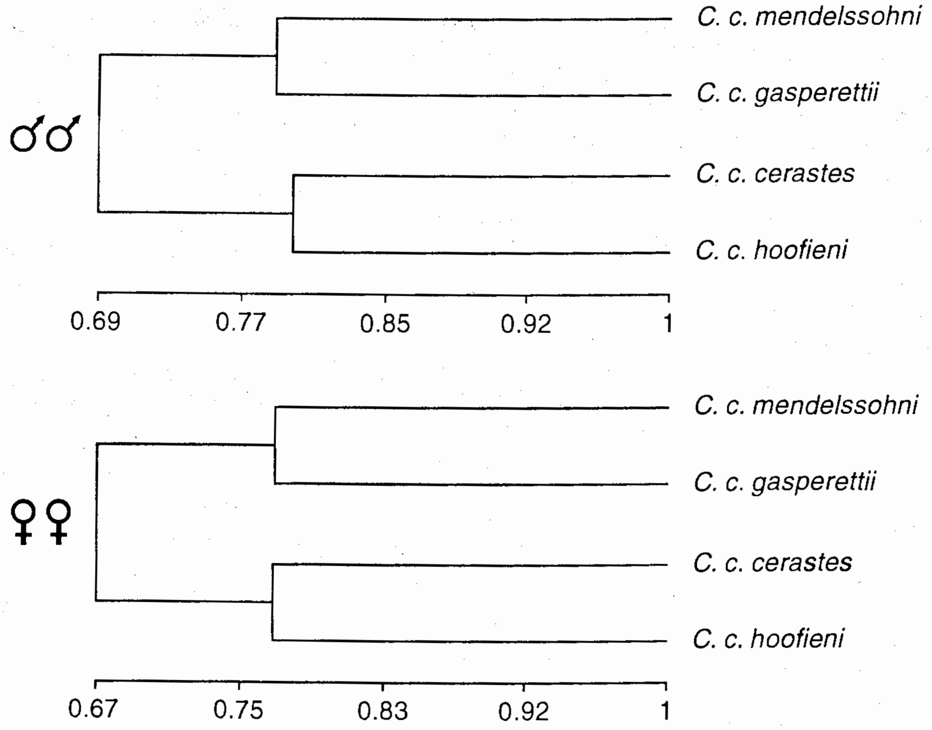

Fig. 8: Phenetic dendrograms relating the four taxa of *Cerastes*, for males and females.

Morphological character displacement?

In the southwestern corner of the Arabian Peninsula *C. c. hoofieni* is sympatric with *C. g. gasperettii*. Morphologically, the former differs from the latter more than does the Egyptian allopatric *C. c. cerastes*. This is the trend in eight out of ten characters listed in Tab. 1, and particularly in the extremely short and deep head and the outstandingly low count of ventrals in *C. c. hoofieni* (Tab. 1). This pattern seems compatible with divergent character displacement (Brown & Wilson 1956, Grant 1972) and resembles a possible example of this phenomenon described by Gallagher et al. (1986) in *Kentropyx* (Sauria: Teiidae). When more material from the area of sympatry becomes available, it would be interesting to explore this aspect.

Phenetic relationships

The taxonomic relations implied by the foregoing description of subspecies are derived from the cluster analysis of the whole material as described above but also agree with a qualitative evaluation of key characters. In order to verify and demonstrate the relations among the four resulting taxa, *Cerastes cerastes cerastes, C. c. hoofieni, C. gasperettii gasperettii* and *C. g. mendelssohni*, we undertook a further cluster analysis. Because many characters are sexually dimorphic, the analyses were conducted separately for the two sexes. In Fig. 8 both dendrograms show the expected phenetic relations: *Cerastes cerastes cerastes* and *C. c. hoofieni* are next to each other on one major branch (despite the geographical separation), while *C. gasperettii gasperettii* and *C. g. mendelssohni* are neighbours on the other major branch.

It is interesting that by our method the dendrograms for the two sexes emerged identical. This is perhaps not a matter of course when pronounced sexual dimorphism is involved. Indeed, Eiselt et al. (1991) used Ward's cluster analysis to test the relative similarity of eight populations of *Lacerta rudis* (six subspecies). The dendrogams for males and females differed (sample sizes ranged from 6 to 19 specimens per sex and population, except for one sample of 4 specimens, which branched equally in both dendrograms). The male dendrogram was more "taxonomically correct", in that the three populations of one subspecies really emerged closest. (In the female dendrogram, one of these populations was separated from the other two by another subspecies.)

Conclusions

1. Based on the examination of 139 museum specimens, the *Cerastes cerastes* population of southwestern Arabia, which is geographically disjunct from the nominate population of northern Africa, northern Sinai and southwestern Israel, merits recognition as a subspecies, *Cerastes cerastes hoofieni* n. ssp. Werner & Sivan.
2. Based on the examination of 143 museum specimens, the hornless *Cerastes gasperettii* population of the 'Arava Valley (in the Great Rift Valley) differs from the nominate population in

the Arabian Peninsula and merits recognition as a subspecies, *Cerastes gasperettii mendelssohni* n. ssp. WERNER & SIVAN.

3. The variation in the number of ventrals among these four populations cannot be explained as a temperature effect.
4. In both head shape and the number of ventrals, difference from *Cerastes gasperettii gasperettii* is greater in the sympatric *Cerastes cerastes hoofieni* than in the allopatric *Cerastes cerastes cerastes*. This suspected case of character displacement merits further study.
5. *Cerastes gasperettii mendelssohni* is endemic to a very small area, and thus requires careful protection.

Acknowledgements

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