A new species of saw-scaled viper of the *Echis coloratus* complex (Ophidia: Viperidae) from Oman, Eastern Arabia

**Abstract** A study of 353 museum specimens of the *Echis coloratus* complex from its entire range of distribution revealed an undescribed species in the United Arab Emirates and northern Oman. The results of UPGMA clustering and principal coordinate analysis of 138 male and 142 female specimens yielded for both sexes two major clusters, one with specimens from the UAE and northern Oman and one from southern and western Arabia, the Levant and Egypt. The new species has a longer tail with higher subcaudal counts; the lower prenasal scale is often missing and the upper prenasal is frequently fused with the nasal; the subnasal is often missing or fused with the nasal. The gular scales between the chin-shield and the preventrals are round or only slightly elongate, not elongate as in *Echis coloratus*, and the number is higher. Other differences in characters of the gular area indicate a different scale structure of the ventral surface of the head. The new species is allopatric or parapatric with *E. coloratus*, but sympatric with *Echis carinatus sochureki*.

**Key words** *Echis coloratus*, taxonomy, northern Oman, Arabia, zoogeography

**Introduction**

Despite its epidemiological importance (Wüster, 1996), the genus *Echis* remains poorly understood taxonomically (Leviton et al., 1992). All the *Echis* populations with the exception of *Echis coloratus* were regarded, at one time or another, as conspecific with *E. carinatus* or *E. pyramidum* (McDiarmid et al., 1999). Cherlin (1990) and Cherlin & Borkin (1990) made a major step to resolve the taxonomic problems within *Echis* concluding that *Echis* comprises 12 species totalling 20 forms. Their conclusions were partly rejected or questioned by others (Auffenberg & Rehman, 1991; Schätti & Gasperetti, 1994; Wüster et al., 1997). However, Cherlin (1990) and Cherlin & Borkin (1990) left *Echis coloratus* (*Echis froenatus* in their work, see explanation below) intact. In this species, several authors have noted extreme intraspecific colour variation (Mendelssohn, 1965; Gasperetti, 1988; Kochva, 1990), which may reflect taxonomic distinctness. In addition, collection data reveal an unexplained gap in the distribution of *E. coloratus* in southern Oman, NE of Dhofar (Joger, 1984; Gasperetti, 1988). Some authors (Arnold, 1980; Gasperetti, 1988) have described the northern Oman population as isolated. The gap actually coincides with the geographic boundary of other taxa of Asian affinity inhabiting northern Oman and of African taxa inhabiting southern Oman or areas west of it, as well as of some South Arabian endemics (Arnold & Gallagher, 1977). Even though this area is quite poorly sampled from a zoological point of view, results from other groups suggest that sufficient collecting has taken place there showing that the gap is not an artefact due to poor sampling (Arnold, 1987; Gasperetti, 1988). In the literature, the gap between the populations of *E. coloratus* in the United Arab Emirates (UAE) and in central Arabia is not discussed in depth. Actually, *E. coloratus* is not arenicolous and hardly seems able to inhabit and cross the sandy desert of the Rhub al Khali that separates these populations. This distribution gap may reflect a taxonomic discontinuity within *E. coloratus*. A preliminary study of morphological characters in *E. coloratus* (Babocsay, 2001) revealed several differences between the sample from the UAE and northern Oman and those from the rest of its distribution range (southwestern and western Arabian peninsula, the Levant and Egypt). The present study is based on these differences and shows that the population of the *Echis coloratus* complex in the UAE and northern Oman is a distinct species.

**Materials and methods**

**Material**

Three hundred and fifty-three museum specimens from The Natural History Museum, London (BMNH); CAS; FMNH;
Methods

Of 47 characters, 37 were entered into cluster and principal coordinate (PCO) analyses. Of the body proportions, only relative tail length and relative dorsal scale length were used; the former was not included in the cluster analysis. Other body proportions listed here for the sake of completeness were not used in this study as they were not available from a sufficient number of specimens or showed no differences between the samples from the UAE and northern Oman and the rest. Mensural characters were assessed using a tape measure and standard callipers, or for axial head length, modified calliper was used (Goren & Werner, 1993). Rostrum-anus length (RA; Werner, 1971) was measured with a piece of string. For counting and measuring small items, a dissecting microscope was used. RA and tail length were measured to the nearest 1 mm and all other mensural characters, to the nearest 0.1 mm. Characters marked by an asterisk (*) were recorded from both sides of the body where possible and then averaged. In multistate characters, asymmetry counted as an intermediate state. For example, if in FPN (fusion of prenasal with nasal) on one side the prenasal was fused with the nasal (state 1) but on the other side it was separate (state 0), then that specimen was scored 0.5.

Characters

Abbreviation: PERCRA = percentage of RA (Werner, 1971).

Meristic characters:

Dors1 Number of dorsal scale rows, counting across the forepart of the body (one head length behind the head).
Dors2 Number of dorsal scale rows at mid-body.
Dors3 Number of dorsal scale rows counted five ventrals anterior to the anal plate.
Lat Number of oblique serrated ‘lateral’ scale rows at mid-body * (counted from the ventrals to the uppermost serrated one (included)).
PreV Number of preventrals (gular scales anterior to ventrals, which are broader than long; Nilson & Andrén, 1986).
PreV2 Number of slightly enlarged (but not broader than long) scales between preventrals and the small elongated or round gular scales along the midline of the ventral side of the head.
Vent Number of ventrals (Dowling, 1951).
SubC Number of subcaudals (apical spine and the first, divided, set excluded). If they were divided elsewhere or asymmetrical then were counted on the right side.
SupraL Number of supralabials * (counted from the one in contact with the rostral to and including the one with the aperture of the external superior labial gland).
InfL Number of infralabials * (counted from the one in contact with the mental to and including the one entirely opposite the last supralabial).
InfL2 Number of infralabials in contact with the chin-shield.*
Gul Number of scales, other than chin-shield, in contact with infralabials. *
Gul2 Number of gular scales between the second preventral (counted from the ventrals) and the infralabials. *
Gul3 Number of gular scales along the ventral midline, between the chin shield and PreV2. *
Gul4 Number of gular scales in contact with the chin-shield. *
CircO Number of scales in the inner circumocular ring * (scales in contact with the eye).
CircO2 Number of scales in the outer circumocular ring * (scales in contact with and distal to the scales in the inner circumocular ring).
ScBE Number of scales between the eyes at the smallest distance.
PreO Number of scales between the anterior edge of the eye and the nasal. *
SubO Number of subocular scale rows between the eye and the supralabial shields. Incomplete intruding scale row is recorded as half. *
IntSc Number of interstitial scales, other than supranasals and prenasals, in contact with the rostral.
SubN Number of subnasal scales, between the nasal and the supralabials. *
IntN Number of scales other than supralabials in contact with the rostral.
IntN2 The minimum number of scale columns separating the supranasals.

Computed meristic characters:

PreV2 + Gul3 Number of scales between chin-shield and preventrals (for gul3 the average of the two sides was used).

Multistate characters:

LPreN Lower prenasal. 0, absent; 1, present. *
FPSN Prenasal and subnasal. 0, separate; 1, fused. *
FPN Prenasal and nasal. 0, separate; 1, fused. *
GulS Gulars between chin-shield and PreV2. 1, mostly elongated; 3, mostly rounded; 2, intermediate.
ShH Conspicuously enlarged (or fused) shield in the centre of the top of the head. 0, absent; 2, present; 1, intermediate.
SOc Enlarged (or fused) supraocular shield in the inner circumocular ring. 0, absent; 2, present; 1, intermediate. *
SOc2 Enlarged (or fused) supraocular shield in the outer circumocular ring. 0, absent; 2, present; 1, intermediate. *
SupLG Aperture of the external superior labial gland on the supralabial. 1, positioned antero-ventrad; 2, positioned medio-ventrad. *

**Mensural characters:**
RA Rostrum-anus length (Werner, 1971).
TailL Tail length (if complete).
HL Head length, taken axially with Goren & Werner’s (1993) modified callipers from the tip of the snout to behind the mandible.
HW Head width (at the widest part of the head).
EyeD Eye diameter (the longest diameter of the visible part of the eye). *
RostH Height of the rostral shield at its midline.
RostW Rostral shield width at the widest point above or at the upper edge of the adjacent infra labial scales.
DorsL Combined length of five consecutive mid-dorsal scales at mid-RA.

**Computed mensural characters:**
RDorsL Relative (PERCRA) length of five consecutive mid-dorsal scales at mid-RA.
RTail Relative (PERCRA) tail length.

**Colour pattern:**
HPat Dark dorsal head pattern. 0, missing; 1, X shaped; 2, Y shaped; 3, a small V shaped marking between the eyes and two small triangular markings behind it; 4, small spots of any shape and arrangement.
FacB Number of scales, excluding supralabials, included in the facial band (dark band between the caudal edge of the eye and the corner of the mouth).
PFB Position of the facial band. 0, not reaching the postmandibular blotch; 1, fused with the postmandibular blotch.
VentP Dark ventral pattern. 0, absent; 1, lateral sides of the ventrals dotted; 2, a mid-ventral row of dots; 3, both lateral and mid-ventral dots; 4, lateral edge of ventrals marbled; 5, entire ventral surface dotted.

**Characters used in cluster and principal coordinate analyses:**

**Statistics**
The sexes were treated separately. Character redundancy was avoided by testing for high intra-locality correlation (Thorpe, 1976) among characters (Pearson’s correlation coefficient). For multivariate analyses, only one of those characters which correlated with each other in all subsamples was kept ($r > 0.8$ in meristic, $r > 0.9$ in mensural characters).

In order to show group similarity of individuals phenetic cluster analysis and principal coordinate analysis (PCO) were applied using Multivariate Statistical Package, MVSP 3.0 for Windows. Clustering followed the unweighted pair-group method, using the Gower general similarity coefficient treating discrete, continuous and categorical characters together. PCO was run on the same Gower similarity matrix. Only the first three principal coordinates were extracted as they showed the main taxonomic differentiation (Thorpe, 1976) aimed for in this study, although they together accounted for only 24% in males and 24.9% in females of the total variation in the entire sample. Both cluster analysis and PCO were performed on a set of specimens with almost all data points recorded. In order to achieve this, some characters and some specimens were omitted. The last few missing data points were replaced with the local sample means, instead of the grand mean, to avoid bias from the quantitative dominance of the Levant material. For gular shape and ventral pattern, the state commonest in the local sample was used. For this analysis, eight geographical samples were defined on the basis of the results of ANOVA among local samples, geographic features and collection activity: 1, Sinai-Elat; 2, Yotvata-Hazeve-Sedom; 3, Negev; 4, En Gedi; 5, Jordan Valley-Judea Desert-Mt. Gilboa; 6, Mecca; 7, Jizan-N Yemen; 8, UAE–northern Oman. For reconstructing missing data points of specimens from poorly sampled areas I pooled them with local samples above as follows: A, Egypt with Sinai-Elat; B, N Arabia: specimens from Arabia north of Jizan (excluded) with Mecca; C, S Arabia: all the Arabian specimens south of Jizan (included) with Jizan-N Yemen.

The differences between the two main groups derived from cluster analysis and from PCO were tested for significance. Meristic and continuous characters were tested by means of a two-tailed $t$-test. The frequencies of character states were tested by applying a Chi-square test. The significance level was $P = 0.05$ in each test.

**Results**
The dendrograms derived from this study are deposited in the herpetological collection of the Hebrew University of Jerusalem, Israel. The dendrogram of each sex showed two main branches. One contained only the specimens of the UAE and northern Oman, and the other comprised the remainder. All 14 male specimens from the UAE and northern Oman clustered to the ‘correct’ branch but one out of 12 females from northern Oman (BMNH 1977.86) clustered with the closest cluster of the other main branch. For each sex, the PCO scores of the axes 1 and 2 plotted in scatter diagrams (Fig. 1) show two non-overlapping groups of specimens. Similarly, in the two main branches of the dendrograms, one group comprises the specimens from the UAE and northern Oman and the other group the remainder.

Characters which seemed to differentiate the UAE–northern Oman sample are summarized in Tables 1 and 2.
Figure 1  Principal coordinate analysis case scores for male (A) and female (B) specimens of the *Echis coloratus* complex. △ = Specimens from the UAE and northern Oman. • = Specimens from the rest of the distribution area of *E. coloratus*.

For comparison, the same characters are shown for the sample from the area of the type locality s.l. (Jebel Sharr, Midian, Saudi Arabia) of *Echis coloratus* of Günther, 1878 (holotype included) and for Hadramaut-Dhofar, the geographic unit closest to northern Oman, which is inhabited by *E. coloratus*. The lowest values in subcaudals (Table 1) should be regarded with caution as healed tail-tip injuries might have passed unnoticed. Small round gular scales were found on the throats (GulS) of two very young specimens of samples other than UAE–northern Oman (Table 2), where perhaps final scale shape had not developed. In three snakes from samples other than UAE–northern Oman a third scale appeared between the upper and lower prenasal (Table 2). Frequencies of seven multistate characters differed between the UAE–northern Oman sample and the other samples (Chi-square; $P \leq 0.05$, Tables 3 and 4).

The combination of morphological distinction and geographical isolation of the UAE and the northern Oman populations of the *Echis coloratus* complex suggests that this population has a separate evolutionary history, and therefore (Frost & Hillis, 1990), the results are interpreted as showing the existence of an undescribed species in the UAE and northern Oman.

**Echis omanensis n. sp. (Fig. 2)**

*Echis colorata* Günther: Boulenger, 1887:408 (Muscat; coll: A. S. G. Jayakar.


*Echis froenatus* Duméril, Bibron et Duméril: Cherlin 1990:203 (part, taxonomic review, map; the name was suppressed by Opinion 1176 (ICZN 1981)).

Proposed English name: Oman saw-scaled viper.

Holotype. BMNH 1973.2113; Male; Wadi as Siji, region of Masafi (25°18'N 56°10'E), United Arab Emirates; collected on 28 May 1973 by E. N. Arnold.

**Paratypes (32)**

<table>
<thead>
<tr>
<th>Character</th>
<th>Sex</th>
<th>E. omanensis</th>
<th>E. coloratus pooled</th>
<th>E. coloratus Type locality s.l.</th>
<th>E. coloratus Hadramaut-Dhofar</th>
</tr>
</thead>
<tbody>
<tr>
<td>RA, max (mm)</td>
<td>m</td>
<td>606 (17)</td>
<td>716 (149)</td>
<td>539 (4)</td>
<td>435 (3)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>603 (14)</td>
<td>658 (152)</td>
<td>610 (4)</td>
<td>540 (5)</td>
</tr>
<tr>
<td>Tail length, percra</td>
<td>m</td>
<td>16.3 ± 1.4 (14)</td>
<td>15.0 ± 1.4 (122)</td>
<td>15.2 ± 0.1 (3)*</td>
<td>16.0 ± 1.4 (2)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>15.2 ± 0.9 (10)</td>
<td>13.0 ± 1.0 (122)*</td>
<td>12.8 ± 0.4 (4)*</td>
<td>14.3 ± 0.8 (3)</td>
</tr>
<tr>
<td>Ventral m</td>
<td></td>
<td>187.3 ± 3.2 (15) (184–194)</td>
<td>190.0 ± 5.3 (148) (175–204)</td>
<td>195.8 ± 6.6 (4)* (186–200)</td>
<td>177.7 ± 3.8 (3)* (175–182)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>191.5 ± 2.9 (13) (187–195)</td>
<td>194.4 ± 6.5 (148)* (175–210)</td>
<td>198.3 ± 3.9 (4)* (193–202)</td>
<td>178.8 ± 3.4 (5)* (175–184)</td>
</tr>
<tr>
<td>Subcaudal m</td>
<td></td>
<td>55.6 ± 2.2 (14) (49–58)</td>
<td>49.8 ± 3.3 (127)* (45–50)</td>
<td>50.8 ± 1.7 (4)* (49–53)</td>
<td>50.5 ± 3.5 (2)* (48–53)</td>
</tr>
<tr>
<td>Subcaudal f</td>
<td></td>
<td>50.7 ± 2.3 (10) (48–56)</td>
<td>45.1 ± 1.8 (125)* (40–50)</td>
<td>45.0 ± 1.0 (3)* (44–46)</td>
<td>44.0 ± 2.5 (3)* (43–48)</td>
</tr>
<tr>
<td>Gular m</td>
<td></td>
<td>12.1 ± 0.7 (15) (11–13.5)</td>
<td>11.1 ± 0.8 (147)* (9.5–13.5)</td>
<td>11.4 ± 0.7 (5)* (11–12.5)</td>
<td>10.3 ± 0.6 (3)* (10–11)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>12.3 ± 0.6 (14) (11–13.5)</td>
<td>11.1 ± 0.8 (148)* (9.5–13)</td>
<td>11.2 ± 0.3 (3)* (11–11.5)</td>
<td>11.0 ± 1.0 (5)* (10–12.5)</td>
</tr>
<tr>
<td>Gular2 m</td>
<td></td>
<td>7.9 ± 0.5 (17) (7–8.5)</td>
<td>7.0 ± 0.6 (157)* (6–9)</td>
<td>6.7 ± 0.3 (5)* (6.5–7)</td>
<td>7.3 ± 0.8 (3)* (6.5–8)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>8.4 ± 0.8 (12) (7–9.5)</td>
<td>7.3 ± 0.6 (152)* (5–9)</td>
<td>7.0 ± 0.7 (4)* (6–7.5)</td>
<td>7.2 ± 0.4 (5)* (6.5–7.5)</td>
</tr>
<tr>
<td>Gular3 +</td>
<td>m</td>
<td>7.0 ± 1.1 (14)</td>
<td>5.4 ± 0.8 (140)*</td>
<td>4.6 ± 0.5 (5)*</td>
<td>5.8 ± 1.4 (3)</td>
</tr>
<tr>
<td>Prevenral2</td>
<td>f</td>
<td>8.7 ± 1.0 (13) (6–10)</td>
<td>5.5 ± 0.7 (138)* (4–7.5)</td>
<td>5.4 ± 0.9 (4)* (4–6.5)</td>
<td>5.5 ± 0.6 (5)* (5–6.5)</td>
</tr>
<tr>
<td>Facial band</td>
<td>m</td>
<td>40.1 ± 3.0 (11) (36–44)</td>
<td>27.4 ± 3.9 (94)* (17–38)</td>
<td>29.5 ± 0.7 (2)* (29–30)</td>
<td>24.5 ± 2.1 (2)* (23–26)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>41.0 ± 4.9 (12) (34–49)</td>
<td>27.9 ± 3.7 (89)* (17–35)</td>
<td>28.5 ± 0.7 (2)* (28–29)</td>
<td>30.0 ± 3.9 (4)* (26–35)</td>
</tr>
</tbody>
</table>

Table 1: Characters most clearly separating *Echis omanensis* from *E. coloratus*. m = males; f = females. Data in the column 'E. coloratus pooled' include the samples in the two following columns. Values marked with an asterisk (*) differ significantly from northern Oman (two-tailed t-test; P ≤ 0.05).

**Diagnosis (based on 32 specimens preserved in alcohol)**

*Echis omanensis* differs from *E. coloratus* (characteristics in parentheses: n = 321) as follows (see also Tables 1, 2, and 4): ventrals 184–194 (175–204) in males, 187–195 (175–210) in females; subcaudals 49–58 (45–56) in males, 48–56 (40–50) in females; nasal often fused with the upper prenasal (almost never); lower prenasal often missing (usually present); 6–10 scales between the chin-shield and the preventral (3.5–7.5); round or only slightly elongated gulars along the two sides of the midline of the throat (conspicuously elongated; Fig. 3).

Head dorsally usually uniform grey, rarely a dark X-shaped marking or, in young specimens, marked by small spots (mostly with an X-shaped marking, rarely spots); facial band covers from 36 to 44 (17–38) temporal scales in males and 34–49 (17–35) temporal scales in females, facial band often...
abruptly ends before the postmandibular blotch, not merging with it (mostly merges with it); usually barely visible dark bands below the eye and anterior to the nasal in adults (usually dark and often fuse with each other or with the facial band); mostly moderately dark infralabial blotches in adults (usually contrasting); dark, sometimes faded mid-dorsal band 5–6 dorsal scale wide connecting the dorsal blotches (usually missing or narrower).

Grows to 606 mm RA in males and 603 mm in females (716 mm, En Gedi, Israel; 658 mm, northern ‘Arava, Israel); tail relatively long 16.3 PERCRA in males and 15.2 PERCRA in females (15.0/13.0).


**Description of the holotype**


Nasal fused with the subnasal and in contact with the supralabial on both sides; supransals separated by one scale column; lower prenasals missing; prenasals divided from the nasals and the subnasals; gulars between the chin-shield (Fig. 3) and the preventrals rather small, barely elongated and in an irregular arrangement; in the inner circumocular ring no enlarged supraocular shields; on the right slightly, on the left conspicuously enlarged shields in the dorsal section of the outer circumocular ring; aperture of the supralabial glands on the middle of the first supralabial.

Head dorsally uniform grey; infralabial blotches (4/4), faded, the posterior one conspicuous; facial band moderately dark; bands under eyes and the one below the nasals almost invisible; ground colour of body grey; dorsal blotches lighter than ground colour (44/43) from occiput to cloaca; blotches (9/8) from cloaca to tip of tail; last third of tail brown dorsally in contrast with grey ground colour of body; blotches slightly lighter than ground-colour cranially and more contrasting caudally; a ring-like dark frame surrounds each blotch; frame extends laterally in a dark rectangular patch, almost always merging with lateral bands; blotches on anterior two-thirds of body often broken up along midline or oblique, more regular caudally (but some broken up or oblique); a faint (lighter than ground colour) mid-dorsal band connecting blotches; lateral bands less contrasting than frame of dorsal blotches; usually

<table>
<thead>
<tr>
<th>Characters and their states</th>
<th><strong>E. omanensis</strong></th>
<th><strong>E. coloratus pooled</strong></th>
<th><strong>E. coloratus Type locality s.l.</strong></th>
<th><strong>E. coloratus Hadramaut-Dhofar</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
<td>Males</td>
<td>Females</td>
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<tr>
<td>Subnasal</td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>0</td>
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<tr>
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<td>10</td>
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<tr>
<td>Lower prenasal</td>
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<td>3</td>
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<tr>
<td>Fusion of prenasal with nasal</td>
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<td>Gular shape</td>
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<td>3</td>
<td>11</td>
<td>13</td>
<td>1</td>
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</tbody>
</table>

Table 2 Frequencies of the states of multistate characters most clearly separating _Echis omanensis_ from _E. coloratus_. The column ‘_E. coloratus pooled_’ includes the samples in the two following columns. Asterisk (*) on top indicates significant difference from _E. omanensis_ (Chi-square test; \( P \leq 0.05 \)).
A new species of the Echis from Oman

<table>
<thead>
<tr>
<th>Characters and their states</th>
<th><strong>E. omanensis</strong></th>
<th><strong>E. coloratus</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>Infracantal 2</td>
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</tr>
<tr>
<td>2.5</td>
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<td>0</td>
</tr>
<tr>
<td>3</td>
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Table 3 Distribution of character states of characters appearing in different frequencies between *Echis omanensis* and *E. coloratus*. The frequency of the states of all differed significantly between the samples (Chi-square test; \( P \leq 0.05 \)).

a series of two, sometimes merging, blotches composes the lateral bands; lateral blotches extend to edge of ventral scales; ventral surface yellowish-white, with faint array of dots both medially and on lateral sides of ventrals.

**Variation in scalation**

The distribution of character states of scalation in the samples of *Echis omanensis* and *E. coloratus* is shown in Tables 1, 2, 3 and 4.

**Variation in colour pattern**

Ground colour of the body grey with dark edged, conspicuous dorsal blotches; the dark frame may surround the entire blotch or may partly disappear, remaining only laterally and as two transversally positioned spots across the mid-dorsal line, one at the caudal end, one at the cranial end of the blotch; the frame often merges with the lateral band or the upper blotch of the lateral band. Usually a series of two large grey blotches composes each lateral band; the upper blotch often rectangular and below the dorsal blotch; the lower blotch is positioned more cranially, thus the bands appear oblique; lateral bands sometimes paler than the frame of the dorsal blotches. Ventral surface yellowish-white or greyish-white, mostly with a faded line of dots medially and an array of faded dots toward each lateral side of the ventrals or with only one of these components; it may lack any pattern.

**Distribution**

*Echis omanensis* seems to be endemic to northern Oman and the eastern United Arab Emirates from the Musandam Peninsula to the eastern tip of the Eastern Hajar (Al Hajar ash Sharqi) in northeastern Oman. The species ranges from sea level to 1000 m (Fig. 4).

**Ecology**

*Echis omanensis* was mostly collected in the spring months (February–May) and less frequently in autumn (November–December). In part this is probably due to the activity of zoological expeditions (Büttiker, 1989), which are probably scheduled for the months with moderate weather conditions. In Israel, where *E. coloratus* is often collected by locals and presented to collections, specimens were frequently collected also in other seasons of the year, especially in summer. On the basis of the few records on the tags, *E. omanensis* was found abroad either early in the morning (7–9 am) or in the afternoon and in the evening (3–8 pm).

**Comments**

The only photograph known to me showing a supposedly *E. omanensis* specimen was published by Gallagher (1990), but regrettably the origin of the specimen is not given.
Figure 3 Comparison of ventral aspect of heads of *Echis* spp.: A *Echis omanensis*, holotype BMNH 1973.2113; B *Echis coloratus*, male BMNH 1986.455, Jabal as Sina, Saudi Arabia; C *E. coloratus*, female HUI-R 8866, Muyet Lulya, Sinai; D *E. coloratus*, female BMNH 1994.134, Jiddat al Harasis, Oman. Note the scales along the midline: in *E. omanensis* these are more numerous and less elongated (Scale bar = 10 mm. Head lengths: A. 30.0 mm; B. 23.8 mm; C. 31.9 mm; D. 27.6 mm).

Figure 4 Distribution of *Echis omanensis* and *Echis coloratus* based on the examined material. Symbols indicate at least one specimen. △ = *E. omanensis*; ● = *E. coloratus*.

Discussion

Morphology

The shape and size of the gulars is of special interest. Cherlin (1983) found that in *Echis* the shape of gular scales along the midline of the throat varies considerably among zoogeographic units and employed it in his division of *Echis* into subgenera (Cherlin, 1990). My results support the use of this character at least at the species level. Moreover, the variation in different characters in the gular area seems to be correlated,
reflecting an overall variation in the ventral pholidosis of the head. Thus these characters are recommended for use in *Echis* taxonomy.

The difference in the RA length I recorded of the largest specimens of each species is great. However, because the encountered maximum RA length is expected to increase with sample size and the sample sizes used here differed, the two species could actually attain similar RA maxima.

**Distribution**

The gap in the distribution of the species complex south of the mountainous area of Oman was previously shown on the maps of Joger (1984) and Gasperetti (1988). It separates the distributions of *E. omanensis* and *E. coloratus*. The distribution gap between the mountains of the UAE and northern Oman and the escarpment of Jabal Tuwayq in the central regions of Arabia, the easternmost outpost of *E. coloratus* in the north, seems to be real as the two regions are separated by the sands of the Rub al Khali. Sand seems to be an ecological barrier for both species. Joger (1984) indicated the occurrence of *E. coloratus* on the coast opposite Qatar, somewhere in the middle of the gap. This locality cannot be confirmed from the material I used. The only specimen (BMNH 1986.457) at my disposal that suggested this locality turned out to be recorded in the catalogue of the British Museum erroneously (Gasperetti, 1988; Mrs P. Gasperetti, pers. comm.). In the south, the boundary seems more dubious. *Echis coloratus* extends east to Jiddat Al Harasis (BMNH 1994.134; 20°13′N, 57°17′E). The gap that remains unsampled (or uninhhabited by either species) is still wide, approx. 300 km. Certainly, the presence of *E. coloratus* even further to the east cannot be ruled out, but its presence in the mountains of Oman seems improbable, considering that the latter area is much better sampled than the former. Thus, *E. coloratus* and *E. omanensis* may be parapatric, but the Wahibah Sands (Ramlat al Wahibah) may impose a barrier for both species, leaving them allopatric.

Separated from *Echis coloratus*, *E. omanensis* might have differentiated in northern Oman and remained allopatric. The zoogeographic isolation of the mountains of northern Oman is known (Arnold & Gallagher, 1977; Arnold, 1987), but in the Pleistocene some migration of reptiles probably took place across the Persian Gulf (Arnold & Gallagher, 1977; Joger, 1984; Anderson, 1999). However, some reptiles with Asian affinity, endemic to northern Oman, remained confined to northern Oman (Arnold & Gallagher, 1977; Arnold, 1987; Joger, 1987). These endemics and some other species also occurring in Iran, do not reach Dhofar in southern Oman. Interestingly, no vipers of the *Echis coloratus* complex have been reported from Iran. *Echis carinatus sochureki* and *Pseudocerastes persicus persicus* are among the snakes that probably have crossed the Persian Gulf toward Arabia. The question arises why *E. omanensis* did not cross in the opposite direction. The distribution of potentially competing species may be restricted by interspecific competition (Arnold & Gallagher, 1977). Possibly in Iran, *E. omanensis* would have been eliminated in competition with *P. p. persicus* if it all had arrived there, while in northern Oman topographic segregation enabled these species to share the same geographic unit. In sympathy, *E. omanensis* occurs at lower altitudes whereas *P. p. persicus* occurs higher up (Arnold & Gallagher, 1977). Nevertheless one cannot exclude a future discovery of an unknown population of *E. omanensis* in Iran, as happened with the gecko *Tropiocolotes cf. steudneri* (Anderson, 1999). However, an *Echis*-like venomous snake is less likely to remain undiscovered. Until proved otherwise, I consider *E. omanensis* endemic to the UAE and northern Oman.

The origin of *Echis omanensis* and its separation from *E. coloratus* remain to be studied. *E. coloratus* occurs in the Arabian subregion of the Saharo–Iranian region (Haas, 1952; Joger, 1984), Cherlin (1990) postulates that the genus *Echis* originated from the Irano–Turanian region in Asia and that it radiated to the west across Mesopotamia, then forking to Oman and to northwestern Arabia and Africa. On the basis of this hypothesis one may postulate two scenarios in which *E. omanensis* evolved: (1) The common ancestor of *E. coloratus* and *E. omanensis* radiated into two directions after reaching Arabia from Mesopotamia. The ancestor of *E. omanensis* spread to Oman and the ancestor of *E. coloratus* to the Levant, Africa and western Arabia. (2) The common ancestor of *E. coloratus* and *E. omanensis* radiated only northwest after reaching Arabia, but not toward Oman, and the ancestor of *E. omanensis* arrived to northern Oman from southwestern Arabia after inhabiting western Arabia. Further analysis of populations of *E. coloratus* and *E. omanensis* is necessary to substantiate any of the above-mentioned hypotheses. On the other hand, studies of the phylogeny of vipers (Herrmann & Joger, 1997; Herrmann et al., 1999) suggest that the genus *Echis* is related to the African *Atheris*. This may put a question mark on the theory of a westerly radiation of *Echis* from Asia to Africa, but does not change the basic question whether the ancestor of *E. omanensis* arrived in northern Oman from northern or southern Arabia.

**Ecology and behaviour**

Little is known about the ecology of *Echis omanensis*. It may resemble that of *E. coloratus*. *Echis omanensis* is often encountered in wadis with surface water (Arnold & Gallagher, 1977; Gallagher, 1990). Like *E. coloratus*, it prefers rocky or hard terrain and is absent from sandy areas, where *E. carinatus sochureki* prevails (Arnold & Gallagher, 1977). It was found abroad either early in the morning or in the afternoon. The afternoon agrees with the observations of Gasperetti (1988) on *E. coloratus*. Its presence outside of shelter in the morning parallels similar observations by amateurs on *E. coloratus* in Israel. It may ambush overnight starting in the afternoon, then retreat in the morning after a short basking period. But this scenario may in part reflect the daily activity pattern of the observers. Indeed, Cherchi & Spanò (1963) reported *E. coloratus* in Hadramaut active also in mid-day, at high (40 °C) air temperature, in mid-April. But then those snakes could have been abroad in mid-day because they were in a reproductive period.

*Echis omanensis* sometimes feeds on the local species of *Bufo* (Arnold & Gallagher, 1977) as does *E. coloratus* in Israel (Mendelsohn, 1965). However, songbirds are considered an important part of the diet of *E. coloratus* in the
Levant (Bouskila & Amitai, 2001). In the HUJ-R material in two cases out of >100 the bad condition of the specimens enabled me to examine the stomach content without further destruction; in both I found bird feathers. The habit of E. coloratus of perching on desert trees and bushes or close to surface water (Bouskila & Amitai, 2001), their head usually pointed upwards (Hawlena, unpublished), suggests similar behaviour to Macroviper a schweizer i in the western Cyclades, which ambushes migrant birds coming to rest and to drink (Nilson et al., 1999). The hypothesis that E. coloratus regularly feeds on birds is compatible with the experimental results of Hawlena and Bouskila (2001), which showed that E. coloratus does not choose its ambush site by smell and with the fact that many avian migration routes coincide with the distribution of E. coloratus (Yom-Tov, 1988; Shirihai, 1996). Migrant passerines appear also in northern Oman (Gallagher, 1977). Besides migrant birds, desert passerine birds, approaching surface waters of wadis for drinking, may also be a regular source of food for both species. Mendelsohn (1965) suggested that migrant birds might be a regular diet of Pseudocerastes persicus fieldi in the Negev. However, both E. coloratus and E. omanensis may consume a wide range of invertebrates and vertebrates (Mendelsohn, 1965; Arnold & Gallagher, 1977; Gasperetti, 1988).

Epidemiological implications
Venom composition may vary in venomous snakes at any systematic level (Wüster et al., 1997), thus the taxonomic distinction presented here suggests a reconsideration of the use in the UAE and northern Oman of antivenin developed for Echis coloratus. A study of venom composition of E. omanensis is desirable.

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References


Appendix

Specimens used in this study

The specimens used in the cluster and principal coordinate analyses are marked with an asterisk (*).

Specimens referred to the type locality s.l. of *Echis coloratus* and to Hadramaut-Dhofar in Tables 1 and 2 are underlined. The former is pooled for statistics with the N Arabian and the latter with the S Arabian pool.

**Males**


Jizan-N Yemen (n = 9): CAS 140409*, 148620*, MHNG 2427.21*, 2427.22, 2457.18, 2582.12*, 2593.45*, 2593.46*, 2593.49*.

Egypt (pooled for statistics with the sample from Sinai-Elat; n = 6): BMNH 1900.5.12.7*, 1900.5.12.8*, FMNH 143998, 143999, 171884, USNM 130616.


Specimens pooled for statistics with the sample from Jizan-N Yemen to a S Arabian group (n = 5): BMNH 1897.3.11.119*, 1953.1.8.58*, 1985.662*, MHNG 2554.27*, 2554.28*.
Females


Jizan-N Yemen (n = 8): CAS 140408, 140496*, 140497, 145302, MHNG 2582.13*, 2593.47, 2593.48*.

Egypt (pooled for statistics with the sample from Sinai-Elat; n = 5): BMNH 1913.2.24.48*, FMNH 164705*, 171883*, Giza Zool. Gardens, Cairo (Magid, 1949), USNM 130615.


Specimens pooled with the sample from Jizan-N Yemen to a S Arabian group (n = 6): BMNH 1881.3.5.5*, 1897.3.11.118*, 1974.4050*, 1994.134*, MSNG 15/APR/1962, MSNG 17/APR/1962.