# Systematics and distribution of the *Acanthodactylus pardalis* group (Lacertidae) in Egypt and Israel

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Abstract: Examination of 385 specimens of the *Acanthodactylus pardalis* group from eastern Libya, Egypt and Israel confirmed the occurrence of two allopatric species in this area: *Acanthodactylus pardalis* (Lichtenstein, 1823) distributed in Egypt and eastern Libya and a hitherto undescribed species endemic to the Negev (Israel). The species differ most markedly in body size, hemipenial structure, colouration and details of sexual dichromatism. Other significant differences involve scalation and biometrics. A simple method for artefact-free use of discriminant analysis in multivariate classification is presented. Redescription of *A. pardalis* (Lichtenstein, 1823), description of a new species *Acanthodactylus beershebensis* sp.n. and corrected geographical ranges of the two species are provided. Both species, each endemic to a small area, appear to be markedly endangered by habitat destruction.

Kurzfassung: Die Untersuchung von 385 Exampiaren aus der *Accnthodactylus pardalis*-Gruppe aus dem östlichen Lybien, Ägypten und Israel bestätigte die Existenz von zwei allopatrischen Arten: *Acanthodactylus pardalis* (Lichtenstein, 1823), in Ägypten und dem östlichen Lybien vorkommend, sowie eine bislang noch nicht beschriebene Art, die in der Negev (Israel) endemisch ist. Diese Art unterscheidet sich deutlich in der Körpergröße, der Struktur des Hemipenis, der Färbung, sowie in Details des Sexualdimorphismus. Außerdem gibt es signifikante Unterschiede in der Beschuppung und der Biometrie. Eine einfache Methode zur Anwendung der Diskriminanz-Analyse bei der multivarianten Klassifikation wird dargestellt. Außerdem werden eine erneute Beschreibung von *A. pardalis* (Lichtenstein, 1823), die Neubeschreibung von *Acanthodactylus beershebensis* sp.n., und die geographische Verbreitung beider Arten mitgeteilt. Die Areale beider Arten sind relativ klein, und sie sind durch Habitatzerstörungen stark gefährdet.

Key words: *Acanthodactylus pardalis*, Lacertidae, Middle East, Egypt, Israel, endemism, new species, discriminant analysis.

## Introduction

The first nominal taxa of the *Acanthodactylus pardalis* group (Lacertidae; North Africa) were described from Egypt (*Lacerta pardalis* Lichtenstein, 1823) and from "Perse et de l'Asie mineure" (*Lacerta deserti*, Milne-Edwards, 1829; interpreted by BOULENGER, 1921, as "probably Syria" on p. 69 and as "Levant" on p. 73). In subsequent years several other related forms were described from different parts of Northern Africa.

The genus *Acanthodactylus* was first revised by BOULENGER (1918). He considered the *Acanthodactylus pardalis* group a single species comprising five varieties (*bedriagai*, *latas-*

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*tii, maculatus, pardalis, spinicauda*). *Lacerta deserti* was placed in the synonymy of *A. pardalis* (BOULENGER 1921).

At present *spinicauda* and *maculatus* of western North Africa are regarded as full species, *latastii* being considered a synonym of *maculatus* (PASTEUR & BONS 1960, SALVADOR 1982, ARNOLD 1983). The forms *bedriagai* in the west and *pardalis* in the east are then treated either as full species (SALVADOR 1982), or as subspecies of the polytypic species *A. pardalis* (ARNOLD 1983). The West Moroccan population related to *bedriagai* was described as a new species, *A. busacki* (SALVADOR 1982).

However, there are open questions in the eastern part of the range of the *A. pardalis* group. *A. pardalis* (or *A. p. pardalis* sensu ARNOLD 1983) appears to comprise several more or less distinct forms distributed in eastern Libya, Egypt, Israel and Jordan. The Israeli (Negev) population is disjunct from the Egyptian one. The species does not occur in the intervening Sinai or the Eastern Desert of Egypt, presumably because correct soils, loess or clay, are absent (WERNER 1982). The Jordan population is disjunct again (WERNER 1991).

Although several authors (ANDERSON 1898, BOULENGER 1921, FLOWER 1933, SALVADOR 1982) have mentioned or even shown differences, in several characteristics, between the Egyptian and Negev populations (e.g. body size, division of the first supraocular, number of transverse rows of ventrals), no study has compared these populations in detail.

We aimed to (1) describe and analyse the variation of *A. pardalis* in Egypt and the Levant, (2) elucidate the taxonomic and nomenclatural status of the Negev population and (3) contribute to the knowledge of distribution, biology and status of the Egyptian and Israeli forms (The term "Egyptian form" here includes the population of *A. pardalis* from Cyrenaica.).

This first paper presents the results of our recent field data and an analysis of morphological characters, leading to the description of a new species from the Negev of Israel.

## Material and methods

Abbreviations and geographical names

BMNH: Natural History Museum, London. – FMNH (CNHM): Field Museum of Natural History, Chicago. – HUJ-R: Zoological Museum, Hebrew University of Jerusalem, Herpetology. – LACM: Los Angeles County Museum of Natural History. – MNHN: Museum National d'Histoire Naturelle, Paris. – MZUF: Museo Zoologico de "La Specola", Firenze. – MZUT: Museo di Zoologia della Universita di Torino. – NMP6V: National Museum (Natural History), Prague. – TAU-R: Zoological Museum, Tel Aviv University, Reptilia. – USNM: Smithsonian Institution, Washington D.C. – ZFMK: Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn. – ZMB: Zoologisches Museum, Humboldt Universität, Berlin.

DS = for scutellation characters, the difference between a specimen's multivariate similarity to the Egyptian sample, and its multivariate similarity to the Israeli sample. – E = material originating from Egypt. – I = material originating from Israel. – percra % of ra (WERNER 1971). – ra = rostrum–anus length (WERNER 1971).

Geographical names in Egypt (and Libya) are mostly spelled following the TIMES ATLAS (1997) or as in the source quoted with explanation in square brackets according to the TIMES ATLAS (1997) or WEBSTER'S GEOGRAPHICAL DICTIONARY (1955). Locality spellings in Israel follow the Survey of Israel 1:250,000 (1971) English map, rather than museum labels or catalogue entries.

## Summary of material

We externally examined all museum specimens of the *Acanthodactylus pardalis* group in HUJ-R and NMP6V; type material from MNHN and ZMB; and part of the material from the other museums listed above. The 368 specimens are listed in Appendix 1. For osteological characters we used existing radiographs (filed in HUJ) of 154 individuals; these are marked (*) in Appendix 1 or listed in Appendix 2. We also examined live material: from Egypt, 12 adults and one juvenile collected by BAHA EL DIN and MORAVEC in June 1995 in the El Nasr area (HUJ-R 18990-99, 19007, 19159, 19169); and from Israel, one male collected in January 1997 by SELIGMANN and SHACHAM, two males and one female collected in May 1997 by SELIGMANN and THIEBERGER (HUJ-R 19191-92) and one young male collected in January 1998 by SELIGMANN and BABOCSAY (HUJ-R 19261); all at Negev Junction, Be'er Sheva' Subdistrict; and photographic documentation of several others collected earlier.

## Characters

Where possible, we examined the following mensural, meristic (pholidotic and osteological), computed (mensural and meristic), and qualitative characters in all specimens investigated.

We examined several meristic (pholidotic and osteological) characters bilaterally and compared the right and left sides to verify the possible presence of directional asymmetry (WERNER et al. 1991). Further we used the individual means of the right and left side. These characters are indicated by an asterisk (*) in the character lists below.

Mensural characters. Rostrum–anus length (ra): Distance from tip of snout to cloaca. – Head length: Distance from tip of snout to posterior edge of ear, measured parallel to long axis of body with special calipers (GOREN & WERNER 1993). – Head width: Greatest width of head. – Head depth: Greatest depth of head. – Forelimb length: From axilla to tip of distal claw. – Hindlimb length: From groin to tip of distal claw. – Fourth toe length: From insertion of 5th toe, claw included. – Tail length: From cloaca to tip of tail, if original.

Except for ra and tail length which were measured to the nearest 0.5 mm, all characters were measured to the nearest 0.1 mm. Except ra, all are presented as percra.

Meristic pholidotic characters. Supralabials*: Number of labials anterior to the centre of eye. – Gulars: Number of gular scales in a straight median series. – Plates in collar: Number of larger scales in collar. – Dorsals: Number of dorsal scales across midbody. – Ventrals across belly: Number of ventral scales in longest row across belly. – Transverse rows of ventrals: Number of complete transverse series of ventral scales counted along the ventral side to (and excluding) the row of scales separating, if present, the series of femoral pores. – Preanals: Number of preanal scales in straight median series between cloaca and the row of scales separating, if present, the series of femoral pores. Femoral pores*: Scales between the rows of femoral pores (number of scales separating the two series of femoral pores). Subdigital lamellae*: Along underside of fourth toe, defined by their width, the one touching the claw included.

Measures of asymmetries in the four characters examined bilaterally are calculated by the subtraction of the left side from the right side (for directional asymmetry, DA), and the absolute value of DA is the fluctuating asymmetry (FA).

Computed characters. Head index: Head length divided by head width, x 100. We also computed three ratios between meristic characters (Tab. 3) because we expected them to differ between samples.

Tab. 1. Mensural characters of the specimens of *Acanthodactylus pardalis* group from Egypt and Israel: males. CD, coefficient of difference; N, sample size; P, significance of difference between Egypt and Israel from two-tailed t-tests between means of residuals of body parts (from means of regressions of body parts over ra); SD, standard deviation (See also Material and Methods: Abbreviations; Statistics.). Variation of N results from missing measurements among specimens. percra except: ra and head index. Head index is % head length from head width. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; n.s., not significant.

| Character | N | | percra (mean, SD, range) | | regression (coefficient, intercept) | | Egypt versus Israel |
|---|---|---|---|---|---|---|---|
| | Egypt | Israel | Egypt | Israel | Egypt | Israel | CD, P |
| ra (mm) | 67 | 130 | 56.38±4.97<br>45.0-66.5 | 66.26±5.86<br>55.0-87.0 | – | – | 0.91 *** |
| Head length | 63 | 130 | 25.54±1.03<br>23.7-28.2 | 24.52±1.20<br>17.4-27.1 | 0.167<br>48.93 | 0.200<br>29.74 | 0.09 n.s. |
| Head width | 60 | 129 | 17.74±0.98<br>14.9-20.2 | 17.80±0.96<br>14.4-20.6 | 0.143<br>18.67 | 0.180<br>-1.69 | 0.20 ** |
| Head depth | 59 | 129 | 13.59±0.99<br>11.1-15.7 | 13.79±0.87<br>11.2-16.1 | 0.111<br>13.47 | 0.136<br>0.40 | 0.21 ** |
| Forelimb length | 61 | 127 | 34.95±2.21<br>30.3-41.5 | 33.97±1.65<br>30.2-38.3 | 0.214<br>74.66 | 0.239<br>66.96 | 0.34 *** |
| Hindlimb length | 57 | 128 | 61.87±3.89<br>53.0-75.0 | 57.26±3.03<br>49.4-64.9 | 0.359<br>143.87 | 0.356<br>142.75 | 0.09 n.s. |
| Fourth toe length | 63 | 129 | 27.05±2.46<br>22.0-34.5 | 24.32±1.53<br>20.0-29.9 | 0.120<br>83.74 | 0.128<br>76.09 | 0.14 n.s. |
| Tail length | 22 | 57 | 175.30±13.60<br>152.5-214.9 | 151.00±8.50<br>125.9-172.1 | 1.682<br>40.32 | 1.276<br>149.00 | 0.99 *** |
| Head index | 59 | 129 | 144.24±8.33<br>126.3-177.8 | 137.83±7.84<br>98.6-157.9 | 0.844<br>79.29 | 1.100<br>62.89 | 0.30 *** |

Meristic osteological characters. From the radiographs we counted vertebrae in the following regions of the vertebral column (which in part are nested and redundant): Cervical vertebrae without ribs*; cervical vertebrae with ribs*; cervical vertebrae, total; dorsal vertebrae with ribs attached to sternum* (directly or indirectly); dorsal vertebrae with floating ribs*; dorsal vertebrae without ribs*; dorsal vertebrae, total; sacral vertebrae*; precaudal vertebrae, total; pygal vertebrae; caudal vertebrae, total.

Qualitative characters. *Pholidosis*. Two qualitative pholidotic characters were each scored for 3 character states: Contact of the suborbital with the mouth (0, excluded from the mouth by supralabials on both sides; 0.5, reaching the mouth on one side; 1, reaching the mouth on both sides) and division of the first supraocular* (0, undivided on both sides, or nearly intact with a small granule medially; 0.5, divided on one side; 1, divided on both sides).

*Colouration.* We describe hues in Ostwald's terminology (STRELLER 1939) by comparing colour diapositives of living animals photographed with a scale of Ostwald colours, with the colour tables in the book; and patterns, in terms of the pholidosis.

*Hemipenis.* To examine the clavulae (ARNOLD 1983), we dissected the retracted hemipenes of eight males from Israel (HUJ-R 1289-90, 1293, 5061, 17161-62, 17167, 10892) and, to visualise ARNOLD's description based on many specimens, we also opened two males from Egypt (HUJ-R 18992, 18995).

## Systematics

In this project of taxonomy we adopt Ernst MAYR's views (MAYR et al. 1953, MAYR 1969, MAYR & ASHLOCK 1991) but consider also other and later opinions, reviewed by FROST & KLUGE (1994).

## Statistics

Univariate Statistics. We used two-tailed t-tests to compare the means of characters in the two populations. The coefficient of difference was calculated by the formula:

$$CD = (X_e - X_i)/(SD_e + SD_i)$$

where X is the mean of a character, SD its standard deviation, and E and I stand for the sample origins, Egypt and Israel. Because expressing body measurements as a percentage of total body length does not always neutralise allometry, we calculated for each sample the least squares linear regression for each body measurement as a function of ra, and for each individual its residual of the mean of the regressions for E and I (REIST 1986). In the case of the head index, we calculated the residual of head width as a function of head length. These residuals express the extent to which, for example, the head of an individual lizard is long, as compared to the mean length predicted for its size class.

Multivariate statistics. We applied discriminant analysis to separate the E and I subsamples at multivariate level. For this we used the 20 pholidotic characters, and asymmetries within them, because a preliminary study of the genus *Acanthodactylus* showed congruence between a phylogenetic hypothesis of the genus based on morphological characters (ARNOLD 1983) and a dendrogram derived from only the measure of asymmetry in four characters (SELIGMANN 1997).

Results of discriminant analyses are biased (WILLIAMS et al. 1997), mainly because the data used to generate the discriminant function are those on which the predictive accuracy of the function is tested. We overcame this difficulty by a method ("refined discriminant analysis"), to our knowledge, first reported here. (1) We compute the discriminant functions on n-1 observations (n = number of specimens with complete character sets). The discriminant function predicts the geographic origin of the specimens, E or I of the nth specimen. (2) The result of the classification for the excluded specimen is then compared to its real origin. (3) The procedure is repeated n times, each time excluding another specimen, until each specimen has a geographic origin predicted from a discriminant function computed without the data of that particular specimen. (4) This analysis was done separately for each sex.

We also compared among all individuals (of one sex) by calculated multivariate similarities for the 20 meristic scale characters, asymmetries included. All characters are range-standardised, according to the equation: $x_{is} = (x_i - X)/SD$, where xi is the value observed for an individual, xis the range-standardised value of character i, X the grand mean for that character (mean of means for E and I), and SD the standard deviation of the pooled samples from both localities.

Tab. 2. Mensural characters of the specimens of *Acanthodactylus pardalis* group from Egypt and Israel; females. Explanations as in Tab. 1.

| Character | N | | perca (mean±SD, range) | | regression (coefficient, intercept) | | Egypt versus Israel |
|---|---|---|---|---|---|---|---|
| | Egypt | Israel | Egypt | Israel | Egypt | Israel | CD, P |
| ra (mm) | 39 | 138 | 55.69±3.70<br>47.5–62.5 | 63.80±4.76<br>50.5–76.0 | – | – | -0.96 *** |
| Head length | 37 | 138 | 23.99±1.27<br>19.8–27.6 | 22.87±1.00<br>20.6–27.1 | 0.109<br>73.46 | 0.158<br>44.38 | 0.00 n.s. |
| Head width | 36 | 137 | 16.90±1.00<br>14.7–19.0 | 16.38±0.90<br>13.4–18.7 | 0.058<br>62.15 | 0.132<br>19.22 | 0.08 n.s. |
| Head depth | 36 | 138 | 12.99±1.14<br>10.7–15.2 | 12.69±0.79<br>10.6–14.9 | 0.016<br>38.44 | 0.100<br>15.70 | 0.20 * |
| Forelimb length | 36 | 134 | 34.16±3.71<br>29.6–52.3 | 32.14±2.03<br>26.3–39.6 | 0.165<br>95.05 | 0.149<br>109.99 | 0.24 ** |
| Hindlimb length | 36 | 137 | 58.07±5.21<br>46.4–77.1 | 52.10±3.80<br>32.2–65.3 | 0.246<br>182.54 | 0.179<br>217.43 | 0.14 n.s. |
| Fourth toe length | 38 | 138 | 25.32±2.81<br>20.3–36.8 | 22.56±1.71<br>19.1–29.1 | 0.064<br>103.56 | 0.068<br>100.43 | 0.04 n.s. |
| Tail length | 9 | 56 | 154.22±16.73<br>134.4–201.9 | 132.24±10.57<br>101.7–155.4 | 1.040<br>271.02 | 0.901<br>263.56 | 0.76 *** |
| Head index | 36 | 138 | 142.12±6.46<br>125.8–157.5 | 139.97±6.25<br>123.8–157.1 | 0.844<br>79.28 | 1.100<br>62.89 | 0.45 *** |

The multivariate similarity between every two individuals is estimated by least squares correlation coefficient. We calculate this mean similarity of each individual to all E individuals, and again to all I individuals. The difference between these two means (DS) defines the relative distance of the individual to the E morphological type in that group of characters.

## Field observations

During short field investigations in Egypt in June 1995 and 1996, the Mediterranean coast between Alexandria and El Salum (As Salum), and the area along the road Cairo-Alexandria, were inspected. The distribution of *Acanthodactylus pardalis* and conditions of its habitats were noted. With the same aim an excursion to the Negev, west and east of Beer Sheva (Negev, Israel), was carried out in June 1995. Earlier and later field observations of the co-authors were also taken into consideration.

Tab. 3. Meristic characters of the specimens of *Acanthodactylus pardalis* group from Egypt and Israel. P, significance of difference between Egypt (E) and Israel (I) (from two-tailed t-tests between means). Other explanations as in Tab. 1.

| Character | Sex | Egypt N | Egypt mean, SD | Egypt range | Israel N | Israel mean, SD | Israel range | E versus I CD, P |
|---|---|---|---|---|---|---|---|---|
| Supralabials | ♂ | 67 | 4.12±0.29 | 4–5 | 120 | 4.02±0.28 | 3–5 | 0.17 * |
| | ♀ | 39 | 4.06±0.30 | 3–5 | 107 | 4.11±0.33 | 3–5.5 | 0.06 n.s |
| Gulars | ♂ | 67 | 28.85±2.09 | 25–34 | 120 | 30.63±2.55 | 24–37 | 0.38 ** |
| | ♀ | 39 | 27.67±2.19 | 24–32 | 107 | 30.56±2.25 | 25–37 | 0.65 *** |
| Plates in collar | ♂ | 67 | 11.88±1.34 | 9–16 | 120 | 12.18±1.32 | 10–16 | 0.11 n.s. |
| | ♀ | 39 | 11.44±1.28 | 10–14 | 107 | 12.14±0.96 | 9–16 | 0.34 *** |
| Dorsals | ♂ | 65 | 60.29±4.04 | 52–71 | 120 | 64.03±3.80 | 56–76 | 0.48 *** |
| | ♀ | 38 | 58.58±3.79 | 50–65 | 107 | 62.01±3.58 | 53–72 | 0.47 *** |
| Ventrals across belly | ♂ | 66 | 11.83±0.71 | 10–14 | 120 | 12.47±0.81 | 10–14 | 0.42 ** |
| | ♀ | 39 | 12.03±0.62 | 10–14 | 107 | 12.42±0.82 | 10–14 | 0.27 * |
| Transverse rows of ventrals | ♂ | 66 | 30.55±1.35 | 28–34.5 | 119 | 33.06±1.41 | 29–37 | 0.91 *** |
| | ♀ | 39 | 32.40±1.51 | 29–35.5 | 107 | 35.46±1.43 | 32–39 | 1.04 *** |
| Femoral pores | ♂ | 66 | 21.64±1.45 | 19–25 | 119 | 20.29±1.59 | 16–24.5 | 0.45 *** |
| | ♀ | 38 | 18.87±1.62 | 15–24 | 107 | 17.05±1.39 | 14–22 | 0.61 *** |
| Scales betw. rows of femoral pores | ♂ | 65 | 0.66±0.81 | 0–4 | 120 | 1.12±0.77 | 0–3 | 0.29 ** |
| | ♀ | 38 | 1.58±0.96 | 0–4 | 106 | 3.29±1.05 | 2–7 | 0.85 *** |
| Preanals | ♂ | 66 | 7.38±1.14 | 5–10 | 120 | 7.52±0.83 | 6–10 | 0.07 n.s. |
| | ♀ | 38 | 5.55±0.71 | 5–8 | 106 | 5.27±0.78 | 4–8 | 0.19 n.s. |
| Subdigital lamellae | ♂ | 66 | 20.64±1.56 | 17.5–27 | 119 | 20.17±1.17 | 17–23 | 0.17 n.s. |
| | ♀ | 39 | 20.40±1.55 | 18–25 | 106 | 19.71±1.20 | 17–22.5 | 0.25 ** |
| Transver. rows of ventrals/fem. pores | ♂ | 65 | 1.42±0.11 | 1.22–1.71 | 118 | 1.64±0.13 | 1.31–2.09 | 0.87 *** |
| | ♀ | 38 | 1.73±0.17 | 1.42–2.13 | 107 | 2.09± 0.18 | 1.57–2.54 | 1.03 *** |
| Dorsals/femoral pores | ♂ | 64 | 2.80±0.25 | 2.31–3.58 | 119 | 3.17±0.25 | 2.5–4.13 | 0.73 *** |
| | ♀ | 37 | 3.12±0.25 | 2.67–3.73 | 107 | 3.66±0.32 | 2.91–4.73 | 0.94 *** |
| Scales betw. rows of fem. pores/fem. pores | ♂ | 66 | 0.03±0.04 | 0–0.19 | 119 | 0.06±0.04 | 0–0.16 | 0.32 *** |
| | ♀ | 38 | 0.08±0.05 | 0–0.23 | 107 | 0.19±0.06 | 0–0.42 | 0.94 *** |

# Results

## Comparing Egyptian and Israeli samples

### Mensural (including computed) characters

The most significant difference between the samples of the two populations (beyond the known difference in ra) was in tail length (both sexes) and forelimb length (especially in males). Tab. 1 (males) and 2 (females) present the statistical reductions of the mensural characters examined, in terms of percra, and compare between the means. Because percra are correlated with ra, the probability test is between the residuals of the regression of body measurements on ra.

### Meristic pholidotic (including computed) characters

Tab. 3 presents statistical reductions of the meristic pholidotic characters examined in the two samples, and compares them by two methods: (a) coefficient of difference, (b) t-test. Although most characters, especially the computed ratios between characters, differed significantly between the E and I samples, the CD was generally <1. The direction of almost all E-I differences in scale counts was in line with the larger body size in I. In femoral pores the trend was reversed and so all ratios involving this character showed particularly significant E-I differences.

Tab. 4 presents the percentages of males and females for which the "refined discriminant analyses" (explained above) correctly predicted the geographic origin. Note that 94.0% of the individuals are correctly classified.

Fig. 1 presents DS of each individual as a function of its ra (males). DS is the difference between the mean similarity to Egyptian specimens and the mean similarity to the Israeli specimens for meristic characters. Similarities are correlation coefficients calculated on the basis of 20 scutellation characters, including asymmetries: values close to 1 indicate high similarity to Egypt and low similarity to Israel; values close to -1, the contrary. Thus Figure 1 gives an overview of the extent of differentiation between these populations, with indication of the positions of specimens of particular interest.

### Osteological meristic characters

Tab. 5 (males) and 6 (females) present statistical reductions of the osteological characters examined in the two samples, and compare them by coefficients of differences and t-tests. Most characters were equal in the two samples. There was a tendency for the I-specimens to have a greater number of dorsal vertebrae, and fewer caudal vertebrae, than in E-specimens (both significant only in the females, perhaps due to sample size). The difference in the number of dorsal vertebrae parallels the difference in body size. The difference in tail vertebrae parallels the difference in relative tail length but is not a matter of course: a shorter tail could involve shorter, rather than fewer, vertebrae (WERNER 1961).

### Sexual dimorphism

Conspicuous differences between the two samples were few. Generally, there was a greater apparent sexual dimorphism in the I-sample. In both samples, sexual dimorphism occurred in most mensural characters; in some pholidotic characters but not the general body cover; and of the osteological characters, I-females (larger sample) tended to have one additional vertebra (a dorsal with free ribs). The data in Tab. 1–6 are separate by sex and Tab. 7 summarises the extent of sexual dimorphism in mensural and meristic (pholidotic and osteological) characters, separately for the E and I samples. The differences between males and females within each sample are expressed in both CD and t-test results. Besides statistics, there was also distinct sexual dichromatism in the Egyptian *A. pardalis* (see below).

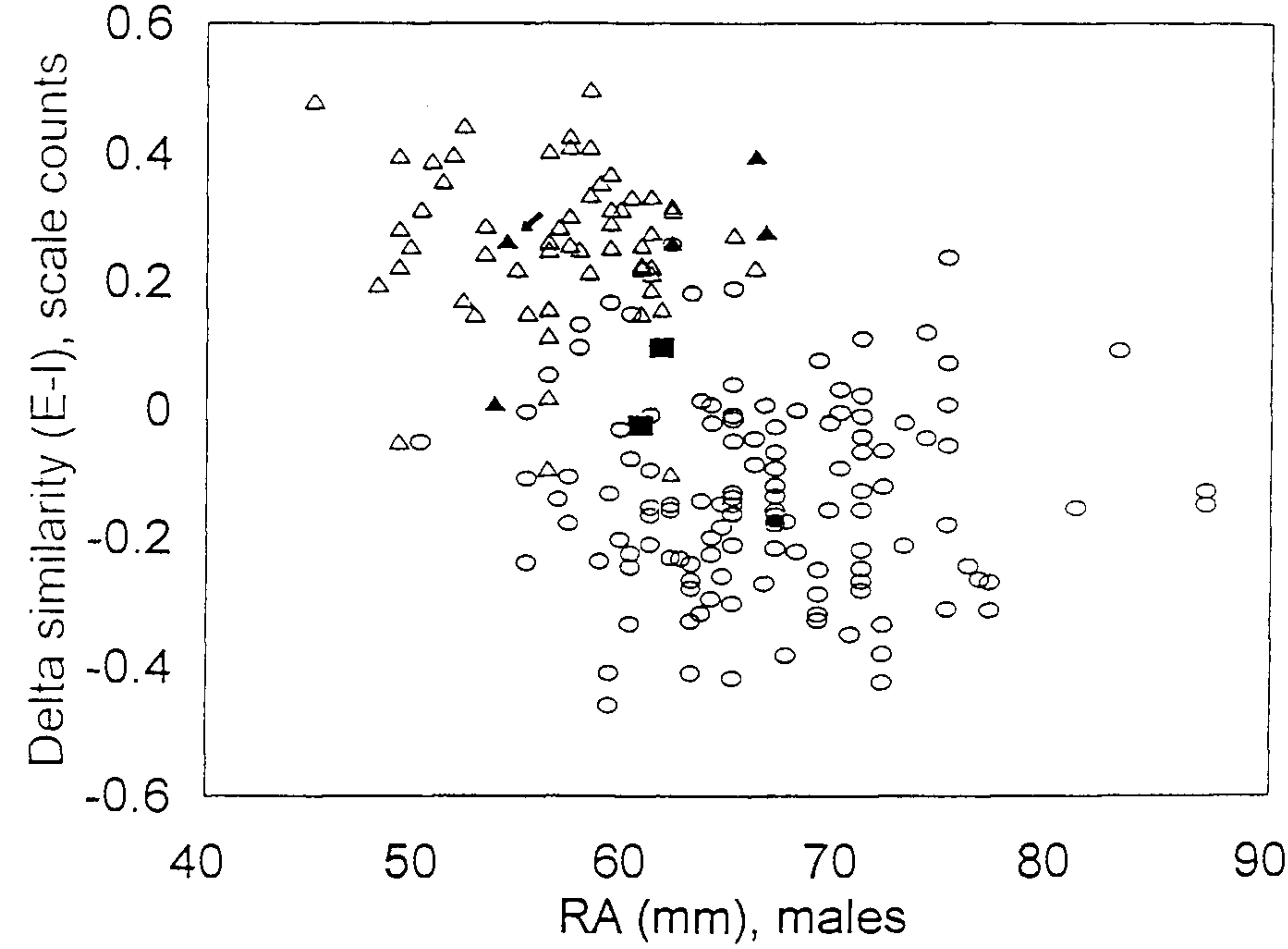


Fig. 1. Multivariate comparison of *Acanthodactylus pardalis* group (males) from Egypt and Israel, showing the position of type specimens. Abscissa, ra size, mm. Ordinate, difference, for each specimen, between its overall similarity to the Egyptian sample, and its overall similarity to the Israeli sample, for scutellation characters (values close to 1 indicate high similarity to the Egyptian sample and low similarity to Israeli sample). Triangles, specimens from Egypt (or Cyrenaica); solid triangles, males of the Lichtenstein 1823 type series (ZMB), the lectotype indicated by arrow. Ellipses, specimens from Israel; solid ellipse, type of *A. beershebensis* n.sp (HUJ-R). Solid squares, syntypes of *Lacerta deserti* Milne-Edwards (MNHN).

## Qualitative characters

Pholidosis: Tab. 8 presents for each of two qualitative pholidotic characters, separately for males and females, a comparison between the E and I samples of the frequency distributions (in %) of the character states. The significance, $p<0.05$ for all four sample pairs, is from chi-square tests.

Colouration (in life): In both samples the dorsal pattern was similarly complex with longitudinal series of whitish specks. In the Egyptian *A. pardalis* sexual dichromatism was distinct. The throat of adult males was bright yellow to bronze; sides of the belly were yellow. Females were uniformly whitish ventrally. In both sexes of the Israeli form the ventral side was whitish.

Hemipenes. Each hemipenis of *Acanthodactylus* is supported by a fibrous armature including a small (or absent) median clavula and a larger lateral clavula presenting variation which is systematically useful (ARNOLD 1983). In Egyptian *A. pardalis* the lateral clavula has two

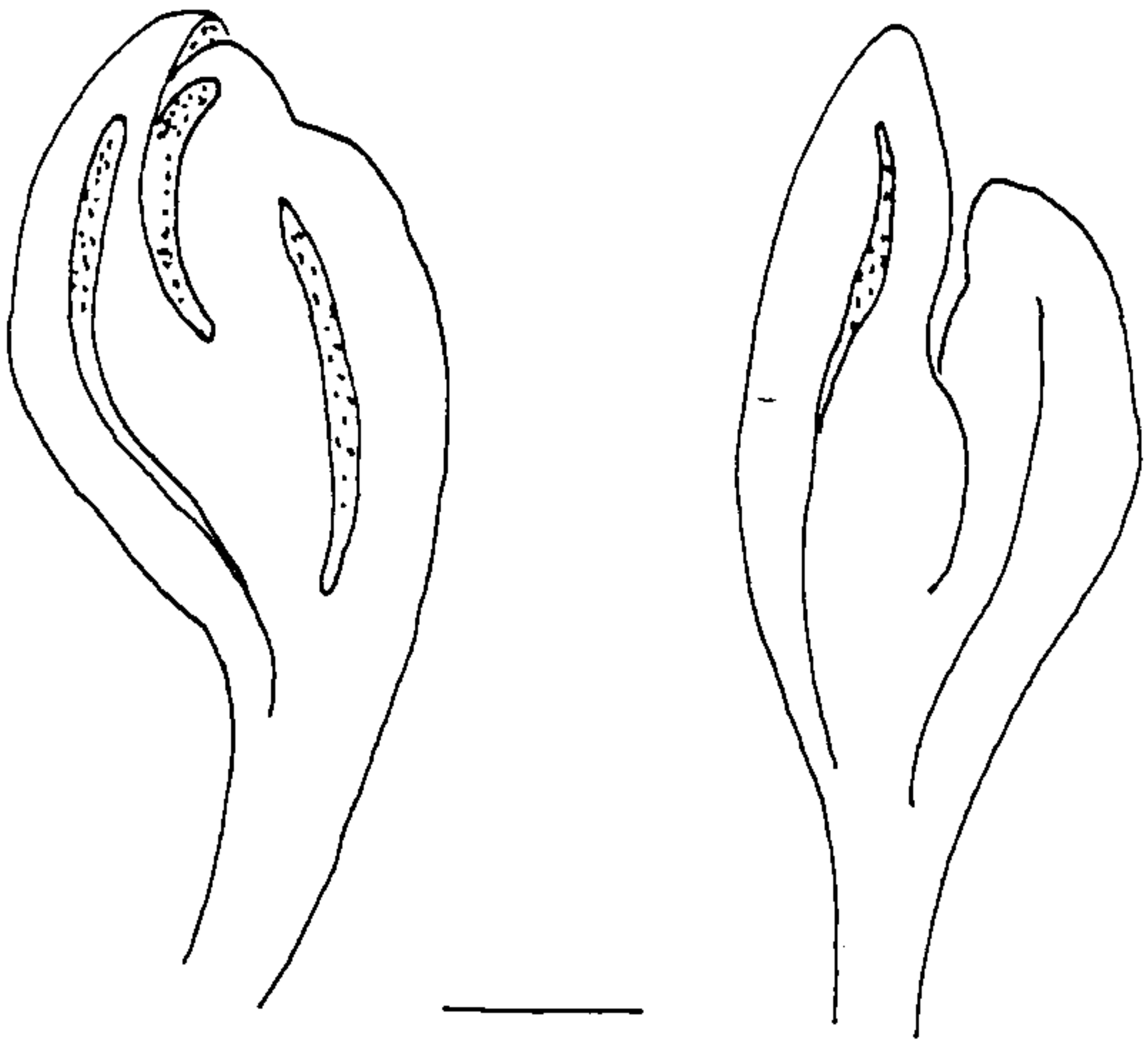


Fig. 2. Comparison of hemipenis armature: Lateral clavula of right hemipenis (ventral view in retracted organ) of: A, *Acanthodactylus pardalis* HUJ-R 18995; B, *A. beershebensis* sp.n. HUJ-R 10892. (Scale bar, 1 mm.).

subequal branches, each with a longitudinal groove or fold (ARNOLD 1983: fig. 6j; Fig. 2). In one of our specimens this is the case, in the other one branch slightly tops the other (by <20%). In Israel the lateral branch is always longer than the median branch by at least 30%, up to 100% in HUJ-R 17162 (Fig. 2).

Conclusions

As further explained and justified in the discussion, from the quantitative and qualitative differences and from the geographical situation, we conclude that the Egyptian and Israeli populations hitherto included in *A. pardalis* are separate taxonomic entities. The difference in hemipenial armature, without overlap between the specific ranges of variation, points to separation at the species level. This calls for verification of applicable names through the examination of type material.

## Comparing type material

Examined externally, the seven syntypes of *Lacerta pardalis* Lichtenstein, 1823 (in ZMB) (Fig. 3), reputedly from Egypt, are fully compatible with our other material from Egypt. When submitted to discriminant analysis, it so happened that one of them (ZMB 1075) was among those few E-specimens classified "wrongly" with the I-specimens. This obviously has no special effect on our considerations. Fig. 1, based on the "multivariate similarity method", places three of the male syntypes among the E-specimens but two in the overlap zone with the I-specimens.

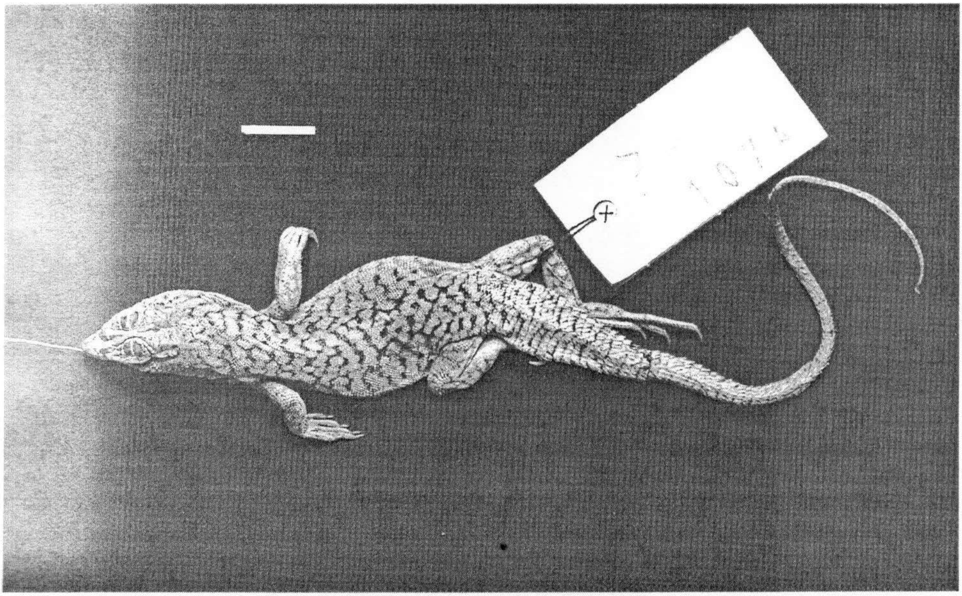

Fig. 3. Photograph (dorsal) of a male paralectotype *Acanthodactylus pardalis* (Lichtenstein, 1823); ZMB 1074 (scale bar, 1 cm.).

We also examined the two syntypes of *Lacerta deserti* Milne-Edwards, 1829 (in MNHN) (Fig. 4). These specimens are problematical in three ways: (a) The locality is given as "Perse et de l'Asie Mineure", areas which seem to be outside the known range of *Acanthodactylus pardalis*. (b) There exist important differences between MILNE-EDWARDS' description and the real characters of the given syntypes. The published body length is "77 and 86 mm" (versus 60.5 and 61.5 mm) and the number of femoral pores "18-22" (versus 19/20 and 24/24) (MILNE-EDWARDS 1829: 80, table p. 87). Our morphometric data agree with those recorded from these specimens by BOULENGER (1921: 73). (c) In our analyses, although both were sorted by the "refined discriminant analysis" into I, Fig. 1, based on the "multivariate similarity method", shows them as being intermediate between E and I.

## Nomenclature

We nevertheless considered whether the name *Lacerta deserti*, Milne-Edwards, 1829, was applicable to the Israeli "*A. pardalis*". The locality "Perse et de l'Asie Mineure" was interpreted by BOULENGER (1921), as "probably Syria" on p. 69 and as "Levant" on p. 73. But three considerations contradict the validity of this name for this population: (a) "Asia Minor" was only very exceptionally conceived as including Syria. Thus BANSE (1916) repented and rejected his earlier wider use of the term, and adopted the usual definition of the peninsula between the Black, Aegean and Mediterranean seas (Anatolia). (b) The lack of correspondence (detailed above) of the two MNHN syntypes with the original description. (c) The somewhat ambiguous sorting, by overall morphology, of the two specimens as E or I. Therefore, we consider it safer to regard the name *Lacerta deserti* Milne-Edwards, 1829 as a nomen dubium. So we name the new taxon after Beer Sheva, the capital of the Negev, because it is restricted to the loess soils surrounding this city, the type series originates from near the city, and the lizard is known in Hebrew as the Beer Sheva fringe-toed lizard.

Tab. 4. Results of classification by discriminant analysis, using 20 scutellation characters. Sample sizes in parentheses.

| Geographic origin | % correctly classified by discriminant function | | |
|---|---|---|---|
| | males | females | total |
| Egypt | 92.45 (53) | 93.75 (32) | 92.94 (85) |
| Israel | 95.04 (110) | 93.85 (101) | 94.97 (211) |
| total | 94.16 (163) | 93.83 (133) | 94.03 (296) |

## *Acanthodactylus pardalis* (Lichtenstein, 1823) – redescribed

### Material

Lectotype: ZMB 1077, male. Type locality "Egypt".
Paralectotypes (6): ZMB 1072–76, 55905.
Other material (n = 108): listed in Appendix 1 as examined from specified localities in Egypt and Libya.

### Differential diagnosis

An *Acanthodactylus* with three series of scales around the fingers and toes, which are not pectinate; usually three (otherwise four) complete supraoculars; subocular very rarely bordering the mouth; dorsal scales small, 50–70 across midbody; ventral plates in 10–14, mode 12, straight longitudinal series; lateral clavula of hemipenis has two branches, branches equal or subequal, lateral branch at most 120% the length of median branch; 24–26 presacral vertebrae (in both sexes).

### Description of the lectotype

Somewhat shrunken specimen. Male; moderate lacertid proportions, neck almost as wide as shoulders, narrower than head; tail base swollen for a stretch equalling head length, wider than inter-femoral distance.

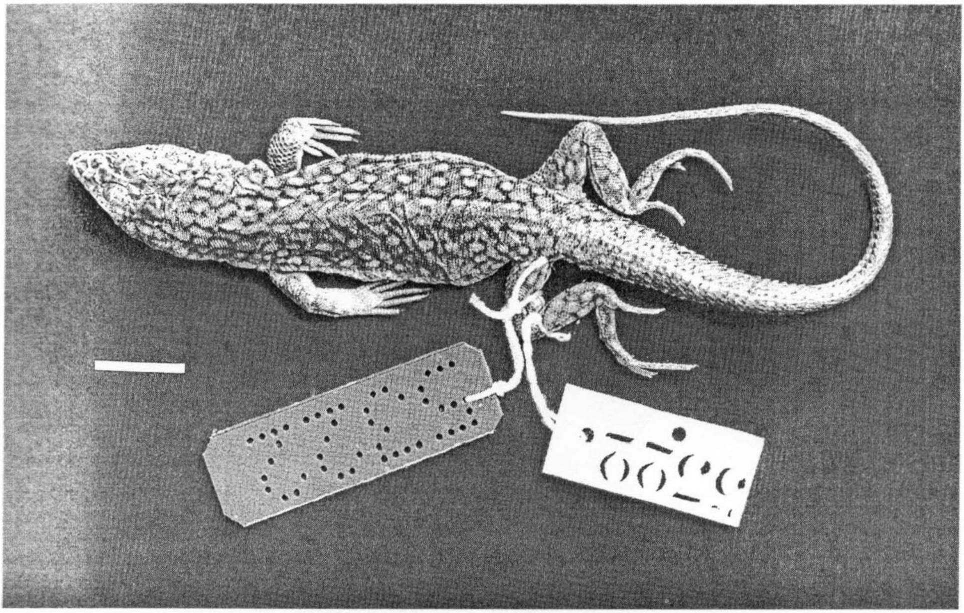

Fig. 4. Photograph (dorsal) of one of the syntypes of *Lacerta deserti* Milne-Edwards, 1829; MNHN 5322. (scale bar, 1 cm.)

Measurements: ra = 54 mm; head length = 15.2 mm (28.1 percra); head width = 9.6 mm (17.8 percra); head depth = 7.6 mm (14.1 percra); head index = 158.3; forelimb length = 19.5 mm (36.1 percra); hindlimb length = 35 mm (64.8 percra); fourth toe length = 14.9 mm (27.6 percra); tail length (incomplete) = 67 mm.

Pholidosis: key head shields symmetrical: second and third supraoculars entire; the first subdivided into a smaller median and a three-times-as-large lateral portion; the fourth fragmented into fragments of varying size, the largest (posterior) about a third of the total; supralabials anterior to the centre of eye, 5 (the 5th small); subocular narrowly excluded from lip by fifth and sixth supralabials; gulars, 31; plates in collar, 13. Dorsals across midbody, 61; ventrals across belly, 14; transverse rows of ventrals, 31; scales separating the two series of femoral pores,1; preanals in straight median series, 8; subdigital lamellae, R, 21; femoral pores, R, 23 & L, 23.

Colouration (in alcohol): head grey, speckled darker, laterally with distinct vertical blackish bar through the eye. Dorsal ground colour grey. Four pairs of longitudinal series of light grey specks, about thirteen specks from shoulder to pelvis, each covering approx. 15-20 granules; the specks are partly framed blackish, i.e., the blackish interspaces form a reticulum of partial longitudinal, transverse or oblique connections, occasionally leaving the light specks interconnected. Limbs with similar oval light specks; tail base mottled blackish-and-light grey in longitudinal semi-stripe pattern. Ventral parts (including tail) light grey.

Tab. 5. Osteological characters of the specimens of *Acanthodactylus pardalis* group from Egypt and Israel: males. L, left side; R, right side. Other explanations as in Tab. 3.

| Character | Egypt N, mean±SD, range | | Israel N, mean±SD, range | | E versus I (CD, P) |
|---|---|---|---|---|---|
| Cervical vertebrae without ribs, R | 8 | 3±0 (3–3) | 27 | 2.96±0.19 (2–3) | 0.21 (n.s.) |
| Cervical vertebrae without ribs, L | 9 | 3±0 (3–3) | 21 | 2.95±0.21 (2–3) | 0.24 (n.s.) |
| Cervical vertebrae with ribs, R | 7 | 5±0 (5–5) | 27 | 5.04±0.19 (5–6) | 0.21 (n.s.) |
| Cervical vertebrae with ribs, L | 9 | 5±0 (5–5) | 22 | 5.18±0.65 (5–8) | 0.28 (n.s.) |
| Cervical vertebrae, total | 9 | 8±0 (8–8) | 29 | 8±0 (8–8) | 0.00 (n.s.) |
| Dorsal vertebrae with ribs attached to sternum, R | 7 | 4±0 (4–4) | 27 | 4.26±0.44 (4–5) | 0.59 (n.s.) |
| Dorsal vertebrae with ribs attached to sternum, L | 9 | 3.89±0.31 (3–4) | 21 | 4.19±0.39 (4–5) | 0.43 (n.s.) |
| Dorsal vertebrae with floating ribs, R | 7 | 11.29±0.70 (11–13) | 26 | 11.46±0.63 (10–13) | 0.13 (n.s.) |
| Dorsal vertebrae with floating ribs, L | 8 | 11.25±0.43 (11–12) | 24 | 11.42±0.49 (11–12) | 0.18 (n.s.) |
| Dorsal vertebrae without ribs, R | 7 | 1±0 (1–1) | 28 | 0.93±0.26 (0–1) | 0.27 (n.s.) |
| Dorsal vertebrae without ribs, L | 9 | 0.89±0.31 (0–1) | 24 | 0.92±0.28 (0–1) | 0.05 (n.s.) |
| Dorsal vertebrae, total | 9 | 16.22±0.63 (16–18) | 30 | 16.63±0.55 (16–18) | 0.35 (n.s.) |
| Sacral vertebrae, R | 8 | 2±0 (2–2) | 35 | 2±0 (2–2) | 0.00 (n.s.) |
| Sacral vertebrae, L | 9 | 2±0 (2–2) | 33 | 2±0 (2–2) | 0.00 (n.s.) |
| Precaudal vertebrae, total | 9 | 26.22±0.63 (26–28) | 32 | 26.56±0.55 (26–28) | 0.29 (n.s.) |
| Pygal vertebrae | 9 | 7.33±0.67 (6–8) | 31 | 7.42±0.66 (6–9) | 0.07 (n.s.) |
| Caudal vertebrae, total | 2 | 50±5 (45–55) | 13 | 47.62±4.75 (38–54) | 0.24 (n.s.) |

## Variation

The variation of mensural and meristic (pholidotic and osteological) characters is shown in Tab. 1-3 and 5–6; the extent of sexual dimorphism of these characters is shown in Tab. 7; and variation in two qualitative pholidotic characters is shown in Tab. 8. The colouration, in

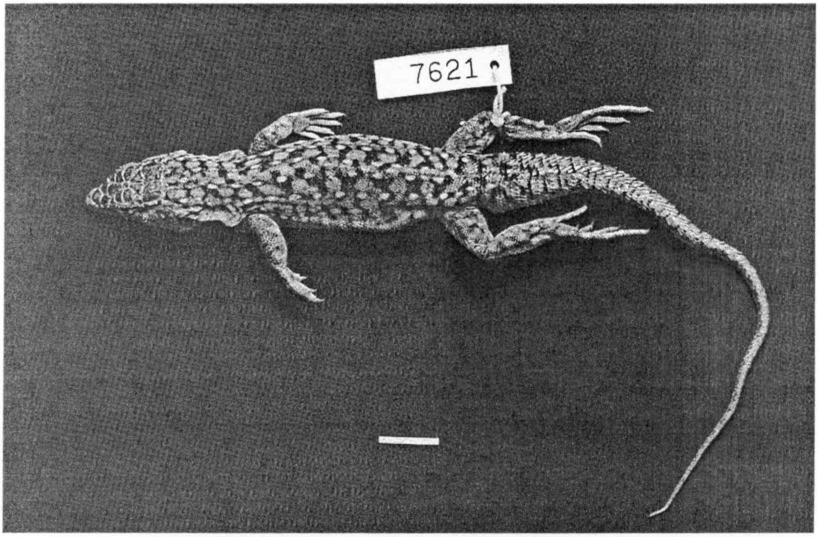


Fig. 5. Photograph (dorsal) of the male holotype of *Acanthodactylus beershebensis* sp.n.; HUJ-R 7621. (scale bar, 1 cm).

our live series, comprised three series of yellowish (to bright yellow in males during the breeding season) spots on each side of dorsum, longitudinally and transversally bridged black, on a reddish-brown (Ostwald 5gc) background; alive, females appeared less bright and less contrasting than males. Moreover, males differed in bright yellow or bronze throat and yellow sides of belly (up to 3rd-4th row of ventrals).

According to ANDERSON (1898:152) the "general colour, in the adult, olive-green, fawn, or even almost orange-red. Very variable in the degree to which the markings are developed." (He does not comment on sexual dichromatism, though his painting shows the female paler). Hence the reddish colouration in our sample may be local. ANDERSON describes the juvenile as "lineated ... with six white and seven black bands"; our one juvenile (27 mm ra, HUJ-R 18999) accorded with this, except that some of the white bands were broken, the mid-dorsal dark band was partly split by a whitish broken line, and the tail was bluish.

Verification of body size: One pair of adults caught by MORAVEC and BAHA EL DIN in June 1995 in Egypt was kept alive in the vivarium facility of the Hebrew University described elsewhere (WERNER et al. 1993). The male died on 14.1.1996 at 59 mm ra, the female on 11.2.1997 at 60 mm ra (HUJ-R 19159, 19169).

## Distribution

Restricted to northern Egypt west of the Nile and north-eastern Libya. ANDERSON (1896, 1898) and BOULENGER (1921) only reported on specimens from Maryut [Lake Mareotis] near Alexandria and from Alexandria. FLOWER (1933) stated that the species was known only from the neighbourhood of Alexandria and Maryut extending as far west as Daba [El

Daba]. SCORTECCI (1935) reported a specimen from Agedabia [road junction in Cyrenaica, near E coast of Gulf of Sirte]. MARX (1968) and SALVADOR (1982) listed specimens mostly from the coastal desert between Salum and Alexandria and from the general vicinity of Wadi Natroun [Wadi el Natrun], Giza and Fayoum [El Faiyum], but erroneously reported the species from localities in south Sinai and from the hinterland of the Sahara Desert west of the Nile (see also "Distribution" under the next species).

Tab. 6. Osteological characters of the specimens of *Acanthodactylus pardalis* group from Egypt and Israel: females. Explanations as in Tab. 3.

| Character | Egypt N | Egypt mean±SD, range | Israel N | Israel mean±SD, range | E versus I (CD, P) |
|---|---|---|---|---|---|
| Cervical vertebrae without ribs, R | 16 | 2.94±0.24<br>2–3 | 71 | 2.93±0.26<br>2–3 | 0.02 n.s. |
| Cervical vertebrae without ribs, L | 18 | 2.94±0.23<br>2–3 | 69 | 2.86±0.35<br>2–3 | 0.14 n.s. |
| Cervical vertebrae with ribs, R | 16 | 5.13±0.33<br>5–6 | 68 | 5.07±0.26<br>5–6 | 0.10 n.s. |
| Cervical vertebrae with ribs, L | 15 | 5.07±0.25<br>5–6 | 69 | 5.19±0.49<br>5–8 | 0.16 n.s. |
| Cervical vertebrae, total | 17 | 8.06±0.24<br>8–9 | 83 | 8±0<br>8–8 | 0.25 * |
| Dorsal vertebrae with ribs attached to sternum, R | 16 | 4.25±0.43<br>4–5 | 71 | 4.22±0.42<br>4–5 | 0.04 n.s. |
| Dorsal vertebrae with ribs attached to sternum, L | 15 | 4.20±0.40<br>4–5 | 71 | 4.25±0.44<br>4–5 | 0.06 n.s. |
| Dorsal vertebrae with floating ribs, R | 16 | 11.81±0.63<br>11–13 | 73 | 12.15±0.63<br>11–14 | 0.28 n.s. |
| Dorsal vertebrae with floating ribs, L | 15 | 11.87±0.62<br>11–13 | 68 | 12.13±0.59<br>11–14 | 0.21 n.s. |
| Dorsal vertebrae without ribs, R | 17 | 0.76±0.42<br>0–1 | 76 | 0.89±0.35<br>0–2 | 0.17 n.s. |
| Dorsal vertebrae without ribs, L | 17 | 0.82±0.38<br>0–1 | 71 | 0.94±0.29<br>0–2 | 0.18 n.s. |
| Dorsal vertebrae, total | 17 | 16.88±0.47<br>16–18 | 82 | 17.32± 0.64<br>16–19 | 0.40 ** |
| Sacral vertebrae, R | 17 | 2±0<br>2–2 | 86 | 2±0<br>2–2 | 0.00 n.s. |
| Sacral vertebrae, L | 17 | 2±0<br>2–2 | 83 | 2±0<br>2–2 | 0.00 n.s. |
| Precaudal vertebrae, total | 17 | 26.94±0.54<br>26–28 | 87 | 27.31±0.65<br>26–29 | 0.31 * |
| Pygal vertebrae | 18 | 6.50±0.50<br>6–7 | 84 | 6.55±0.56<br>6–8 | 0.05 n.s. |
| Caudal vertebrae, total | 8 | 50.63±3.00<br>44–55 | 35 | 43.11±4.38<br>36–53 | 1.02 *** |

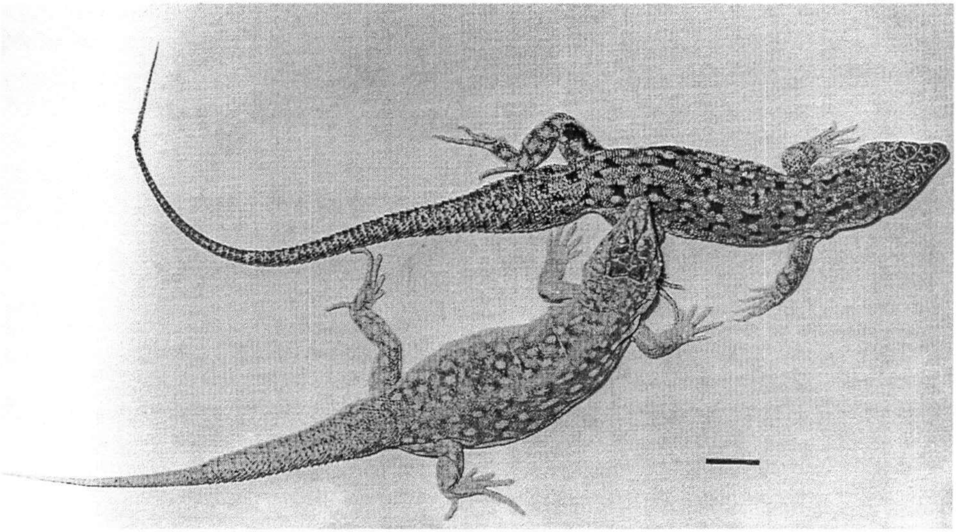

Fig. 6. Photograph (dorsal) of a live pair of *Acanthodactylus beershebensis* sp.n.; the upper, darker, animal is the male (Scale bar, 1 cm).

The re-examination of much material referred to *A. pardalis* from Egypt indicates that the species had a fairly restricted range along the Mediterranean coast from the Libyan borders to Alexandria, extending south along the western edge of the Nile delta & valley to the El Faiyum depression. All reports of the species outside this range are erroneous. The species has been often confused with *A. scutellatus*, *A. longipes* and *A. boskianus* in Egypt.

There is only one specimen of *A. pardalis* from east of the Nile; FMNH 78822, collected one mile south of Helwan in 1952 by H. HOOGSTRAAL. The specimen is rather peculiar in having only three upper labials anterior to the eye, two chin shields in contact and fused loreals. The possibility of a locality error should not be excluded: the region of reported origin has no suitable habitat for *A. pardalis*, and has been fairly intensively covered by many other workers, who found no evidence of the species.

In Libya *A. pardalis* is found in a narrow band across northern Cyrenaica from the Egyptian borders, as far west as Agedabia (SALVADOR 1982, ARNOLD 1983, SCHLEICH et al. 1996).

Recent extensive field observations in Egypt by S. BAHA EL DIN have revealed that *A. pardalis* has apparently disappeared from much of its previous range, largely due to habitat degradation and loss. The species is now mainly found in fragments of suitable habitats thinly scattered along the coast from El Alamein to Marsa Matruh. Only west of the last-named locality towards the Libyan borders are there reasonably healthy populations of the species.

*Acanthodactylus pardalis* is found in open semi-desert under Mediterranean influence, receiving 50–150 mm of rain annually, where it is confined exclusively to fairly hard substrates.

Tab. 7. Sexual dimorphism of mensural, meristic and osteological characters of the specimens of *Acanthodactylus pardalis* group from Egypt and Israel. For each area, the coefficient of difference between males and females, and the significance of two-tailed t-tests between male and female means are given.

| Character | Egypt | | Israel | |
|---|---|---|---|---|
| | CD | P | CD | P |
| ***Mensural*** | | | | |
| ra (mm) | 0.08 | n.s. | 0.23 | ** |
| Head length | 0.57 | *** | 1.00 | *** |
| Head width | 0.14 | n.s. | 0.86 | *** |
| Head depth | 0.19 | n.s. | 0.71 | *** |
| Forelimb length | 0.31 | ** | 0.76 | *** |
| Hindlimb length | 0.63 | *** | 1.14 | * |
| Fourth toe length | 0.54 | *** | 0.95 | *** |
| Tail length | 0.92 | *** | 1.04 | *** |
| Head index | 0.54 | *** | 0.39 | *** |
| ***Scale counts*** | | | | |
| Supralabials | 0.10 | n.s. | -0.15 | *** |
| Gulars | 0.28 | n.s. | 0.01 | n.s. |
| Plates in collar | 0.17 | n.s. | 0.02 | n.s. |
| Dorsals | 0.22 | n.s. | 0.27 | n.s. |
| Ventrals across belly | -0.15 | n.s. | 0.03 | n.s. |
| Transverse rows of ventrals | -0.65 | * | -0.85 | *** |
| Femoral pores | 0.90 | ** | 1.09 | *** |
| Scales between the rows of femoral pores | -0.52 | ** | -0.45 | n.s. |
| Preanals | 0.99 | *** | 1.40 | *** |
| Subdigital lamellae | 0.08 | n.s. | 0.19 | n.s. |
| Transverse rows of ventrals/femoral pores | -1.11 | *** | -1.45 | *** |
| Dorsals/femoral pores | -0.64 | *** | -0.86 | *** |
| Scales betw. rows of femoral pores/ femoral pores | -0.56 | *** | -1.30 | *** |
| ***Osteological*** | | | | |
| Cervical vertebrae without ribs, R | 0.26 | n.s. | 0.08 | n.s. |
| Cervical vertebrae without ribs, L | 0.24 | n.s. | 0.17 | n.s. |
| Cervical vertebrae with ribs, R | -0.38 | n.s. | -0.08 | n.s. |
| Cervical vertebrae with ribs, L | -0.27 | n.s. | -0.01 | n.s. |
| Cervical vertebrae, total | -0.25 | n.s. | 0.00 | n.s. |
| Dorsal vertebrae with ribs attached to sternum, R | -0.58 | n.s. | 0.04 | n.s. |
| Dorsal vertebrae with ribs attached to sternum, L | -0.44 | n.s. | -0.08 | n.s. |
| Dorsal vertebrae with floating ribs, R | -0.39 | n.s. | -0.54 | *** |
| Dorsal vertebrae with floating ribs, L | -0.59 | * | -0.66 | *** |
| Dorsal vertebrae without ribs, R | 0.55 | n.s. | 0.06 | n.s. |
| Dorsal vertebrae without ribs, L | 0.09 | n.s. | -0.05 | n.s. |
| Dorsal vertebrae, total | -0.60 | ** | -0.58 | *** |
| Sacral vertebrae, R | 0.00 | n.s. | 0.00 | n.s. |
| Sacral vertebrae, L | 0.00 | n.s. | 0.00 | n.s. |
| Precaudal vertebrae, total | -0.62 | ** | -0.62 | *** |
| Pygal vertebrae | 0.71 | * | 0.71 | *** |
| Caudal vertebrae, total | -0.08 | n.s. | 0.49 | ** |

## *Acanthodactylus beershebensis* sp. n.

### Material

Holotype: HUJ-R 7621 male (Fig. 5); 1 March 1963; Coll. Y. L. WERNER et al.
Type locality: Israel: Be'er Sheva' Subdistrict: 5 km E of 'Omer-Hebron–'Arad crossroads (Israel Grid 14350770) [i.e., around the Nahal Yattir crossing of the Zomet Shoqet – 'Arad road]
Paratypes (5): HUJ-R 7617, 7619, 7620; NMP6V 35698 (=HUJ-R 7622); MZUF 19954 (=HUJ-R 7618); all from the type locality. Other paratypes (n = 247) listed in Appendix 1 as examined from specified localities in Israel.

### Differential diagnosis

An *Acanthodactylus* with three series of scales around the fingers and toes, which are not pectinate; usually four (otherwise three) complete supraoculars; subocular bordering the mouth or not; dorsal scales small, 50-70 across midbody; ventral plates in 10-14, mode 12, straight longitudinal series; lateral clavula of hemipenis has two branches, lateral branch at least 130% the length of median branch; 24-26 presacral vertebrae in males, 24-27 in females.

### Description of the holotype

Male; moderately robust, neck as wide as shoulders, barely narrower than head; tail base swollen for a stretch equalling head length, wider than inter-femoral distance.

Measurements: ra, 67 mm; head length, 16.2 mm (24.2 percra); head width, 11.8 mm (17.6 percra); head depth, 9.0 mm (13.4 percra); head index, 137.3; forelimb length, 22 mm (32.8 percra); hindlimb length, 36 mm (53.7 percra); fourth toe length, 16.9 mm (25.2 percra); tail length (complete), 97 mm (144 percra).

Pholidosis: key head shields symmetrical: first, second and third supraoculars entire, the fourth fragmented; supralabials anterior to the centre of eye, 4; subocular narrowly excluded from lip by fourth and fifth supralabials; gulars, 32; plates in collar, 12. Dorsals across midbody, 65; ventrals across belly, 12; transverse rows of ventrals, 35; scales separating the two series of femoral pores,1; preanals in straight median series, 8; subdigital lamellae, R, 21 & L, 20; femoral pores, R, 23 & L, 22.

Colouration (in alcohol): head grey, speckled darker, laterally with distinct vertical white-framed blackish bar through the eye. Dorsal ground colour grey. Four pairs of longitudinal series of white specks, about ten specks from shoulder to pelvis, each covering approx. 10 granules; the two central pairs of speck-series conspicuous, the third series barely indicated, the fourth moderate. Specks are partly framed in black, this frame merging between successive specks; these longitudinal black designs are transversely connected, in black, sometimes at the level of white specks, sometimes between them. In this black-and white reticulum the remnants of the ground colour appear as grey, semi-ordered, oval spots. Limbs dotted whitish; tail base with a few black-and-white ocelli. Ventral parts (including tail to tip) unmarked whitish.

Tab. 8. Frequency distributions (%) of two qualitative characters in the specimens of *Acanthodactylus pardalis* group from Egypt and Israel: Contact of the subocular with the mouth (0, excluded from the mouth on both sides; 0.5, reaching the mouth on one side; 1, reaching the mouth on both sides) and division of the first supraocular (0, undivided on both sides; 0.5, divided on one side; 1, divided on both sides). For each character and in each sex, the frequency distribution differs between Egypt and Israel ($p<0.05$, Chi-square tests).

| Character state | Contact of subocular with mouth | | | | Division of the first supraocular | | | |
|---|---|---|---|---|---|---|---|---|
| | males | | females | | males | | females | |
| | Egypt | Israel | Egypt | Israel | Egypt | Israel | Egypt | Israel |
| 0 | 92.5 | 69.2 | 89.7 | 52.3 | 4.5 | 75.6 | 12.8 | 82.2 |
| 0.5 | 1.5 | 8.3 | 2.6 | 11.2 | 13.4 | 9.2 | 23.1 | 9.3 |
| 1 | 6.0 | 22.5 | 7.7 | 36.4 | 82.1 | 15.1 | 64.1 | 8.4 |
| N | 67 | 120 | 39 | 106 | 67 | 119 | 39 | 106 |

## Variation

The variation of mensural and meristic (pholidotic and osteological) characters is shown in Tables 1-3 and 5–6; the extent of sexual dimorphism of these characters is shown in Tab. 7; and variation in two qualitative pholidotic characters is shown in Tab. 8. In the hemipenis, the long branch of the lateral clavula is 130% the length of the shorter branch in 6 males, but 150% in the 7th and 200% in the 8th (HUJ-R 17162).

In the colouration, the stable component are the dorsal series of white spots, usually four on each side, but may be reduced to three or two. Laterally (ventro-lateral) of these may be one or two additional series of larger and dimmer light spots. The connecting, or framing, black markings may be arranged mainly longitudinally, mainly transversely, or as reticulation. The pattern is more contrasting in males than in females, alive or preserved (WERNER 1995: 57 and fig. 6; fig. 6). Only exceptionally are the white spots missing, with the black markings on a uniform grey back (e.g., female HUJ-R 6931). Juveniles (31–32 mm ra) are striped in high contrast: on each side four whitish lines (complete or broken), on brown-blackish background. The mid-dorsal dark space is partly split by a median white line of very variable extent. In the living adult male from Negev Junction (6.1.1997, H. SELIGMANN and B. SHACHAM), the ground colour was pinkish brown (Ostwald 3gc).

## Distribution

Endemic to the Negev of Israel (Fig. 7). Its restriction to loess and loessy soils would seem to confine it to an area approximating 2000 km² (ZOHARY 1947 - incomplete towards south; RAVIKOVITCH 1970 - incomplete towards north; ), and has thus been mapped by WAHRMAN (1970: map k). This population is separated from that in Egypt by the absence of suitable soil in Sinai. MARX (1968) recorded *A. pardalis* from Santa Katherina monastery in southern Sinai, and this was accepted by SALVADOR (1982) and SALEH (1997). Actually on re-examination the specimen turned out to be *A. boskianus* (WERNER 1982: 157). The only other record from Sinai is ZFMK 22768-78 "Aegypten: noerdl. Sinaihalbinsel, A. Koenig 5-6.4.1896, Nilreise Koenig 1896"; this record we do not consider acceptable: (1) It lacks a specific locality and so does not fulfil the requirement of scientific reporting: to enable verification by repetition. (2) According to the expedition's itinerary, which actually was in 1898 (KOENIG 1964: 33), these specimens seem to have been collected within the agricultural western Negev, today in Israel. (3) According to multivariate similarity analysis, 10 of the 11 specimens conform to the Negev population. The Negev population is also separated by soil discontinuity from the apparently very different Jordanian population (WERNER 1991), so far known from one specimen, HUJ-R 1296. The other, listed by SALVADOR (1982) and WERNER (1991), LACM 74540, originated not from Ara'ir in Jordan but from Ara'ir = Be'erot Aro'er in Israel.

Ecological comments

*A. beershebensis* lives in steppe with loess soil; the physics and chemistry of this soil were described by REIFENBERG (1939). In the lizard's range the mean annual temperatures are 19–21°C and August temperatures 26–28°C; annual rainfall ranges 0–150 mm in a dry year but 150–400 mm in a wet year (AMIRAN et al. 1970). The vegetation of the area has been variously described by ZOHARY (1962, 1982) as of the Irano-Turanian Territory and by DANIN & PLITMANN (1987) as mixed Saharo-Arabian & Irano-Turanian with some Mediterranean and other chorotypes. Where the natural vegetation survived, the dominant shrub is *Artemisia herba-alba*.

In museum material, 23 females, 59–74 mm ra (mean = 66 mm) carried 3–7 shelled eggs (mean = 4.8) during March–July (FRANKENBERG & WERNER 1992).

*A. beershebensis* typically inhabits loess plains with sparse shrub coverage, taking refuge in small shrubs, soil cracks or under stones. *A. beershebensis* seems to be strongly territorial, because aggressive chasing was observed in the three cases of encounters between 2 animals. Many individuals are taken by the Great Grey Shrike, *Lantus excubitor*, and impaled on thorns of scattered *Acacia* trees (WERNER, unpublished).

Most of this endemic taxon's habitat, including the type locality, is now occupied by agriculture employing deep motorised ploughs; in some places housing projects cover former choice habitats. In June 1995 we could observe none, and during several later field trips we found single individuals. CROCHET (1997) observed only one individual despite active search in an extensive loess area. Only little of the former range is included in nature reserves; the occurrence of the lizard there requires verification.

# Discussion

## Systematics

Taxonomically, the first question is whether to recognise two populations as distinct taxa. MAYR et al. (1953) regarded subspecies as geographically defined subunits of species, not fully reproductively isolated from adjacent subspecies. MAYR & ASHLOCK (1991) expanded the discussion to cover various problems, opinions and precedents. They advised that if the samples clearly differ in one respect or several, or if there are pronounced steps in a cline (and depending on additional obvious conditions), then widespread species should be split

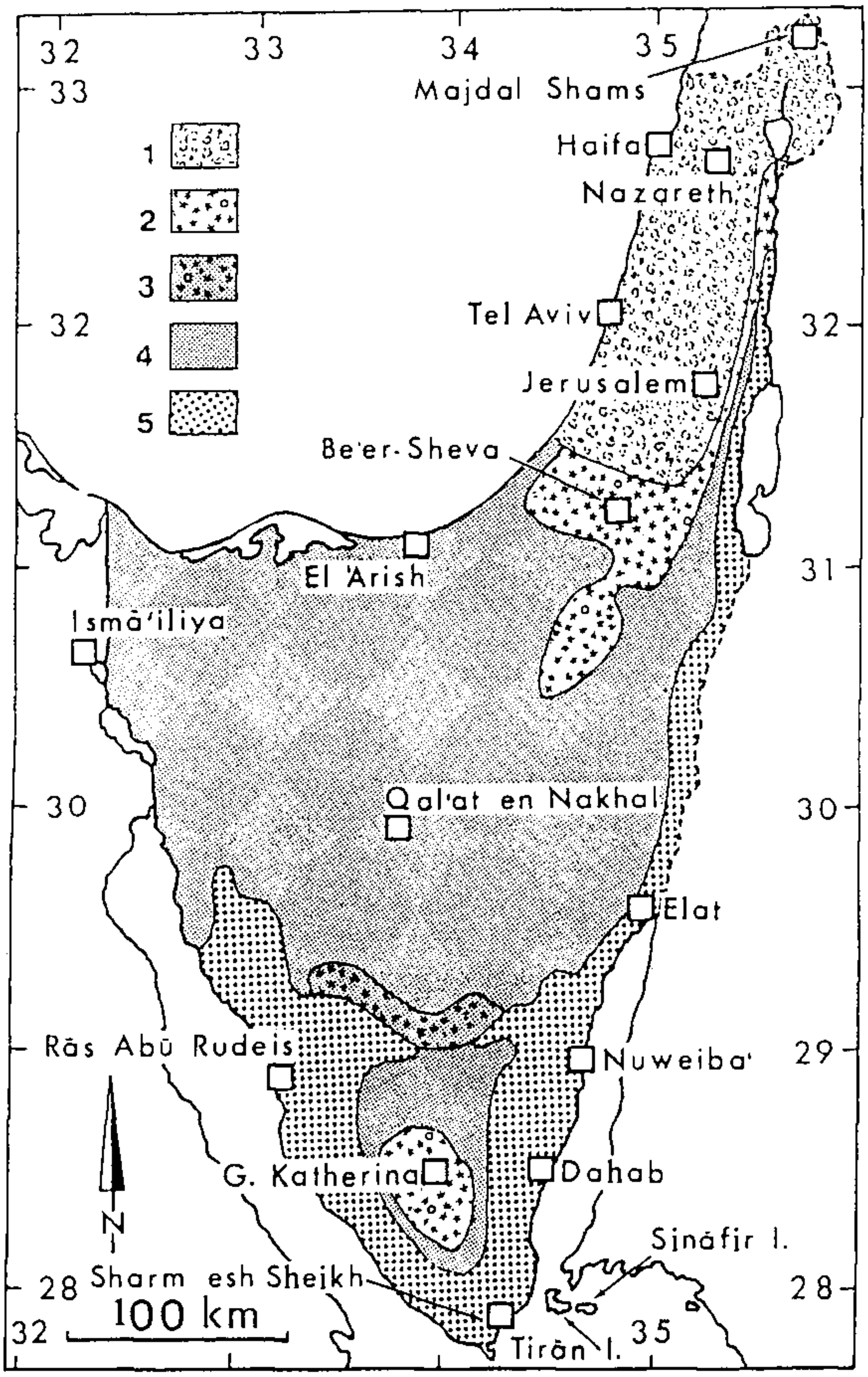


Fig. 7a. The survey area of Israel and Sinai after WERNER (1988), with localities for orientation. Biogeographical regions are indicated by shading: 1, Mediterranean; 2, Irano-Turanian; 3, Irano-Turanian - Saharo-Arabian transition; 4, Saharo-Arabian; 5, Sudanian penetration zone.

into subspecies. They commented (p. 97) that "subspecies that are isolates are incipient species" and concluded (p. 105) that "it is preferable to treat allopatric populations of doubtful rank as subspecies."

On the technical level, MAYR et al. (1953: 146) proposed, with reservations, the 1.28 value of the coefficient of difference as a threshold for recognizing subspecies. But MAYR & ASHLOCK (1991: 98) say, "in the decision whether to recognize subspecies, so many additional considerations enter the picture, that extreme accuracy in the determination of the amount of overlap ... is not important. Other kinds of information, such as degree of isolation ... may be more important..."

Thus apparently despite the partial overlap between the quantitative characters of the samples (usually CD<1), in view of the geographical separation, some taxonomic distinction is

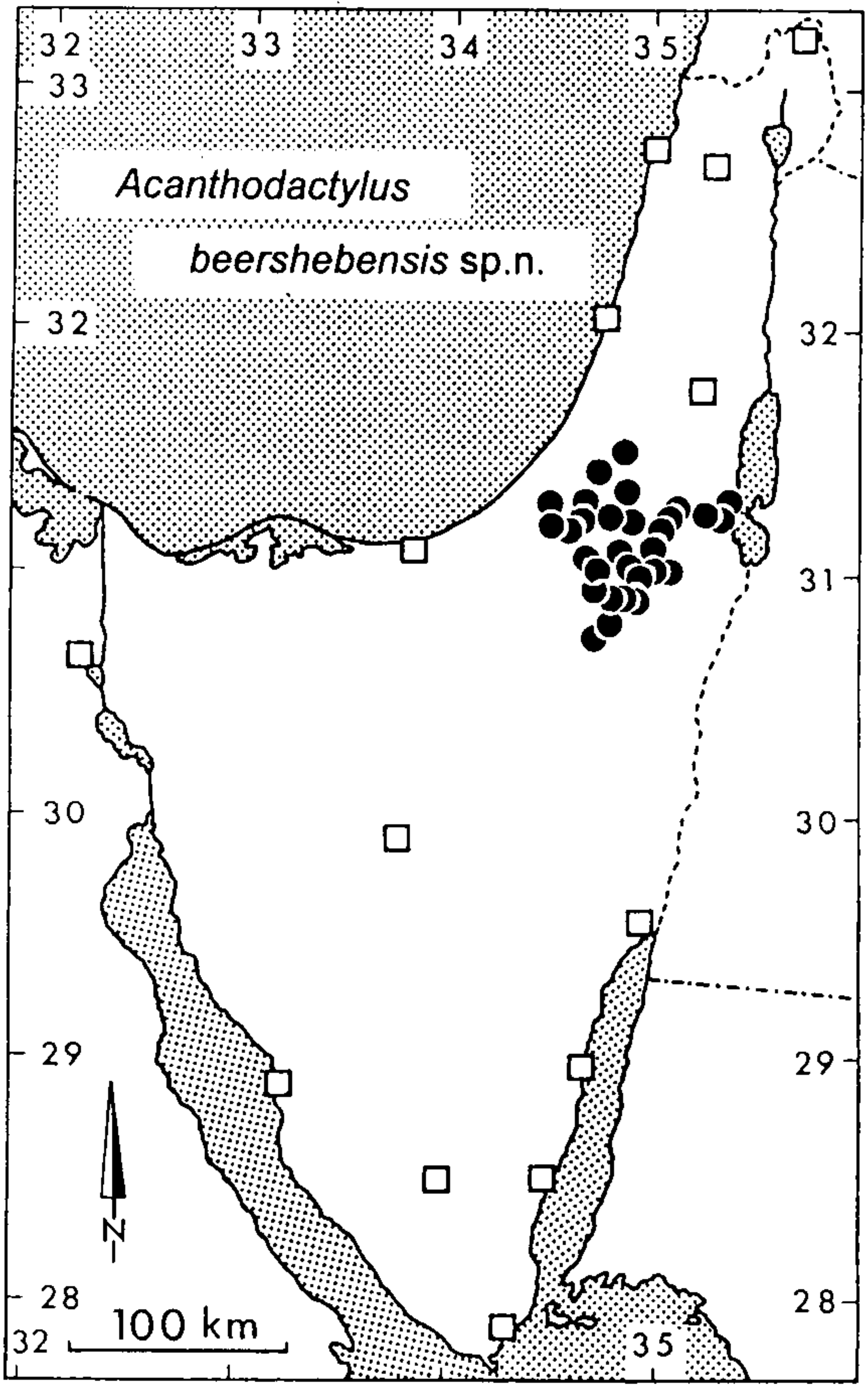


Fig. 7b. World distribution range of *Acanthodactylus beershebensis* sp.n.: Locality records in the survey area of Israel and Sinai (WERNER 1988). Each solid circle represents a locality from which at least one specimen is in HUJ-R, TAU-R or both. Hollow squares are towns for orientation (see Fig.7a); Be'er Sheva' is in the middle of the range.

justified. So the second question is, what level of distinction? According to the "biological species concept" in the literature cited, if reproductive isolation is indicated, the species level is appropriate. Further, in the absence of direct indication to this effect, one should be guided by the magnitude of differences among established related species. In our case mainly the difference in hemipenial armature tips the scales in favour of the species level; not so much as a hinderance to cross-mating (which is unknown) but as morphological non-overlap.

Moreover, as we view species primarily as distinct populations that merit conservation, the "phylogenetic species concept" is also of interest. FROST & KLUGE (1994) have discussed the contribution of species descriptions to the study of evolution, and pointed out that the modern phylogenetic species concept promotes the recognition of new species. The phylogenetic species concept tends to recognize species where previously one would only have recognized subspecies, when the populations are sufficiently separate to raise an expectation of future separate evolution.

## Eco-morphological differences

The best known difference between *A. beershebensis* sp.n. and *A. pardalis*, is the greater body size in samples of the former (ANDERSON 1898, BOULENGER 1921, FLOWER 1933). But the quantification of body size is problematic (FITCH 1981). Moreover, for demographic reasons, modal adult body size in the field may underrepresent the population's characteristic maximum size (ADOLPH & PORTER 1993). The individuals of *A. pardalis* which in captivity failed to exceed the size sampled in nature (after 20 months the adult female remained at 60 mm ra) tend to support the notion, that the maximum size of *A. pardalis* resembles the minimum reproductive size of *A. beershebensis*.

Tail length also differs conspicuously, the tail being relatively shorter in *A. beershebensis* than in *A. pardalis*. Because among lacertids tail length is correlated to foraging mode and related life history syndromes (HUEY & PIANKA 1981, PERRY et al. 1990), this difference predicts biological differences. A comparative study of the biology of the two species would be of particular interest, in view of their close relationship, as evidenced above.

Another difference potentially of biological relevance is in sexual dichromatism. Our observations do not support the statement of SCHLEICH et al. (1996: 389), "Sexual dimorphism: Males with an irregular reticulated pattern ... females with two light dorsal bands" – we saw no such dimorphism in either Egypt or Israel. But whereas in Israeli material we observed distinct dichromatism only in the dorsal colouration (more contrasting in males), in Egypt the males differed markedly also in the colouration of the throat and belly sides.

## Conservation

In Egypt, land reclamation for agriculture and urban expansion has almost completely destroyed the habitats of *Acanthodactylus pardalis* in the vicinity of Alexandria, and south towards Wadi el Natrun, Giza and El Faiyum. Coastal tourist development, overgrazing and large-scale ploughing for growing winter cereals are rapidly devouring valuable habitats between Alexandria and Salum (BAHA EL DIN, unpubl., KASPAREK 1993). The threatened *Testudo kleinmanni*, which in Egypt largely shares the habitat of *A. pardalis*, also suffers from the same plight (BAHA EL DIN, unpublished). Similarly in Israel much of the original area of *A. beershebensis* is now in agricultural use or built up, as described above (MORAVEC, SELIGMANN AND WERNER, unpublished).

So far, conservation authorities in Libya, Egypt and Israel could only assign low priority to the protection of "*A. pardalis*", which appeared to have a reasonably wide range of distribution. The discovery that there are two different species, one restricted to a small area in Libya and Egypt, the other endemic to an even smaller area in Israel, should stimulate greater responsibility in all three states.

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## References

ADOLPH, S. C. & W. P. PORTER (1993): Temperature, activity, and life histories. – American Naturalist 142: 273–295, Salem/Chicago.

AMIRAN, D. H. K., J. ELSNER, M. GILEAD, N. KADMON, U. PARAN & N. ROSENAN (1970): Atlas of Israel. 2nd ed. – Survey of Israel, Jerusalem & Amsterdam.

ANDERSON, J. (1896): A contribution to the herpetology of Arabia. With a preliminary list of the reptiles and batrachians of Egypt. – London, 122 pp.

ANDERSON, J. (1898): Zoology of Egypt: Reptilia and Batrachia. – London, 371 + 44 pp.

ARNOLD, E. N. (1983): Osteology, genitalia and the relationship of *Acanthodactylus* (Reptilia: Lacertidae). – Bulletin of the British Museum (Natural History), Zoology Series, 44: 191–339, London.

BANSE, E. (1916): Die Türkei: eine moderne Geographie. – Berlin, 452 pp.

BOULENGER, G. A. (1887): Catalogue of the Lizards in the British Museum (Natural History). 2nd ed. vol. 3. – London, 575 + 40 pp.

BOULENGER, G. A. (1918): Sur les lézards du genre *Acanthodactylus* Wiegm. – Bulletin de la Societe zoologique de France 43: 143–155, Paris.

BOULENGER, G. A. (1921): Monograph of the Lacertidae, Vol. 2. – London, 451 + 8 pp.

CROCHET; P. A. (1997): Herpetological observations in southern Israel. – British Herpetological Society Bulletin 60: 13–24, London.

DANIN, A. & U. PLITMANN (1987): Revision of the plant geographical territories of Israel and Sinai. – Plant Systematics and Evolution 156: 43–53, Vienna.

FITCH, H. S. (1981): Sexual size differences in reptiles. – University of Kansas Museum of Natural History, Miscellaneous Publication 70: 1–72, Lawrence (Kansas).

FLOWER, S. S. (1933): Notes on the recent reptiles and amphibians of Egypt, with a list of the species recorded from that kingdom. – Proceedings of the zoological Society of London 1933: 735–851, London.

FRANKENBERG, E. & Y. L. WERNER (1992): Egg, clutch and maternal sizes in lizards: intra- and interspecific relations in Near-Eastern Agamidae and Lacertidae. – Herpetological Journal 2: 7–18, London.

FROST D. R. & A. G. KLUGE (1994): A consideration of epistemology in systematic biology, with special reference to species. – Cladistics 10: 259–294, London.

GOREN, M. & Y. L. WERNER (1993): On measuring head length in fishes, amphibians and reptiles and on modified caliper rules. – Journal of Zoology 230: 187–191, London.

HUEY, R. B. & E. R. PIANKA (1981): Ecological consequences of foraging mode. – Ecology 62: 991–999, Washington, DC.

KASPAREK, M. (1993): Marine Turtle Conservation in the Mediterranean: Marine Turtles in Egypt. Phase I. Survey of the Mediterranean coast between Alexandria and El-Salum. – MEDASSET, RAC/SPA and NIOF, Heidelberg, 63 + xvi pp.

KOENIG, A. (1964): Reisen am Nil (ed. G. NIETHAMMER). – Alexander-Koenig-Stiftung, Bonn 174 pp.

MAYR, E. (1969): Principles of Systematic Zoology. – New York, 488 + 11 pp.

MAYR, E. & P. D. ASHLOCK (1991): Principles of Systematic Zoology. Ed. 2. – New York, 475 + 20 pp.

MAYR, E., E. G. LINSLEY & R. L. USINGER (1953): Methods and Principles of Systematic Zoology. – New York, 328 + 9 pp.

MARX, H. (1968): Check list of the reptiles and amphibians of Egypt. – Special Publication of the United States Naval Medical Research Unit No. 3.

MILNE-EDWARDS, M. H. (1829): Recherches zoologiques pour servir à l'histoire des Lézards, extraites d'une Monographie de ce genre. – Annales des Sciences Naturelles 16: 50–89, Paris.

PASTEUR, G. & J. BONS (1960): Catalogue des reptiles actuels du Maroc. – Travaux de l'Institut scientifique chérifien, Série Zoologie, 21: 1–132, Rabat.

PERRY, G., I. LAMPL, A. LERNER, D. ROTHENSTEIN, E. SHANI, N. SIVAN & Y. L. WERNER (1990): Foraging mode in lacertid lizards: variation and correlates. – Amphibia-Reptilia 11: 373–384, Leiden. [cf. also 13, 1992: 96].

RAVIKOVITCH, S. (1970): Map II/3 in AMIRAN et al. (1970).

REIFENBERG, A. (1939): The loess soils of the Beersheba region of Palestine. – Empire Journal of Experimental Agriculture 7: 305–310, Oxford.

REIST, J. D. (1986): An empirical evaluation of coefficients used in residual and allometric adjustment of size covariation. – Canadian Journal of Zoology 64: 1363–1368, Ottawa.

SALEH, M. A. (1997): Amphibians and Reptiles of Egypt. – Publication of National Biodiversity Unit No. 6 (Egyptian Environmental Affairs Agency, Ministry of State for Environmental Affairs), 236 + 11 pp.

SALVADOR, A. (1982): A revision of the lizards of the genus *Acanthodactylus* (Sauria: Lacertidae). – Bonner zoologische Monographien 16: 1–167, Bonn.

SCHLEICH, H. H., W. KAESTLE & K. KABISCH (1996): Amphibians and Reptiles of North Africa. – Königstein, 630 pp.

SCORTECCI, G. (1935): Rettili raccolti nel Deserto Libico dalla Missione Desio della Reale Accademia d'Italia. – Atti della Societa Italiana di Scienze Naturali 74: 185–190, Milano.

SELIGMANN, H. (1997): Phylogenetic and ecological aspects of directional asymmetry in *Acanthodactylus* (Sauria: Lacertidae). – Journal of Morphology 232: 187, Boston/New York.

STRELLER, G. (1939): Die kleine Farbmesstafel nach Wilhelm Ostwald. – Göttingen, Frankfurt & Berlin, 10 + 4 pp.

TIMES ATLAS (1997): The Times Atlas of the World. Comprehensive Edition, 9th Ed., Times Books. – London, XLVII + 123 pis. + 218 pp.

WAHRMAN, J. (1970): Distribution of Vertebrates, plate VII/1 in AMIRAN et al. (1970).

WEBSTER'S GEOGRAPHICAL DICTIONARY (1955): Revised Ed. Springfield, Massachusets, XXXI + 1293 + 24 pis.

WERNER, Y. L. (1961): The vertebral column of the geckos (Gekkonoidea), with special consideration of the tail [in Hebrew, with English parts]. – Ph.D. Thesis, The Hebrew University of Jerusalem, 267 pp.

WERNER, Y. L. (1982): Herpetofaunal survey of the Sinai Peninsula (1966–77), with emphais on the Saharan sand community. p. 153–161. In: N. J. (Jr.) SCOTT (Ed.), Herpetological communities: a symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League, August 1977.– U.S. Fish and Wildlife Service, Wildlife Research Report 13, Washington.

WERNER, Y. L. (1991): Notable herpetofaunal records from Transjordan. – Zoology in the Middle East 5: 37–41, Heidelberg.

WERNER, Y. L. (1995): A Guide to the Reptiles and Amphibians of Israel [in Hebrew]. – Nature Reserves Authority, Jerusalem, 88 pp. + 108 photographs.

WERNER, Y. L., E. FRANKENBERG, M. VOLOKITA & R. HARARI (1993): Longevity of geckos (Reptilia: Lacertilia: Gekkonoidea) in captivity: an analytical review incorporating new data. – Israel Journal of Zoology 39: 105–124, Jerusalem.

WERNER, Y. L., D. ROTHENSTEIN & N. SIVAN (1991): Directional asymmetry in reptiles (Sauria: Gekkonidae: *Ptyodactylus*) and its possible evolutionary role, with implications for biometrical methodology. – Journal of Zoology 225: 647–658, London.

WILLIAMS, B. K., K. TITUS & J. E. HINES (1990): Stability and bias of classification rates in biological applications of discriminant analysis. – Journal of Wildlife Management 54: 331–341, Bethesda/Lawrence.

ZOHARY, M. (1947): A geobotanical soil map of Western Palestine. – Palestine Journal of Botany 4: 24–35, Jerusalem.

ZOHARY, M. (1962): Plant life of Palestine: Israel and Jordan. – London, 262 pp., 6 pls.

ZOHARY, M. (1982): Vegetation of Israel and adjacent areas. In: Tübinger Atlas des Vorderen Orients, Beiheft A007. – Wiesbaden, 183 pp.

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# Appendix 1: specimens examined

Localities are in west-to-east order. The material from Israel is listed in condensed manner; dates and collector names are omitted. Locality names are followed in parentheses by Israel Grid coordinates (six or eight digits, the first 3–4 being longitude); then by cataloge numbers of the relevant specimens. H. = Hirbet, Hurbat, Horvot (ruin, ruins). N. = Nahal (wadi). * = Also radiograph. {...} = Excluded from statistics (extralimital or extratemporal). [...] = Our interpretations.

**Libya:** Gwemines (Cyrenaica) [Ghemines]: {MZUF 770}. • Benghazi [Banghazi]: MZUF 852, 12688. • Near Benghazi [Banghazi]: BMNH 1988.189, 1988.191-192. • Fuchat, Benghazi [Banghazi]: {MZUF 853}.

**Egypt:** Without details: ZMB (syntypes of *A. pardalis*) 1072, {1073}, 1074-77, 55905. • Matruh: Sellum & Matruh [Matruh: Salum]: BMNH 1924.12.8.8-9. • Sidi Barrani: FMNH 78831. • Sidi Barrani, 19.2 km S of: FMNH 78832. • El Nasr, W of (31°28'06"N, 26°23'38"E): HUJ-R 18995. • El Nasr (31°18'05"N, 26°58'46"E): HUJ-R 18990-4, 18996-8, {18999, 19007, 19159, 19169} • Mersa Matruh [Marsa Matruh]: FMNH 63042-3, {63044}, 63046, 63048, 63050, USNM 130333-5, {130336} • Burg el Arab: BMNH 1924.12.8.3*-4*-5*-6*, FMNH 68858, 78825, USNM 134176-85. • Burg el Arab, 8 mi S of: FMNH 78824. • Bahig: FMNH 152612, 152614-15, 152617. • El Hauwariya: FMNH 78849-61. • Ikingi Mariut [Maryut], Alexandria: USNM 195477, 343182-4. • El Amiriya, Western Desert: USNM 136413. • Maryat, Alexandria [Maryut = El Amiriya]: BMNH 97.10.28.323*-324*-325*-326*-327-328*-329*-330*. • Surroundings of Alexandria: NMP 34941-46, {34947}, 34948-51. • Beheira: Abu el Matamir: FMNH 66115, 66117-9, 66122-3. • Matruh: 179 km NW of Cairo-Alexandria road: FMNH 78863. • Wadi Natroun [Wadi el Natrun]: FMNH 77976-9. • Faiyum: Kom O Shim: FMNH 58698. • Kfar Mahfuz: FMNH 77980. • Giza: Abu Rawash: USNM 133329. • Giza Pyramids: FMNH 78829. • Damietta: Kafr el Battikh: FMNH 78866.

**Egypt** (additional specimens examined by S. BAHA EL DIN): Burg El Arab: FMNH 78826-8, 78833-5. • 179 km NW of Cairo (on Alex. road): FMNH 78864-5. • El Hauwariya: FMNH 78836-48. • 1 mile S of Helwan: FMNH 78822. • Kom Oshim: FMNH 77981. • Maryout or Alexandria: FMNH 608. • Sidi Barrani: FMNH 78830. • 1 mile W of Sidi Barrani: FMNH 204527. • Wadi El Natroun: FMNH 77972-5. • 5 km W of Wadi Natroun: FMNH 164617.

**Negev:** Gaza (09941015): HUJ-R 1293*,{5061}. • Nirim (09950828): TAU-R 2438. • Sharuhen, W of: (101078): TAU-R 1054. • Sharuhen, 8 km S of (10410690): TAU-R 1052. • H. Abu-Suheiban (11600724): HUJ-R 2252* • Gilat (117082): HUJ-R 5277. • Matred (120019): HUJ-R 1577. • Shivta, nr. (120038): HUJ-R 2063* • Be'er Mash'abbim, 5 km NW of (12100480): TAU-R 1058. • N. Hadeqa (12100405): HUJ-R 1299. • Sede Zevi (12270951): TAU-R 9719. • Revivim (12350504): HUJ-R 1876, TAU-R 1043, 1049. • Be'er Sheva', 5 km W of (125073): HUJ-R 2488*-9*. • Be'er Sheva', 34 km S of (127044): HUJ-R 1289, 1294*. • 'En Mor (12740265): TAU-R 997-8. • 'Avdat (12820228): HUJ-R {6992*}. • Be'er Sheva', nr. (12890730): TAU-R 1039, 1044. • N. Boqer (129036): HUJ-R {1298}. • Be'er Sheva' (130073): HUJ-R 1290*, 1777*, 2188*, {5071*}, 5398*, 10873, TAU-R 1586-7, 2804, 2830, 6299, {7161, 7169}, 7172-4, {7326}, 7329-34, 7336-38, 9209, 9222. • Be'er Sheva', 3 km S of (130070): HUJ-R 7331, 7333. • Sede Boqer (13040315): HUJ-R 2172*, 2259, 2261, 2814*, 2817*, {2818*}, 2820*, 5067, {5068}, MZUF {19952}, 20002, TAU-R 1628-9, 8835-6. • Holot Haluza (131058): HUJ-R 11275, 11276*, 11278*-9*. • Be'er Sheva', 2 km S of (13110690): TAU-R 2805. • Be'er Sheva', 12 km S of (13150600): HUJ-R {6293*, 6294*, 6295*}. • Be'er Sheva', 10 km S of, way to Yeroham (13150610): HUJ-R 6993. • Be'er Sheva', 5 km S of, highway to Yeroham (13150660): HUJ-R 5714, 5715*. • Bet Eshel, 10 km E of (13220703): HUJ-R 1297. • Holot Mashash (133056): HUJ-R {12292*, 12293}, 12294, {12295, 12296*, 12297}, 12298, 12299*, 12300, {12301*}, 12302. • Be'er Sheva – Asluj road (dunes) (133057): HUJ-R 2070*, 2149*, 5066*. • N. Mashash (13310565): TAU-R 1040-2, 2105-6. • N. Mashash oil road crossing (13350555): HUJ-R 12195. • Mishor Haluqim (134036): HUJ-R 1773, 5056*, 5057*, 5058, 5059. • Be'er Sheva', 20 km S of (13400540): HUJ-R 2061*. • Be'er Sheva', 18 km S of (13400555): HUJ-R 6791*. • Tel-Yeroham – Revivim jnct., 3 km S of (13450499): HUJ-R 6931*. • Negev junction (13450528): HUJ-R 10892*, 11265, 11266*, 11267, 11268*, 11269, 11270*, 11271, 11272, 12582. • 'Omer (13480751): HUJ-R 6308*, {6309*}, ZMUF {19954}. • Oil Road km 1 (13500525): HUJ-R 2147. • Bor Mashash (13510538): HUJ-R 11274*, 11366*, 13488, {13489}. • Lahav, 1 km W of (13640876): TAU-R 4870. • H. al Leiqiya (N of Omer) (13650815): HUJ-R 7264*. • 24 km S of Be'er Sheva' (137050): HUJ-R 7762*. • Lahav area (13740876): TAU-R 5166. • Imara (139049): TAU-R {3675}. • Nevatim (13900700): TAU-R 905, 906, 13902. • Tel Shoqet (14110799): TAU-R 10706. • Be'er Yeroham (14140449): HUJ-R 1878*, TAU-R 940-42, 1046, 1048. • Tel Yeroham (14220450): HUJ-R 2623*, TAU-R 1051. • Kefar Yeroham (143044): TAU-R 3917-8. • Rekhes Yeroham (143043): TAU-R 13870. • 'Omer–Hebron–'Arad jnct., 5 km E of (14350770): HUJ-R 7617*, 7619*, 7620*, 7621*, 7622* (type and topotypes). • 'Aro'er, 7 km SW of (14400565): TAU-R 3854. • Kefar Yeroham, 3 km NE of (14500465): TAU-R 3644-5. • Tel Masos (14650688): HUJ-R 1292*, 5070*, TAU-R 2909, 2918-9, 2924-5. • Be'erot 'Aro'er, 11 km W of (14840508): HUJ-R 7798*. • Be'erot 'Aro'er (14840619): HUJ-R 1291*, 5064-5, {LACM 74340}, TAU-R 3824-5, 4248. • Dimona, 3-4 km SW of (15000515): HUJ-R 6788. • Dimona, W of (150054): HUJ-R {5748*}, 7662*, 7685*, 7686*, 7687*. • Tel Malhata (15250696): HUJ-R 1774*, TAU-R 958, 960, 1733-4, 2472-3. • Dimona (15300525): TAU-R 2207, 2209, 2505. • N. Malhata (15600694): HUJ-R 1289*, 5062, 5063*, 5296*. • H. Mamshit (15610483): HUJ-R 1582*, 5060*. • H. Kasif (15650740): HUJ-R 7581*, 7582*, 7583*, 7584*, 7585*, 7586, 7587*, 7588*, 7589*, 7590*, 7591*, 7592*, 7595*-6*, 7598*, 7599*, 7600*, 7601*, 7602*, 7603*, 7604*, 7605*, 7606*, 7607*, 7608*, 7609*, 7610*, 7613*, TAU-R 14230. • Tel 'Arad (16210766): HUJ-R 7278*, 7279*, 7280*. • 'Arad (170074): HUJ-R, 12286*-7*, 12289*, 12290*, 12291*, 13546-58, {13559-61}, TAU-R 14074. • Har Menahem (17590776): TAU-R 916. • Between Hasruta [=Mezad Hatrurim] and Berekhat Zefira (17610746): TAU-R 922-3. • Berekhat Zefira (17650822): HUJ-R 1775*, 5069, TAU-R 892. • N. Revivim: HUJ-R 1776. • N. Be'er Sheva': TAU-R 8834, 8837, 8839-44, 9172, {9207}, 9224-5.

Israel and Sinai (problematic locations): South Palestine: HUJ-R 1581*. • E of Be'er Sheva': HUJ-R 1295. • N. Be'er Sheva': TAU-R 7969. • S. of Yeroham: TAU-R 10908. • Sede Tzafar [Sede Zofar, a name not heard of]: TAU-R 10022. • Biq'at Bet-Shean: TAU-R 10736 [presumably erroneous]. • No locality stated: TAU-R 9198. • "Aegypten, noerdl. Sinaihalbinsel": ZFMK 22768-78 [discussed in the text].

Jordan: 30 km S of Amman: HUJ-R {1296}*.

Asia Minor and Persia: MNHN 5322, 1991.3235 [see Discussion].

# Appendix 2: specimens radiographed

Order and abbreviations as in Appendix 1.

**Libya:** Agedabia, Cyranaica: BMNH {1965.1262-4}.

**Egypt:** Burg el Arab: BMNH 1924.12.8.7. • Maryat, Alexandria: BMNH 97.10.28.331-2. • Alexandria: BMNH 1920.1.20.387 a-i.

**Negev:** Gevulot (09800683): TAU-R 1055. • Be'er Sheva', 15 km W of (11500725): TAU-R 1050. • 'En Mor (12740265): TAU-R 996. • N. Boqer (129036): HUJ-R {1569}. • Be'er Sheva', 3 km S of (130070): HUJ-R {7332}. • N. Mashash (13310565): TAU-R 2110. • Negev Junction (13450528): HUJ-R {11273}. • Lahav, 1 km W of (13640876): TAU-R 4869. • Lahav area (13740876): TAU-R 5165, 5167. • Wadi Milkh (14009205): TAU-R {1056}. • Be'er Yeroham (14140449): TAU-R 930, {940}, 1047. • Tel Masos (14650688): TAU-R 2911, 2917, 2920-1, 2923, 2926-7. • Dimona, W of (150054): HUJ-R {7684}. • Dimona (15300525): TAU-R 2206, 2208. • Kasif, 5 km W of Arad (159072): TAU-R 11114. • Arad (170074): HUJ-R {12288}, 12670. • Between Hatrurim and Har Menahem (17650780): TAU-R 939.

**Israel (problematic locations):** N. Be'er Sheva' (110067-161078): TAU-R 7925, 8533. • No locality stated: TAU-R {4586}, 6255, 8538.