Subspeciation or none? The hardun in the Aegean
(Reptilia: Sauria: Agamidae: *Laudakia stellio*)

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Abstract
A study aimed at testing the contested validity of the subspecies *Laudakia stellio daani* yielded novel insights into the essence of subspecies. We examined morphologically museum specimens from Greece, Aegean islands, and Anatolia (*n* = 118; not all could be used in all analyses). Beyond the conventional mensural, meristic and qualitative characters we quantified 14 coloration characters, thus totalling 34 characters (including sex). Biometry was statistically analysed within and between the two geographically defined presumed subspecies, *L. s. daani* and *L. s. stellio*. Excluding or including broken-tailed specimens changed the outcome of tests. Significant minor directional asymmetry occurred in one of four character-taxon combinations. Phenetic cluster analysis poorly separated the two presumed subspecies when all characters, including those with discordant variation, were included; after selection of characters, the separation improved. Some biometric characters distinguish the two presumed subspecies, confirming their validity. The associations of significant inter-character correlations differed between the two subspecies. Additionally, the two differed in parameters reflecting selection pressures and social structure: *L. s. stellio* is more colourful than *L. s. daani*; its sexual dimorphism is mainly chromatic, versus mensural in *L. s. daani*; and its population seems to include many males with underdeveloped callous scales, presumably socially subordinate, versus very few in *L. s. daani*.

Keywords: Aegean islands, Agama stellio, Anatolia, asymmetry, Greece, Laudakia stellio, Seligmann effect, sexual dimorphism, subspeciation

Introduction

Historical

The hardun, a medium-sized rupicolous lizard (Schreiber 1912) of the family Agamidae, is the most conspicuous reptile in natural, rural and urban environments in the eastern Mediterranean (Bodenheimer 1935; Disi et al. 2001). [We follow Böhme (1990) and Baig...]

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The hardun was described by Linnaeus (1758) as *Lacerta stellio*. Names applied by others during the following century were listed by Schreiber (1912) and Wermuth (1967). The hardun became *Agama stellio* in Boulenger’s (1885) edition of the *Catalogue of the Lizards in the British Museum* and retained this name for a century. Moody (1980), in an unpublished thesis, split the genus, making the hardun *Stellio stellio* in Boulenger’s (1885) edition of the *Catalogue of the Lizards in the British Museum* and retained this name for a century. The splitting was accepted by Hertz and Nevo (1981) and others, as reviewed by Leviton et al. (1992, p 12), who regarded Moody’s thesis as a published paper. However, as reviewed more fully by Loveridge (1957, p 192), Henle (1995) and D. R. Frost (1991, manuscript within personal communication to Y. L. Werner, dated 19 February 2004), Laurenti’s genus *Stellio* had been eliminated by Stejneger by retroactively basing it on an invalid type species. Henle (1995) argued for the application of Blyth’s *Plocederma* to the *stellio* (sensu stricto) group of *Agama*. Nevertheless, because of the unresolved phylogenetic situation (Henle 1995), we follow the majority of authors and especially the thorough discussion of Rastegar-Pouyani and Nilson (2002) in accepting Leviton et al.’s (1992) naming the hardun *Laudakia stellio*.

Linnaeus (1758, 1766) gave the origin of *Lacerta stellio* as “The Orient: Delos, Egypt, Africa” despite his collector’s report, “This creature frequents the ruinous walls of Natolia, Syria and Palaestine” (Hasselquist and Linnaeus 1757). The type specimen is lost (Andersson 1900). The type locality was restricted by Mertens and Müller (1928, p 26) to Delos Island, Cyclades. According to Leviton et al. (1992), the species ranges from Corfu, Salonika and the Cyclades through the Turkish Islands, Anatolia, Syria, northern Iraq, Lebanon, Israel and Jordan to Lower Egypt and northern Saudi Arabia. Actually, in Anatolia the hardun does not occur north of approximately 39°N (Başoğlu and Baran 1977).

Over this ecologically heterogeneous expanse the hardun’s morphology varies considerably (Beutler 1981). Accordingly, the hardun of Lower Egypt was recognized early as distinct, *Stellio vulgaris* (now *L. s. vulgaris*) Sonnini and Latereille, 1802. Parker (1935) described the melanistic *A. s. picea* from the Jordanian basalt desert (Werner 1992). Haas (1951) described the robust, large-scaled hardun of Israel’s Negev as *A. s. brachydactyla*. But because from the Aegean eastwards and southwards the geographical variation increases (Wettstein 1953), not all populations between Delos and the Negev could reasonably be lumped under *A. (= L.) s. stellio* (Schmidt 1939). Indeed, Daan (1967) described *A. s. cypriaca* from Cyprus. Later Beutler and Frör (1980) distinguished most of the populations of Greece and those of Turkey as *A. s. daani*, restricting the typical subspecies *A. s. stellio* to five islands in the central Cyclades, the Mykonos archipelago (Delos, Mikro Rhematiaris, Mykonos, Rinia, Tinos). They admitted that the limit of *A. s. daani* to the south-east was unclear. Baran and Öz (1985) assigned the populations of western and southern Anatolia to *A. s. daani* but those of south-eastern Anatolia to *L. s. stellio*, although according to their own data the coloration did not fit very well (e.g. head lighter than body but not yellow-red). Baran and Atatür (1998) considered that although in western Anatolia *L. s. daani* is widespread, the populations in central, southern and south-eastern Anatolia belong to *L. s. stellio*. Recently, Göçmen et al. (2003) confirmed the Hatay population as taxonomically indistinct from the adjacent Anatolian *L. s. stellio* population.

In this taxonomical and nomenclatural scenario the definition of the typical subspecies is of key importance. The distinction, by Beutler and Frör (1980), of *Laudakia stellio daani* from *Laudakia stellio stellio*, relied primarily on coloration. In *L. s. daani* the top of the head is blackish grey, similar to the back, while in *A. s. stellio* the back of the head is yellow to red,
contrasting with the brown trunk (as already noted by Daan 1967). Furthermore, at least dominant male \textit{L. s. daani} (\textit{L. stellio} has a well-developed social structure; Beutler 1981; Arbel 1982) in life have blue markings on the head and legs and often on the back, which are absent in \textit{L. s. stellio}. In \textit{L. s. daani} the throat is mostly amply spotted with black, and only rarely marbled; in contrast, \textit{L. s. stellio} is characterized by an unspotted, at most weakly marbled, throat (see also Daan 1967). Additionally, the two subspecies have distinct sets of albumin-like materials (Beutler 1981). On the other hand, the differences in mensural and meristic characters are small, so that these are shared by both subspecies in comparison with, and distinction from, all other named subspecies (Beutler and Frör 1980).

Xyda (1983, 1986) recognized the distinction of the Mykonos and Delos harduns as yellow-headed and smaller-sized than those of most other Greek islands but surprisingly referred to them as \textit{Stellio s. mykonensis}, considering the others to be \textit{S. s. stellio}.

However, recently the taxonomic distinction of \textit{Laudakia stellio daani} from \textit{Laudakia stellio stellio} was challenged and tentatively rejected by Baig (1992) in his treatise of the \textit{stellio}-group of ‘’\textit{Agama}’’. He demoted \textit{L. s. daani} to the synonymy of \textit{L. s. stellio}, whose distribution, he concluded, extends all the way to Israel. Baig mainly argued that Beutler and Frör (1980) had examined insufficient material but presumably he was aware also of the morphological conformity of the two nominal subspecies.

The present project was aimed at examining the systematic status of \textit{L. s. daani} relative to \textit{L. s. stellio} but it yielded an instructive example of the complexity of identifying subspeciation, and some insight into the essence of subspecies.

\textbf{General research strategy}

We relied on existing museum material, hence on morphology. Beyond the conventional mensural, meristic and qualitative (pholidotic and colour) characters (Daan 1967; Baran and Öz 1985; Baig 1992) we quantified the coloration, which can be very variable even within one island (Calabresi 1923; Zavattari 1929). We did this in terms of shades of grey and the number, shape and size of spots, ignoring hues as these probably vary with season, behaviour and preservation. We did not adopt the sophisticated set of characters used by Moody and Böhme (1984), expecting the main relevant phenomena to be reflected in the simpler basic set. Moreover, we excluded some characters reputedly correlating with others, such as the sublabial count (paralleling the supralabial count). However, two bilateral meristic characters were recorded on both sides, for reasons explained below. Together with ratios computed between characters, we recorded 33 characters, besides sex.

We limited statistical sophistication to the minimum required for solid results. To reduce the problem of allometry, we excluded young specimens and simply expressed measurements as percentages of body length. Initially we also excluded all specimens with broken or regenerated tails (Loumbourdis and Kattoulas 1986; Schall et al. 1989; Lapid and Werner 1991), intending all specimens to participate in all tests. However, in a second round we included specimens lacking complete tails, especially from the Mykonos archipelago, to increase the samples of the two presumed subspecies and to reduce the difference between them.

Our analysis proceeded in steps: (1) testing asymmetry, to see whether bilateral characters should be used separately or averaged, and whether asymmetry itself is an additional taxonomic character (Seligmann 1997). Because asymmetry could vary between sexes and between parapatric taxa (Werner et al. 1991) we did this separately for each sex of each of the presumed subspecies. (2) Testing sexual dimorphism (Abo-Taira et al.
1996), to see for which characters the sexes could be pooled. Because sexual dimorphism could vary between parapatric taxa (Werner 1971a) we did this separately for each presumed subspecies. (3) Because subspecies cannot be defined if most of the geographic variation of characters is discordant (Inger 1961), we tested for correlation within all pairwise combinations of the 33 characters. (4) Phenetic cluster analysis of the whole material, to see whether specimens cluster in geographical coherence (separately for each sex). (5) Statistical testing of the differences between the presumed subspecies, separately for each participating character, to identify diagnostic characters. (6) Statistical reduction of the relevant characters, for each sex and subspecies, and constructing a key. Finally, (7) testing the results by applying the key to additional specimens excluded from the detailed analyses due to juvenile size, bad preservation or timing of becoming available.

Materials and methods

The following abbreviations are used: L, left side; R, right side; r, Pearson coefficient of correlation; RA, rostrum-anus length (Werner 1971b); PERCRA, percent of RA (Werner 1971b). Museum abbreviations follow Leviton et al. (1985) except: LM, Lorenz Müller Collection within the ZSM; NHMC, Natural History Museum of Crete (University of Crete).

Summary of material examined

We examined 118 *Laudakia stellio* specimens: 37 from the Mykonos archipelago (presumed *L. s. stellio sensu stricto*), 50 from other Aegean islands and Greece (presumed *L. s. daani*) and 31 from Anatolia (presumed *L. s. daani* though affinities possibly heterogeneous). The specimens are briefly listed by taxon and locality in the Appendix. As already indicated, not all specimens were used in all tests.

Characters

**Sex.** In *Laudakia stellio* males are easily identified by possessing a preanal field of callous glandular scales and, especially, a longitudinal band of similar glandular scales in mid-belly (Boulenger 1885; Beutler 1981; Baig and Böhme 1991). In a sample of 196 adults from Israel and Sinai (Kosswig et al. 1976) no ambiguous specimens were encountered (Werner, unpublished). For statistics sex was coded 1, male; 2, female. (Figure 1).

**Mensural characters, including computed ones (11).** RA: from tip of snout to cloacal slit, to nearest 0.5 mm. All the following measures were processed, and are presented, as PERCRA. Tail length: from cloacal slit to tip (only if original), to nearest 0.5 mm.

All the following measures were taken by callipers to nearest 0.1 mm. Head length: from tip of snout to rear border of ear, parallel to long axis (by Goren and Werner’s 1993 modified callipers). Head width: at maximum width. Head depth: with closed mouth at maximum height. Head index: (100 head length)/head width. Head flatness: (100 head length)/head depth. Forelimb length: from axilla to tip of claw of longest finger, along mid-width of limb, in two sections: to and from pin in elbow joint. Hindlimb length: from groin to tip of claw of fourth toe, along mid-width of limb, in two sections: to and from pin in knee joint. Fourth toe length: from insertion of fifth toe to tip of claw. Limb ratio: hindlimb length/forelimb length.
Meristic characters, including computed ones (9). Supralabialia (L, R): counted from the most posterior scale sharing the typical appearance of the supralabials, to (and excluding) the rostral. Relative asymmetry in supralabials (the difference between R and L counts, as a
percentage of the average of R and L counts; %D). Dorsal scales index: number of scales in a longitudinal row, along 1 cm (counted within a 1-cm window in a thin plastic ruler), in the largest scaled area vertebrally or paravertebrally, halfway between fore- and hindlimbs, and weighted by trunk length (RA minus head length; Moody and Böhme 1984). Ventral scales index: number of scales in a transverse (obliquely transverse) row, along 1 cm (counted as above), in the middle of the belly (from the midline laterad, located as above), and weighted by trunk length. Preanal glandular scales: their total number in the patch (excluding the mid-abdominal longitudinal patch of males). Subdigital lamellae under fourth toe (L, R), from the junction with the third toe, and including the one sheathing the claw base. Relative asymmetry in subdigitals (the difference between R and L counts, as a percentage of the average of R and L counts).

**Qualitative pholidosis character (1).** Dorsal scutellation pattern: qualitative assessment of the degree of coverage of the dorsum by enlarged scales, based on Figure 6 in Daan (1967), on a scale from 0 to 15, in which Daan’s Figures 6d=2, 6b=6, 6a=10 and 6c=14.

**Coloration characters (14).** Dorsal pattern categories (figure 2): 0, blotches (often longitudinally oblong); 1, thin transverse bars; 2, both the preceding kinds combined; 3, irregular. Level of distinctiveness of dorsal spots: 0, distinct; 2, indistinct. Number of dorsal blotches, or transverse bars (or combination) between head and tail. Transverse bars, presence in dorsal pattern: 0, absent; 1, present. Dorsal blotch length (longitudinal diameter) in mid-dorsum, to 0.1 mm, processed and presented in PERCRA. Dorsal blotch width (transverse diameter) in mid-dorsum, as above. Level of symmetry of dorsal spots (assessment): 0, symmetrical; 2, very asymmetric. Throat ground colour (figure 3): 0, light; 1, dark. Throat pattern, coverage with contrasting spots: 0, none; 4, all over. Venter, ground colour: 0, light; 1, dark. Venter, coverage with contrasting dots: 0, none; 3, many. Tail, distinctiveness of colour rings on tail base: 0, distinct; 1, indistinct. Tail rings, number of colour rings along the tail (only when distinct on the base, and tail complete).

**Statistics**

Basically we applied parametric statistics, using Microsoft Excel, complemented by StatistiXL version 1.1 (2003, from www.statistiXL.com) for the one-sample $t$ test (to test asymmetry) and contingency tables. Correlation within all character pairs was tested via a bivariate matrix in SPSS.

Cluster analyses were done with the MVSP package, using the Gower General Similarity Coefficient or the Euclidian calculation, respectively, depending on inclusion or exclusion of categorical characters. We used the “farthest neighbour” display. When it appeared advisable to select characters for cluster analysis, we applied the “sort” function to all characters and evaluated the distribution of each character over the two (geographically) presumed subspecies.

**Results**

**Sex**

Upon trying to sex 71 presumed *Laudakia stellio daani* specimens by visual examination, they readily segregated into 29 males, 28 females, 13 juveniles and one specimen (SMF 10195 from Chios) that was enigmatic as explained below. But the 36 presumed *L. s. stellio*
specimens segregated into 10 males, 12 females, eight juveniles and six similarly enigmatic specimens. These seven tended to have masculine head proportions (see below) but the glandular scale patches were only most feebly indicated. The scales of the mid-ventral ridge were not callous but flat (flush with the surrounding ventrals), slightly expanded, and under the dissecting microscope each contained the indication of a ring (or ellipse), being reminiscent of the feebly developed femoral pores of some female lacertid lizards (Figure 1). Upon dissection, these seven specimens proved to be “cryptic males” with apparently normal testes.
Asymmetry

The possible occurrence of directional asymmetry was tested in eight character-taxon-sex combinations, i.e. in supralabial plates and subdigital lamellae. Although at the individual level asymmetry was frequent, all eight group averages were insignificant. However, in *Laudakia stellio stellio* the number of supralabials showed in males $%D=0.491$, $P=0.063$ and in females $%D=0.541$, $P=0.191$. Thereupon we repeated the test for pooled sexes (four character-taxon combinations). The results for both characters in *L. s. daani* and subdigital lamellae in *L. s. stellio* ranged $0.3<P<0.7$ but for supralabials in *L. s. stellio*, $%D=5.547$, $P=0.010$. Hereinafter we treat the right and left counts as separate characters and asymmetry itself is reckoned as another character.

Sexual dimorphism

The list of characters showing significant sexual dimorphism radically differed between the presumed *Laudakia stellio daani* and the presumed *L. s. stellio*. In *L. s. daani* (Table I) the sexual dimorphism involved mainly size and head proportions, though when the sample was restricted to whole-tailed specimens, there was also some difference in the width of the dorsal blotches and the frequency of presence of the dorsal transverse bars. In *L. s. stellio* (Table II) the sexual dimorphism involved mainly the dorsal coloration, though when the sample was expanded with broken-tailed specimens, also the difference in ventral coloration became significant. In terms of Fitch's (1981) female-to-male ratio (FMR), in presumed *L. s. daani* FMR=0.897 (Table I) but in presumed *L. s. stellio* FMR=0.948 (not significant).

Correlation among characters

We tested for correlation in all 561 pair-wise combinations of the 34 characters (including sex), separately in each presumed subspecies. In the presumed *Laudakia stellio daani* significant ($P<0.01$) correlation occurred only in 16 character combinations (Table III). It is remarkable that the correlation of right side with left side, in both supralabial plates and subdigital lamellae, was only $r<0.7$. Sex was correlated significantly only with RA and head length.

In the presumed *L. s. stellio* the number of character combinations with significant correlation was only 12 when initially tested for $n=15$ specimens with complete tails, and rose to 30 when tested for $n=23$ specimens, some with broken tails (Table IV). Interestingly in this subspecies the correlation between right and left sides, in both supralabial plates and subdigital lamellae, failed to attain significance. Sex was significantly correlated only with the relative length of the dorsal blotches; and RA, in the sample expanded with broken-tailed specimens, was correlated not only with the relative size of body parts but also with some coloration traits.

However, this enlargement of this sample did not merely increase the number of significant correlations (as expected). It also eliminated from the list of significant correlations three character combinations that in the smaller whole-tailed sample had shown significant correlations: head length with the pattern of ventral spots, the number of tail rings with the ventral color, and the same with throat color.

Cluster analysis

We applied phenetic cluster analysis separately to males and females, initially using only whole-tailed specimens for which a maximum number of characters was recorded, and
Table I. Sexual dimorphism in *Laudakia stellio daani* (RA in mm, other measurements in PERCRA).

| Character            | Males               | Females              |   |   |
|----------------------|---------------------|----------------------|---|---|
|                      | Mean    | SD      | Range    | n  | Mean   | SD      | Range    | n  | P  |
| RA length            | 118.0   | 114.6   | 99.0–135.0| 18 | 106.6  | 94.4    | 90.0–117.0| 15 | 0.002 |
| Head length          | 25.9    | 1.82    | 21.2–29.2| 18 | 23.1   | 2.59    | 17.9–27.5| 15 | 0.006 |
| Head width           | 28.03   | 2.66    | 23.6–32.3| 18 | 25.65  | 3.16    | 19.2–30.6| 15 | 0.046 |
| Head flatness        | 169.3   | 29.39   | 131–264  | 18 | 150.9  | 23.93   | 96.8–198.5| 15 | 0.065 |
| Hindlimb length      | 72.0    | 4.35    | 63.6–79.5| 18 | 66.5   | 8.66    | 41.5–77.2| 15 | 0.059 |
| Dorsal blotch width  | 8.24    | 1.69    | 6–11.5   | 13 | 7.02   | 1.41    | 4.46–8.96| 11 | 0.058 |
| Transverse bars,     | 0.69    | 0.48    | 0–1      | 16 | 0.33   | 0.48    | 0–1      | 15 | 0.051 |
| presence             |         |         |          |    |        |         |          |    |     |
| Transverse bars,     | 22.2    | 25.53   | 16.9–24.8| 10 | 15.1   | 7.71    | 0–0      | 5  | 0.108 |
| length               |         |         |          |    |        |         |          |    |     |

Table II. Sexual dimorphism in *Laudakia stellio stellio* (measurements in PERCRA).

| Character            | Males               | Females              |   |   |
|----------------------|---------------------|----------------------|---|---|
|                      | Mean    | SD      | Range    | n  | Mean   | SD      | Range    | n  | P  |
| Limb ratio           | 143.3   | 18.6    | 112–163.5| 15 | 133.5  | 7.1     | 117.2–149.1| 9  | 0.052 |
| Dorsal pattern categories | 1.87   | 1.58    | 0–3      | 15 | 0     | 0       | 0–0      | 10 | 0.000 |
| Level of distinctiveness | 1.47   | 0.87    | 0–2      | 15 | 0.1   | 0.35    | 0–1      | 10 | 0.000 |
| Number of dorsal blotches | 2.36   | 1.94    | 0–4      | 11 | 3.90  | 0.35    | 3–4      | 10 | 0.024 |
| Dorsal blotch length | 6.09    | 4.99    | 7.63–10.76| 11 | 12.93  | 1.64    | 10.0–14.87| 10 | 0.000 |
| Venter, coverage with dots | 0.6    | 0.44    | 0–2      | 15 | 1.5   | 0.71    | 0–3      | 10 | 0.012 |
| Tail, distinctiveness of colour rings | 0.67   | 0.49    | 0–1      | 15 | 0     | 0       | 0–0      | 10 | 0.000 |
Table III. Correlations among characters in *Laudakia stellio daani*, significant at $P<0.01$ (based on 18 males and 16 females).

| Character                        | Correlated with... | n  | r    |
|----------------------------------|--------------------|----|------|
| Sex                              | RA length          | 34 | -0.498 |
| Head flatness                    | Head length        | 34 | -0.446 |
|                                  | Head depth         | 34 | -0.513 |
|                                  | Fourth toe length  | 34 | 0.460  |
| RA length                        | Throat ground colour | 31 | 0.533 |
| Dorsal scales index              | Ventral scales index | 34 | 0.462 |
| Supralabialia, R                 | Supralabialia, L   | 34 | 0.698  |
|                                  | Dorsal blotch width | 32 | 0.540  |
| Supralabialia, L                 | Subdigitalia, L    | 34 | 0.441  |
| Subdigitalia, R                  | Subdigitalia, L    | 34 | 0.680  |
| Number of dorsal transverse bars | Mid-dorsal pattern | 15 | -0.990 |
|                                  | Dorsal blotch length | 15 | -0.797 |
|                                  | Dorsal blotch width | 14 | -0.833 |
| Dorsal blotch length             | Dorsal blotch width | 32 | 0.825 |

Table IV. Correlations among characters in *Laudakia stellio stellio* significant at $P<0.01$ (based on 15 males and 8 females).

| Character                        | Correlated with... | n  | r    |
|----------------------------------|--------------------|----|------|
| Sex                              | Dorsal blotch length | 19 | 0.614 |
| Head index                       | Head flatness      | 23 | 0.642 |
|                                  | Head width         | 23 | -0.781|
| Head flatness                    | Head depth         | 23 | -0.805|
|                                  | Dorsal scutellation pattern | 23 | 0.606 |
| RA length                        | Tail length        | 15 | -0.652|
|                                  | Head length        | 23 | -0.534|
|                                  | Forelimb length    | 23 | -0.654|
|                                  | Fourth toe length  | 23 | -0.818|
|                                  | Hindlimb length    | 23 | -0.786|
|                                  | Throat pattern     | 23 | -0.535|
|                                  | Tail rings         | 19 | -0.716|
|                                  | Dorsal scales index | 23 | 0.633 |
| Tail length                      | Fourth toe length  | 15 | 0.649 |
| Head length                      | Hindlimb length    | 23 | 0.569 |
|                                  | Dorsal scales index | 23 | -0.585|
|                                  | Ventral scales index | 23 | -0.535|
| Head width                       | Ventral scales index | 23 | -0.607|
|                                  | Head depth         | 23 | 0.540 |
| Head depth                       | Ventral scales index | 23 | -0.567|
|                                  | Dorsal scutellation pattern | 23 | -0.605|
| Forelimb length                  | Fourth toe length  | 23 | 0.614 |
|                                  | Throat pattern     | 23 | 0.609 |
| Hindlimb length                  | Forelimb length    | 23 | 0.645 |
|                                  | Fourth toe length  | 23 | 0.797 |
|                                  | Dorsal scales index | 23 | -0.573|
| Dorsal scales index              | Fourth toe length  | 23 | -0.566|
|                                  | Ventral scales index | 23 | 0.614 |
| Tail rings                       | Dorsal blotch width | 15 | 0.660 |
| Dorsal blotch length             | Dorsal blotch width | 15 | 0.826 |
dropping some specimens and some characters so as to get maximum representation without replacing missing data points by averages. The dendrogram for whole-tailed males (Figure 4; $n=22$; based on 29 characters) shows two main clusters, one wholly comprising animals from Delos and Mykonos islands ($n=8$), presumed $L. s. stellio$; the other containing presumed $L. s. daani$ ($n=13$) from assorted localities and one single individual from Mykonos, a presumed $L. s. stellio$.

The male sample expanded by adding broken-tailed individuals (Figure 5; $n=26$; based on 25 characters) again shows two main branches, but now the one concentrating the Delos and Mykonos lizards ($n=9$), presumed $L. s. stellio$, additionally contains four presumed $L. s. daani$, according to their collection sites, Antakya in east Anatolia, Chios, Naxos and

Figure 4. Dendrogram of 22 male $Laudakia stellio$ sspp., all whole-tailed, based on 29 characters.

Figure 5. Dendrogram of 26 male $Laudakia stellio$ sspp., 22 whole-tailed and four broken-tailed, based on 25 characters.
Rhodos in the Aegean. The other branch contains mainly presumed *L. s. daani* (*n* = 11) but also two presumed *L. s. stellio* (from Delos and Mykonos). Thus, enlarging the sample (with elimination of caudal characters) has resulted in a less clear dichotomy.

In contrast with the males, the dendrogram for whole-tailed females (Figure 6; *n* = 16; based on 26 characters) fails to depict a clear dichotomy: one main branch contains four presumed *L. s. stellio*; its partner has two secondary branches, one with five presumed *L. s. daani*, the other populated equally by the two presumed subspecies. Enlarging the sample with broken-tailed females yielded a dendrogram paralleling that of the expanded male sample (not shown).

Our a priori plan to improve the segregation, in this case of females, by excluding characters not showing correlations was foiled by the fact that the list of correlations greatly differed between the two presumed subspecies. Therefore we resorted to employing those characters that most neatly seemed to sort into two sub-ranges of their ranges of variation. The second dendrogram for whole-tailed females (Figure 7; *n* = 16) is accordingly based on five characters: ventral scales index, dorsal scutellation pattern, asymmetry of supralabials, tail pattern (distinctiveness on tail base), and ventral coverage with dots. One main branch comprises five presumed *L. s. daani* and one presumed *L. s. stellio*; the other main branch contains seven presumed *L. s. stellio* and three presumed *L. s. daani*, from Artemision and Selcuk in west Anatolia, and near Saloniki.

**Validation of quantitative differences between subspecies**

The descriptive statistics of characters that showed significant differences between the subspecies, with emphasis on those used in the dendrograms, are summarized in Tables V (males) and VI (females), with the levels of significance of the differences.

**Summary of additional differences between the subspecies**

Beyond the quantitative differentiation (Tables V, VI), the two subspecies differ in additional ways.

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**Figure 6.** Dendrogram of 16 female *Laudakia stellio* sspp., all whole-tailed, based on 26 characters.
In life, in *Laudakia stellio stellio* (but not in *L. s. daani*) the head is coloured yellow-red in contrast with the grey body (see Introduction), and in museum specimens this often remains indicated (Figure 2).

Sexual dimorphism differs between the two subspecies: as reported above, in *L. s. daani* it concerns mainly body proportions but in *L. s. stellio* mainly coloration. This trend is reflected also in the analysis of correlations (Tables III, IV).

The association of inter-character correlations differs between the two subspecies (compare Tables III and IV): for example the length of the fourth toe is significantly correlated in *L. s. daani* only with head flatness, but in *L. s. stellio* it is, instead, correlated with hindlimb length and tail length, and negatively with RA and the dorsal scales index. The numbers of supralabialia and of subdigital lamellae are correlated only in *L. s. daani*. In contrast, the number of rings on the tail is correlated with RA and with the width of the dorsal blotches only in *L. s. stellio*.

The frequency of occurrence of “cryptic males” may constitute another difference: in *L. s. daani* only one out of 30 males was “cryptic” but in *L. s. stellio* six out of 16 males were “cryptic” (Chi-square test, $P<0.01$). Unfortunately, collecting may have been biased (see Introduction).

Key for identification of Aegean *Laudakia stellio*

The following key is derived from the data in Tables V and VI.

1. A mid-ventral longitudinal crest or band of callous or glandular scales (males) . 2
   - No mid-ventral longitudinal crest or band of callous or glandular scales (females) . 3
2. Head dorsally commonly coloured like back or darker. Mid-dorsal blotch width usually $>7$ PERCRA. Throat spotted at least anteriorly, usually at least over half
Table V. Differences between males of *Laudakia stellio daani* and *Laudakia stellio stellio*.

| Character                      | *Laudakia stellio daani* |               | *Laudakia stellio stellio* |               | n  | P    |
|-------------------------------|--------------------------|---------------|---------------------------|---------------|----|------|
|                               | Mean         | SD           | Range                    | n             |    |      |
| RA length                     | 118.0        | 114.6        | 99.0–135.0               | 18            | 15 | 0.054|
| Head length                   | 25.9         | 1.82         | 21.2–29.2                | 18            | 15 | 0.006|
| Head width                    | 28.0         | 2.66         | 23.6–32.3                | 18            | 15 | 0.046|
| Head index                    | 93.4         | 12.11        | 66.2–112.2               | 18            | 15 | 0.041|
| Head flatness                 | 169.3        | 29.39        | 131.4–263.7              | 18            | 15 | 0.002|
| Forelimb length               | 49.9         | 2.22         | 45.4–54.9                | 18            | 15 | 0.028|
| Hindlimb length               | 72.0         | 4.35         | 63.6–79.5                | 18            | 15 | 0.008|
| Ventral scales index          | 957.6        | 84.5         | 801–1116                 | 18            | 15 | 0.068|
| Preanal glandular scales*     | 41.7         | 10.65        | 13–56                    | 18            | 15 | 0.000|
| Subdigitalia, L              | 19.8         | 1.46         | 17–22                    | 18            | 15 | 0.005|
| Subdigitalia, R              | 19.6         | 1.62         | 16–23                    | 18            | 15 | 0.031|
| Distinctiveness of coloration | 0.27         | 0.59         | 0–2                      | 15            | 15 | 0.000|
| Dorsal blotch width*          | 8.24         | 1.70         | 6.0–11.5                 | 13            | 11 | 0.007|
| Transverse bars, presence    | 0.69         | 0.48         | 0–1                      | 16            | 11 | 0.007|
| Transverse bars, length       | 22.2         | 25.53        | 16.9–24.8                | 10            | 2  | 0.000|
| Throat ground colour          | 0.62         | 0.5          | 0–1                      | 16            | 15 | 0.046|
| Throat pattern*               | 2.5          | 1.32         | 1–4                      | 16            | 15 | 0.000|
| Venter, ground colour         | 0.5          | 0.52         | 0–1                      | 16            | 15 | 0.007|
| Tail, distinctiveness         | 0.31         | 0.48         | 0–1                      | 16            | 15 | 0.051|

*Character used in the key.*
the area. Venter light or dark. Preanal glandular scales usually.

3. Head dorsally commonly coloured yellow or red or lighter than the back. Mid-dorsal blotch width usually <7 PERCRA. Throat usually spotted only anteriorly, or not at all. Venter almost always light. Preanal glandular scales usually <30. L. s. daani

3. Head dorsally commonly coloured like back or darker. Mid-dorsal blotch length usually <11 PERCRA. Ring pattern on tail base distinct or indistinct. L. s. stellio

– Head dorsally commonly coloured yellow or red or lighter than the back. Mid-dorsal blotch length usually >11 PERCRA. Ring pattern on tail base always distinct. L. s. stellio

Finally, we applied this key to the specimens that had not participated in the main analyses (n=60). Juveniles under 90 mm RA usually could not be sexed with certainty and their subspecific characters were poorly differentiated (n=20). Among the adults, most were easily identified to one of the two subspecies, though in a few specimens one of the characters deviated (n=37; 2.5%). One additional specimen was clearly identified (MTKD 27992, as L. s. daani) but in the absence of locality data there was no control for this. Only two specimens, both females, appeared to be intermediate (NMW 24603:15; SMF 39342).

**Table VI. Differences between females of Laudakia stellio daani and Laudakia stellio stellio.**

| Character                  | Laudakia stellio daani |       |       | n  | Laudakia stellio stellio |       |       | n  | P   |
|----------------------------|------------------------|-------|-------|----|-------------------------|-------|-------|----|-----|
| Dorsal scutellation pattern| 7                      | 0.95  | 6–10  | 15 | 8.4                     | 2.14  | 6–10  | 10 | 0.076|
| Subdigitaria, L            | 19.3                   | 1.50  | 17–22 | 15 | 18.4                    | 1.41  | 16–21 | 10 | 0.103|
| Subdigitaria, R            | 19.6                   | 1.32  | 18–22 | 15 | 18.5                    | 1.13  | 17–20 | 10 | 0.045|
| Dorsal pattern categories  | 1.08                   | 1.20  | 0–3   | 12 | 0                       | 0     | 0–0   | 10 | 0.008|
| Dorsal blotch length       | 9.69                   | 2.14  | 4.92–12.36 | 11 | 12.93                   | 1.64  | 10–14.87 | 10 | 0.001|
| Transverse bars, presence  | 0.33                   | 0.49  | 0–1   | 15 | 0                       | 0     | 0–0   | 10 | 0.019|
| Throat pattern             | 2.92                   | 1.33  | 0–1   | 12 | 1.70                    | 1.75  | 0–0   | 10 | 0.071|
| Tail, distinctiveness      | 0.47                   | 0.52  | 0–1   | 15 | 0                       | 0     | 0–0   | 10 | 0.003|

aCharacter used in the key.

**Discussion**

Despite the small samples (due to time constraints), the initial question that generated this project has received, through straightforward statistics, a clear answer. Phenetic cluster analysis of 26 male specimens of Laudakia stellio from localities scattered over Greece, the Aegean islands and much of Anatolia yielded two distinct main clusters. The geographical origin of the specimens of one cluster, from the Mykonos archipelago, and remnants of their live coloration (yellow-red head), identify them as L. s. stellio. Specimens of the other cluster agree in geography and coloration with L. s. daani Beutler and Frör, 1980, which therefore is validated, overruling the doubts of Baig (1992). Similar analysis, but with selectivity of characters, of 16 female specimens yielded a similar, if less clear-cut, picture.
Altogether the “75% rule” for difference between subspecies (Mayr 1969) seems fulfilled. Moreover, viewed by t test, several characters statistically differed between the two subspecies, some without overlap between their ranges of variation. In this context it should be remembered that the heavy criticism of the proliferation of named subspecies (Wilson and Brown 1953) does not equally apply to island systems (Mayr and Ashlock 1991).

Still, our results may seem dubious because the outcomes of tests changed when samples were enlarged—so, are even the enlarged samples appropriate? But in this case the samples, especially that of L. s. stellio, were enlarged by specifically adding broken-tailed individuals to samples originally comprising only whole-tailed individuals. Hence the change in results may be explained by the recently discovered phenomenon, which we might call the “Seligmann effect”, that among conspecific lizards the tail-losers differ biometrically from the tail-retainers (Seligmann 2001; Seligmann et al. 2003). In other words, tail-losers (as a statistical group) differ genetically from tail-retainers, and it is only natural that adding them would affect the biometry. There may be here a general caveat for taxonomic work in comparable cases.

Furthermore, It should be noted that the success of the cluster analysis underlying this validation of systematics depended (for the females) on an advised selection of characters to use. Inger (1961) reviewed discordant variation of characters in several vertebrate species, and discussed how this precludes the definition of subspecies. Highton (1962), in his revision of North American salamanders of the genus Plethodon, depicted the geographically discordant variation of seven colour characters in the monotypic P. jordani, while confirming subspeciation in five other species of the genus. In the case of Laudakia stellio we first tested correlation among all recorded characters, intending to exclude from the cluster analysis those characters not involved in any significant correlation. This approach became impractical when it transpired that the list of correlations differed profoundly between the presumed subspecies. We needed to resort to selecting characters directly for their apparent bimodal distribution; only then did the subspeciation emerge for the females.

The fact that the identification of related taxa seems easier for males than females (compare Tables V and VI) is not surprising in sexually dimorphic, and especially sexually dichromatic, lizards with a social structure involving territoriality and maybe male dominance. A conspicuous example is provided by the Chamaeleonidae of Africa and Madagascar: in many species the males differ from females through carrying species-specific horns or hypertrophied crests, which greatly facilitate their identification to species (Rand 1961; Necas 1995). Similarly, in the diurnal geckos of the genus Gonatodes in Trinidad and Tobago, the colourful males of the four species differ from each other much more sharply than the more cryptically coloured females (Murphy 1997).

Some of the differences between the two subspecies considered here (Table V) parallel differences known between other subspecies of Laudakia stellio. For example, L. s. brachydactyla differs from the parapatric L. stellio ssp. of central Israel, among other things, in relative limb length (Izhaki and Haim 1996). But the reality of the two subspecies as independent entities is especially shown by their being different also in traits other than those quantified and participating in the cluster analyses. First, the fact that the list of significant inter-character correlations differs between the two probably indicates some difference in selection pressures, in the responses to these, or in both. Second there is a group of possibly inter-related phenomena: (1) Compared to Laudakia stellio daani, L. s. stellio is more colourful with yellow or red head. (2) In L. s. daani the sexual dimorphism is chiefly mensural, including a great difference in relative head size, while in L. s. stellio the emphasis is on dichromatism. This difference probably reflects very different
selection pressures, related to food in the former but sexual in the latter (Shine 1989). (3) The L. s. stellio population (unlike L. s. daani) tentatively seems to include many “cryptic males”, which, as has been suggested (W. Böhme, personal communication), may be socially subordinate. The counterpart of this phenomenon may be the documented occurrence of callous glandular scales in some of the females of certain congener, which is presumed to relate to their territorial behaviour (Baig and Böhme 1991). All these peculiarities may reflect a different social structure and also different intraspecific communication, a subject begging investigation. Thus there is more to the essence of these subspecies than a mere biometrical distinction.

The question of the eastern boundary of Laudakia stellio daani remains open. As mentioned in the Introduction, Beutler and Frör (1980), when describing this taxon, were uncertain of this point. Baran and Öz (1985), Baran and Atatür (1998) and Göçmen et al. (2003) accepted the presence of L. s. daani in western Anatolia but assigned the populations of south-eastern Anatolia (including the Hatay region) to L. s. stellio, assuming its disjunct distribution, and without reporting from this area the precise bright head coloration (yellow-red) that characterizes topotypical L. s. stellio. Three specimens from this area (Adana, MTKD 37843; Antakya, HUJ-R 11935; Iskenderun, HUJ-R 7065) participated in our cluster analyses; one (Antakya, HUJ-R 11935) clustered within the L. s. stellio branch (Figure 5) and the other two clustered as L. s. daani (Iskenderun, HUJ-R 7065, Figures 6, 7; Adana, MTKD 37843, broken-tailed female, not shown). Thus our limited project in itself provides no evidence supporting the view of L. s. stellio as a polytopic subspecies (Mayr 1969), and the question of the eastern boundary of L. s. daani remains to be addressed, preferably within a broader study of variation in the species.

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Appendix

Material examined

Laudakia stellio daani (Greece and Aegean)

Antiparos: LM 91/1972/1–91/1972/8.
Chios: NHMC 80.3.93.31; SMF 10195–10200.
Ikaria (terra typical): NMW 24604/8, 24604/9, 30974/1, 30974/3, 30989/3.
Korfu: SMF 56762, 66811.
Kos: NMW 24604/2.
Naxos: NHMC 80.3.93.29, SMF 40009; NMW 24603/10–24603/15.
Paros: NHMC 80.3.93.30; NMW 24603/1, 24603/4.
Piscopi (= Tilos): SMF 37665.
Rhodos: HUJ-R 7929, 14806; MTKD 16062, 16063; SMF 55245, 55403, 55410, 61933, 70164.
Saloniki (nr.): HUJ-R 14810; SMF 36394, 39342.
Samos: NMW 7297/1, 27584/1, 30989/4.

**Laudakia stellio daani** (Anatolia)

Adana: MTKD 41047, TAUR 8703–8706.
Adana (30 km N of): MTKD 37843.
Antakya: HUJ-R 11935.
Artemision: HUJ-R 11938–11946.
Bornova-Manisa: HUJ-R 10617.
Demircili: HUJ-R 18324.
Diarbekir: TAUR 8707.
Ephesus: HUJ-R 10618, 11937.
Iskenderun: HUJ-R 7065.
Kizkalesi: HUJ-R 10616, 11934, 11936.
Lagina: MTKD 25786.
Menderistal (S Selcuk): HUJ-R 10615.
Saimbeyli (Kozan-Devili): HUJ-R 18325.
Selcuk: MTKD 25290, 25291.
Turunc, Loryma peninsula: MTKD 39502.

**Laudakia stellio stellio**

Delos (terra typical): SMF 58553; ZFMK 2060–2075, 3089.
Mykonos: LM 410/1976/1–410/1976/11; MTKD 25701, 25789, 25790; SMF 10194; ZFMK 2076–2079.