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On the Phylogeny and Taxonomy of the Genus *Uromastyx* Merrem, 1820 (Reptilia: Squamata: Agamidae: Uromastycinae) – Resurrection of the Genus *Saara* Gray, 1845

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Abstract. We assessed the taxonomic relationships within the genus *Uromastyx* Merrem, 1820 using morphological and genetic methods, resulting in the resurrection of the genus *Saara* Gray, 1845 for *Saara hardwickii*, *S. asmussi* and *S. loricata* and in changes of the taxonomic rank of *Uromastyx nigriventris*, *U. aegyptia leptieni* and *U. shobraki*. A synopsis of all taxa considered to be valid is provided, including differential diagnosis, description and data on their respective distribution. A key for the species of *Saara* and *Uromastyx* is presented.

Keywords. Reptilia; Sauria; Agamidae; Uromastycinae; *Uromastyx*; *Saara*; *Saara hardwickii*; *Saara asmussi* new comb.; *Saara loricata* new comb.; *Uromastyx aegyptia leptieni* new status; *Uromastyx nigriventris* new status; *Uromastyx shobraki* new status; Phylogeny; Taxonomy; Morphology.

1. INTRODUCTION

Within the Palearctic genus *Uromastyx* Merrem, 1820 a total of 17 species are considered to be valid by Wilms & Schmitz (2007) and Wilms & Böhme (2007). Some of the species respective subspecies belonging to that genus have been described quite recently (e. g. *Uromastyx dispar maliensis* Joger & Lambert, 1996; *Uromastyx occidentalis* Mateo et al., 1998; *Uromastyx leptieni* Wilms & Böhme, 2000; *Uromastyx alfredschmidti* Wilms & Böhme, 2001; *Uromastyx y. yemenensis* Wilms & Schmitz, 2007, and *Uromastyx y. shobraki* Wilms & Schmitz, 2007) reflecting a continuing scientific interest in the phylogeny and taxonomy of these animals.

Uromastyx spp. are medium sized to large lizards inhabiting the old world desert belt from North Africa to north western India. All species are either ground dwellers or saxicolous, with some species climbing occasionally on trees. *Uromastyx* are predominantly herbivorous, feeding on the scarce vegetation in their desert environment. Ecologically these animals are largely limited by the availability of food and by the availability of appropriate thermal refuges.

Uromastyx spp. are currently listed on Appendix II of CITES. Internationally more than 367 000 specimens have been traded legally in the pet trade between 1977 and 2005 (Knapp 2004, Wilms 2007a). But the consumption of spiny-tailed lizards in their countries of origin may be considerably higher due to the fact, that *Uromastyx* are heavily hunted for food and for the production of souvenirs and traditional medicine (Wilms 2007a).

The main aim of the present paper is to evaluate the phylogenetic relationships within the taxa of the genus *Uromastyx* and to establish a hypothesis of the taxonomy of this group, based on a synthesis of morphological and genetic characters.

Taxonomic History

The taxonomic history of the lizards currently assigned to the genus *Uromastyx* dates back to the second half of the 18th century [description of *Lacerta aegyptia* Forsskål, 1775; for more detailed information on the history of this taxon see Wilms & Böhme 2000 a. For a discussion on the spelling of Pehr Forsskål's family name see Friis & Thulin (1984)].

The genus name *Uromastyx* was coined by Merrem in his work 'Versuch eines Systems der Amphibien – Tentamen Systematis Amphibiorum' (Merrem 1820). Of the seven species included in this first synopsis of the genus only

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one is belonging to *Uromastyx* as it is currently defined [*Uromastyx spinipes* (Daudin, 1802) = *Uromastyx aegyptia* (Forsskål, 1775)].

Between 1822 and 1885 a total of five new genera (*Mastigura* Fleming, 1822; *Centrocercus* Fitzinger, 1843; *Saara* Gray, 1845; *Centrotrachelus* Strauch, 1863; *Aporoscelis* Boulenger, 1885) were erected for different members of the genus *Uromastyx* of which only *Aporoscelis* and *Centrotrachelus* were considerably in use (e. g. Anderson 1894, 1896, 1901; Blanford 1874, 1881; von Bedriaga 1879; Murray 1884; Scortecci 1933; Ninni 1933; Parker 1942; Haas & Werner 1969). *Aporoscelis* was used in the rank of a subgenus by Joger (1987). The name *Centrocercus* Fitzinger, 1843 is preoccupied by *Centrocercus* Swainson, 1832 (Aves, Phasianidae) and is therefore not available. The main taxonomic problem within *Uromastyx* was the proper delimitation of taxon boundaries on the specific and subspecific level, which led in the past to considerable confusion on the identity of diverse taxa (for more detailed information see Wilms & Böhme 2000 a, 2000 b, 2001).

Beside studies based on external morphology (e. g. Mertens 1962; Moody 1987; Wilms & Böhme 2000 a, 2000 b; Wilms & Böhme 2001; Wilms & Schmitz 2007) and immunology (Joger 1987), some recent papers also adress this issue by employing molecular genetic methods (Amer & Kumazawa 2005; Wilms & Schmitz 2007; Harris et al. 2007). Nevertheless some aspects of the taxonomy of these highly specialized desert lizards still remain unclear.

On the basis of external morphology and immunological distances it is well established, that several species groups within *Uromastyx* are recognizable, but the relationships and species compositions of these groups are still under debate (Joger 1986; Moody 1987; Wilms 2001; Amer & Kumazawa 2005; Wilms & Schmitz 2007).

2. MATERIAL AND METHODS

Morphological sampling and analysis

621 specimens of the genus *Uromastyx*, including the type material of the relevant taxa have been examined. The specimens are deposited in the following collections (Institutional abbreviations in parenthesis): The Natural History Museum, London (BMNH); Naturhistorisches Museum Wien (NMW); Museo Zoologico de „La Specola", Firenze (MZUF); Muséum d'Histoire Naturelle, Genève (MHNG); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum für Tierkunde, Dresden (MTKD); National Museum, Museum of Natural History Prague (NMP6V); Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt a. M. (SMF); Zoologisches Forschungsmuseum A. Koenig, Bonn (ZFMK); Zoologisches Museum der Universität Hamburg (ZMH); Museum für Naturkunde, Humbold-Universität, Berlin (ZMB) and Zoologische Staatssammlung München (ZSM). For a list of examined specimens see Appendix II.

For each specimen 25 external characters (16 meristic, 6 metric, 3 qualitative) have been routinely recorded: snout-vent length (SVL), length of tail (TL), head width between the anterior margins of the ear openings (HW), head length from the tip of the snout to the anterior margin of the ear opening on the left side (HL), width of tail between the 4th and 5th whorl (TW), maximum tail width at the 5th whorl (TW_{max}), number of tail whorls (W), number of scales beneath the 4th toe on the left side (SD), number of gular scales (from mental to a line between the anterior margins of the ear openings (G)), number of scales around mid-body (MBS), number of scales between gular- and inguinal fold (V; ventrals), number of scales around the 5th whorl (SW), number of preanofemoral pores (PP; left and right), number of enlarged scales at the anterior margin of the ear opening (LS; left and right), number of scales between suboculars and supralabials (SO; left and right), number of scales from the mid of the lower end of the ear opening to the mental scale (HS; left and right), number of scales from the upper to the lower end of the left ear opening (ES; approximately three scale rows before the anterior margin of the ear opening), number of scales from the upper end of the left ear opening to the first enlarged subocular scale (PES), presence or absence of enlarged tubercular scales at the flanks (TF; absent = 0 / present = 1), enlarged tubercular scales at the dorsum (TD; absent = 0 / present = 1 / arranged in rows = 2), intercalary scales between the whorls present or absent (IS; absent = 0 / 1–2 unkeeled present = 1 / 2–6 keeled present = 2). Measurements were taken to the nearest 0.5 mm using a calliper.

To obtain morphological outgroup data from the closest relatives of *Uromastyx* several vouchers of the genus *Leiolepis* from the collection of the ZFMK were examined.

Statistical analyses of morphological data

The Excel 2000 and SPSS (10.0) statistical packages were used to run the analyses. Hierachical Cluster analysis and Principal Component Analysis (PCA) have been selected to evaluate the morphological data and to explore the phenetic relationships between the taxa examined.

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Phylogenetic analysis of morphological data

Phylogenetic analysis was carried out on the basis of twenty-five external characters (16 meristic, 6 metric, 3 qualitative). To assign a polarity to these characters (plesiomorphy vs. apomorphy), ingroup and outgroup comparisons were applied (WATROUS & WHEELER 1981; MADDISON et al. 1984). Species of the genus *Leiolepis* were used as outgroup, because this genus forms the morphologically and genetically proposed sister clade to *Uromastyx* (PETERS 1971; BÖHME 1988; SCHMITZ et al. 2001; AMER & KUMAZAWA 2005). Within the genus *Leiolepis* seven taxa are distinguished: *L. belliana* HARDWICKE & GRAY, 1827; *L. guttata* CUVIER, 1829; *L. revesii* GRAY, 1831; *L. pegnensis* PETERS, 1971; *L. triploida* PETERS, 1971; *L. guentherpetersi* DAREVSKY & KUPRIYANOVA, 1993 and *L. boehmei* DAREVSKY & KUPRIYANOVA, 1993 of which three are 'agamospecies' (*L. triploida, L. guentherpetersi* and *L. boehmei*; DAREVSKY & KUPRIYANOVA 1993), which do not require fertilisation of female gametes to produce offspring.

For thirteen of the twenty-five characters polarity was unanimously assignable. These characters (ten two-state and three multistate) were defined for one outgroup (*Leiolepis*) and all twenty-three taxa in this study. A character matrix (Table 1) was designed using Nexus Data Editor (PAGE 2001) and analysed in PAUP* v4.0b10 (SWOFFORD 2002) using both neighbour-joining (NJ) and maximum parsimony (MP) algorithms. MP was run using a heuristic search and 2000 bootstrap pseudoreplicates. Detail of the character definition and coding is provided in Appendix III.

Genetic sampling

Samples of muscle tissue were taken from fresh specimens as well as from preserved specimens kept in the collection of the ZFMK, Bonn. New voucher specimens are now also kept in the herpetological collection of the ZFMK and the National Museum, Museum of Natural History Prague (NMP6V) (for a complete list of voucher specimens see Table 2).

DNA was extracted from the tissue samples using QuiAmp tissue extraction kits (Quiagen) or a modified Chelex-Protocol (WALSH et al. 1991; SCHMITZ 2003). The primers 16sar-L (light chain; 5' - CGC CTG TTT ATC AAA AAC AT - 3') and 16sbr-H (heavy chain; 5' - CCG GTC TGA ACT CAG ATC ACG T - 3') of PALUMBI et al. (1991) were used to amplify a section of the mitochondrial 16S ribosomal RNA gene. PCR cycling procedure was as described in SCHMITZ et al. (2005).

To get a better resolution within two identified clades of very closely related taxa (compare below), 12S rRNA data for representatives of those clades were added and separate trees were produced. Therefore, in these cases we amplified a section of the mitochondrial 12S ribosomal RNA gene using the primers 12SA-L (light chain; 5' - AAA CTG GGA TTA GAT ACC CCA CTA T - 3') and 12SB-H (heavy chain; 5' - GAG GGT GAC GGG CGG TGT GT - 3') of KOCHER et al. (1989). Cycling procedure was again identical as described in SCHMITZ et al. (2005).

PCR products were purified using Qiaquick purification kits (Qiagen). Sequences (including complimentary strands for assuring the accuracy of the sequences) were obtained using an automatic sequencer (ABI 377). Sequences were aligned using ClustalX (THOMPSON et al. 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (HALL 1999). For the full dataset we performed neighbour-joining (NJ), and Bayesian reconstructions (PP), while for the two extended dataset we also calculated maximum parsimony trees. We used PAUP* 4.0b10 (SWOFFORD 2002) to compute the neighbor-joining tree, maximum parsimony tree and the uncorrected pairwise distances for all sequences. For the additional MP analysis of the combined 16S and 12S datasets, we used the heuristic search algorithm of PAUP* (SWOFFORD 2002) with 100 random additions per replicate and the TBR (tree bisection-reconnection) branch swapping option. Additionally, we used bootstrap analyses with 2000 pseudoreplicates to evaluate the relative branch support in the phylogenetic analysis. For the Bayesian analysis parameters of the model were estimated from the data set using MrModeltest 2.2 (NYLANDER 2004) and the analyses were performed with MrBayes, version 3.0b4 (HUELSENBECK & RONQUIST 2001). The comparison between the different likelihood scores for each model showed that the GTR + Γ model (YANG 1994) was determined to be the optimal model for the data set. For the Bayesian analyses we ran two MCMC analyses for 10^6 generations each. The initial 100000 (10%) trees were disregarded as "burn-in". We consider probabilities of 95 % or greater to be significantly supported. The exact parameters used for the Bayesian analyses followed those described in detail by REEDER (2003).

Sixty-four 16S sequences comprising 555 bp (lengths referring to the aligned sequences including gaps) as well as thirty-two 12S sequences comprising 434 bp were obtained. Sequences have been submitted to GenBank; for accession numbers see Tab. 2. *Tympanocryptis tetraporophora* Lucas & Frost, 1895 (Agamidae: Amphibolurinae), *Agama impalearis* Boettger, 1874 (Agamidae: Agaminae), *A. planiceps* Peters, 1862 (Agamidae: Agaminae), *Leiolepis b. belliana* Hardwicke & Gray, 1827 (Agamidae, Leiolepidinae), *L. r. reevesii* Gray, 1831

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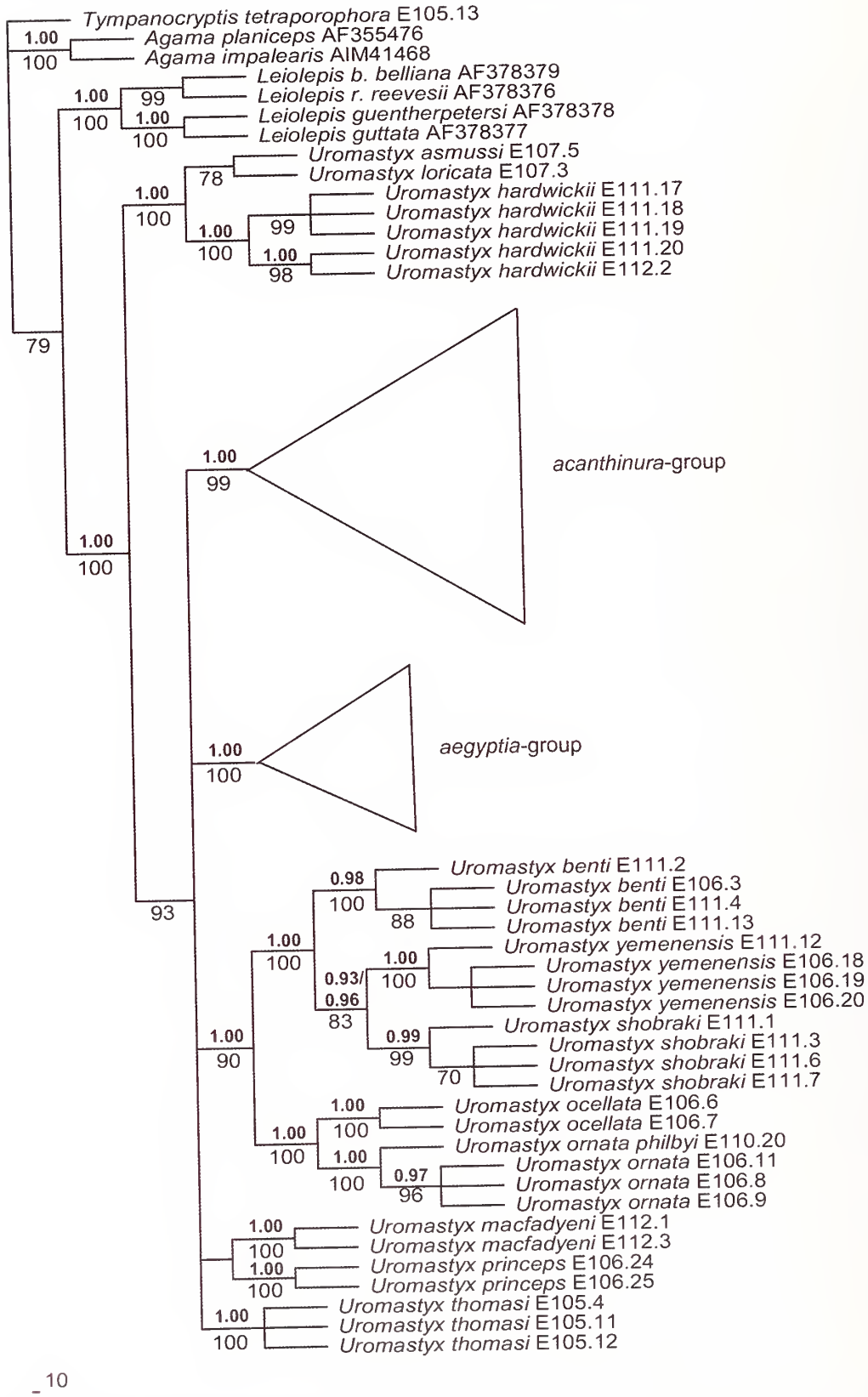

Fig. 1. Cladogram of the tree recovered by the analyses based on 555 bp of the 16S mitochondrial RNA gene. Upper (bold) values at the nodes are Bayesian posterior probabilities (values below 0.5 not shown); lower values are neighbor-joining bootstrap replicates (values below 50 % not shown).

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(Agamidae, Leiolepidinae), *L. guentherpetersi* Darevsky & Kupriyanova, 1993 (Agamidae, Leiolepidinae) and *L. guttata* Cuvier, 1829 (Agamidae, Leiolepidinae) were used as outgroup. 16S Sequences for all species used as outgroup, with the exception of *T. tetraporophora*, have been obtained vom GenBank.

3. RESULTS

Results of the phylogenetic analysis of genetic data

Uromastyx sensu lato and *Leiolepis* group together in a large clade supported by a neighbour joining bootstrap value of 79 (Fig. 1) and is the sister group to a clade including *Agama planiceps* and *A. impalearis*. Within this clade *Leiolepis* and the ingroup are separated in fully supported subclades (PP: 1.00 / NJ: 100 for *Leiolepis*; PP: 1.00 / NJ: 100 for *Uromastyx* sensu lato). The ingroup itself forms again two well separated clades: in the first one *U. hardwickii* groups with the sister species *U. asmussi* and *U. loricata*, while in the second all other taxa of the genus *Uromastyx* are present (*Uromastyx* sensu stricto). Both clades are supported at least by very high and significant NJ bootstrap values (*U. hardwickii*, *U. asmussi*, *U. loricata* clade: PP: 1.00 / NJ: 100; *Uromastyx* s. s.: PP: <0.95 / NJ: 93).

Genetic distances (uncorrected p-distances, 16S rRNA gene) from *U. hardwickii*, *U. asmussi* and *U. loricata* to all other taxa are as follows: *hardwickii*: 10.2–14.2 %, *asmussi*: 8.6–13.0 %, *loricata*: 8.2–12.1 %.

Within *Uromastyx* sensu stricto five well supported clades are recognizable but the direct relationships of these clades are not resolved, as they are forming an unresolved polytomy.

Uromastyx hardwickii, *U. asmussi* and *U. loricata* clade

The clade including these three afore mentioned species shows a substructure with two principal subclades. Beside the clade consisting of the sister taxa *U. asmussi* and *U. loricata* (NJ: 78), a second well supported clade (PP: 1.00 / NJ: 100) comprising all five *U. hardwickii*-specimens. This latter clade also shows another clear separation with taxa-units of three and two *hardwickii*-specimens respectively and both these terminal clades are significantly supported by at least one bootstrap value (ZFMK 83794, 83795, 83797: NJ: 99; ZFMK 83796, sample without voucher specimen: PP: 1.00 / NJ: 98). We preliminarily assigned the second subcluster exclusively to *Uromastyx hardwickii*, but data suggest that in fact two taxa may be involved (see also discussion).

Genetic distances between the taxa of the *Uromastyx hardwickii*, *U. asmussi* and *U. loricata* clade are as follows: *asmussi-loricata*: 2.9 %; *asmussi-hardwickii*: 5.8–6.5 %; *loricata-hardwickii*: 6.1–6.7. Distance between the two identified subclades within *hardwickii* is rather low at 0.9 %.

Uromastyx sensu stricto clade

Based on the genetic data four of the five clearly recognizable clades are strongly supported by bootstrap values: *Uromastyx acanthinura* group (PP: 1.00 / NJ: 99); *U. aegyptia* group (PP: 1.00 / NJ: 100); *U. ocellata* group (PP: 1.00 / NJ: 90) and *U. thomasi* (PP: 1.00 / NJ: 100). The fifth clade comprising *U. macfadyeni* and *U. princeps* is only very weakly supported. To get a better resolution within the *U. acanthinura* and the *U. aegyptia* clades 12S rRNA data were added and separate trees were produced.

Uromastyx acanthinura group

Based on the genetic data the *U. acanthinura* clade (Fig. 1), including the taxa *geyri*, *acanthinura*, *nigriventris*, *dispar*, *flavifasciata* and *maliensis* (*alfredschmidti* was not included in this analysis due to the non-availability of DNA samples), is very well supported by bootstrap values (PP: 1.00 / NJ: 99). Intraspecific genetic distances within all taxa of the *U. acanthinura* group was 0.0–0.4 % (exception *U. geyri*: 0.9 %). Between the taxa of this group, genetic distances are 0.2–1.4 %. On the basis of these data, decisions on the rank of the taxa in question were not possible. To further enhance the resolution of the tree, 12S rRNA data were combined with the 16S rRNA data and new trees were produced using *U. ornata* as outgroup (Fig. 2). The newly calculated tree shows the *geyri* clade basal to all other taxa within the *U. acanthinura* group. This clade is maximally supported (PP: 1.00 / NJ: 100 / MP: 100) and forms the sister taxon to all other members of the *U. acanthinura* group, which form a clade significantly supported by bootstrap values (NJ: 88 / MP: 100). This clade shows a very well supported substructure with *nigriventris* being the sister taxon (PP: 1.00 / MP: NJ: 100 / MP: 100) of the clade including *acanthinura* and *U. dispar* spp. On the basis of this tree, *acanthinura* is the sister taxon to the clade comprising the taxa *dispar*, *flavifasciata* and *maliensis* with both clades being significantly supported by at least NJ and MP bootstrap values (*acanthinura* clade: PP: 0.97/0.95 / NJ: 100 / MP: 100; *dispar* clade: PP: 0.75/0.80 NJ: 85 / MP: 90). As it was not possible to win a 12S DNA-sequence from the only available representative of *maliensis* and we still wanted to include all described taxa in our analyses, we filled the missing 12S sequence information with "N"s and calculated the phylogenetic trees both with and without the inclusion of *maliensis*. This was done to check if the inclusion of the

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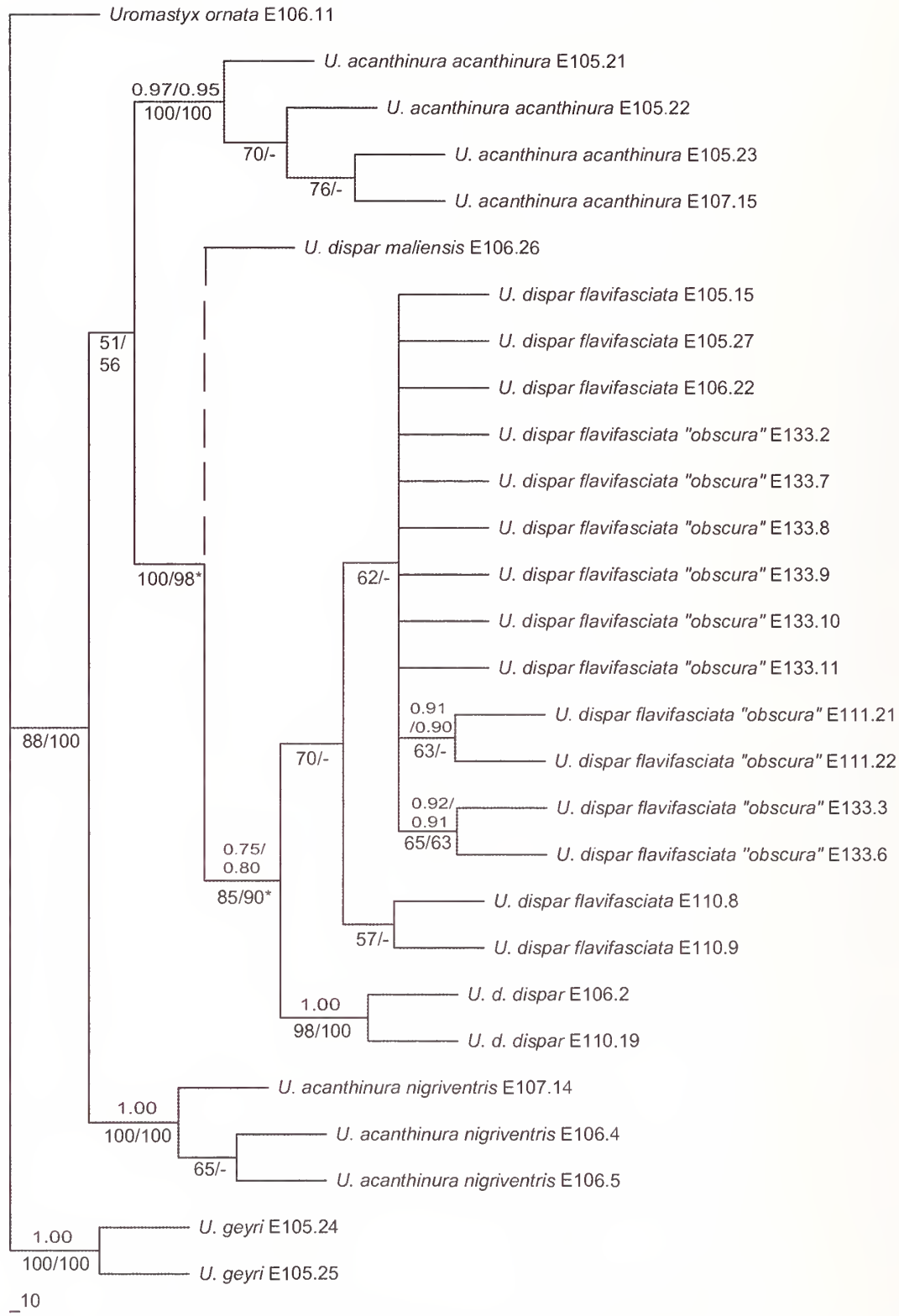

Fig. 2. Cladogram of the tree recovered by the analyses based on 989 bp of the combined 16S and 12S mitochondrial RNA genes. Upper values at the nodes are Bayesian posterior probabilities (values below 0.5 not shown); lower values on the right are maximum-parsimony bootstrap replicates; lower values on the left are neighbor-joining bootstrap replicates (values below 50 % not shown). The line connecting to *Uromastyx dispar maliensis* is dotted to incorporate the fact that we were not able to get a 12S sequence for this species and that we had to fill up the alignment with "N"s to include the species in the calculation.

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incomplete sequence would alter the tree topologies. As this was not the case, we added the sequence and have marked its calculated position with a broken line.

Within the *dispar* clade three fairly well supported subunits are recognizable (for exact bootstrap values see Fig. 2), corresponding to the currently valid subspecies *dispar*, *flavifasciata* and *maliensis*, while the recently described "*obscura*"-form is included in and identical (no genetic difference) with *flavifasciata*.

Intraspecific genetic distances within the terminal taxa (lumping data for the subspecies of *U. dispar*) are: *acanthinura*: 0.0-0.1%, *nigriventris*: 0.0–0.1%, *geyri*: 0.4%, *dispar*: 0.0–0.7%. Distances between the taxa are: *acanthinura-geyri*: 4.57–4.69 %, *nigriventris-geyri*: 4.46–4.57 %, *dispar-geyri*: 4.21–4.99 %, *acanthinura-nigriventris*: 2.0–2.3 %, *acanthinura-dispar*: 1.54–2.44 %, *nigriventris-dispar*: 1.72–3.08 %.

Uromastyx aegyptia group

The calculation for the extended dataset for the taxa of the *U. aegyptia*-group produced an identical topology (tree not shown) for all three algorithms, with the following structure [numbers are bootstrap values (PP/NJ/MP) for the following nodes; significant values in bold; values below 0.90 (PP) or under 50 (NJ/MP) (*) not shown]:

(*Uromastyx ornata*), */**100** (*Uromastyx a aegyptia*, */59/55 (*Uromastyx a. microlepis*, 0.94/55/52 (*Uromastyx a. microlepis*, **1.00**/93/94 (*Uromastyx leptieni*, *Uromastyx leptieni*))))

Within taxa genetic distances are extremely low: *microlepis*: 0.10 %, *leptieni*: 0.13 % (for *aegyptia* only a single specimen was sequenced), while between the different taxa genetic difference were comparatively much higher: *aegyptia-microlepis*: 0.3–0.4 %, *microlepis-leptieni*: 0.3–0.6 %, *aegyptia-leptieni*: 0.7–0.9 %.

Uromastyx ocellata group

The *Uromastyx ocellata* group constitutes a further well supported clade (Fig. 1) which is itself again subdivided: the first main clade comprises the taxa *ornata* (including the single specimen of *philbyi*) and *ocellata* (PP: 1.00 / NJ: 100). Both of the nominal taxa are clearly separate species-units (PP: 1.00 / NJ: 100).

The second clade comprises a well supported substructure, consisting of three subclades which correspond to the taxa *benti*, *yemenensis* and *shobraki* (PP: 1.00 / NJ: 90). Each of these taxa is fully supported (*benti*: PP: 0.98 / NJ: 100; *yemenensis*: PP: 1.00 NJ: 100; *shobraki*: PP: 0.99 / NJ: 99).

Intraspecific genetic difference is very low: *benti*: 0.0–0.4 %, *yemenensis*: 0.0–0.2, *shobraki*: 0.0–0.2, *ocellata*: 0.2 %, *ornata* (without *philbyi*): 0.0 %. As expected, the interspecific genetic distances are much higher: *benti-yemenensis*: 2.2–2.7 %, *benti-shobraki*: 2.2–2.9 %, *yemenensis-shobraki*: 1.8–2.0 %, *benti-ocellata*: 6.5–7.2 %, *benti-ornata*: 5.8–6.3 %, *yemenensis-ocellata*: 7.2–7.4 %, *yemenensis-ornata*: 6.5 %, *shobraki-ocellata*: 7.0–7.4 %, *shobraki-ornata*: 6.5–7.0 %, *ocellata-ornata* (including *philbyi*): 3.6–4.0 %. Genetic difference between *ornata* and *philbyi* is 0.7 %.

Uromastyx macfadyeni / *Uromastyx princeps* clade

This is the only major clade (Fig. 1) which is not significantly supported on its basal node; it therefore comprises two clearly separated species units (each with PP: 1.00 / NJ: 100), whose direct relationships remain unclear. Intraspecific genetic difference is: *macfadyeni*: 0.0 %, *princeps*: 0.2 %. Between those two taxa, the genetic difference is 9.0–9.5%.

Uromastyx thomasi clade

Uromastyx thomasi forms a separate, well supported clade of its own (PP: 1.00 / NJ: 100).

Intraspecific genetic difference is 0.2–0.3 %.

Results of the multivariate analyses of the taxa of the genus *Uromastyx*

A distance phenogram based on the average values of 18 characters for all taxa of the genus *Uromastyx* (number of taxa = 22; *Uromastyx occidentalis* data were not available; for definition of variables see Table 3) was calculated using the complete linkage method (Fig. 3). The resulting distance phaenogram shows two distinct main clusters (OTU I & OTU II), of which one includes *hardwickii*, *loricata* and *asmussi* (OTU II), while the second cluster represents all remaining taxa of the genus (OTU I). Within this second cluster five subcluster based on phenetic similarity are recognizable – the first cluster contains *aegyptia*, *microlepis* and *leptieni*; the second *ocellata*, *yemenensis*, *shobraki* and *benti*, the third *dispar*, *maliensis*, *flavifasciata*, *acanthinura* and *nigriventris*; the fourth *princeps* and the fifth clade contains *alfredschmidti*, *geyri*, *thomasi*, *macfadyeni*, *ornata* and *philbyi*.

Because of these morphological findings based on average values, we suggest, that the genus *Uromastyx* s.l. consist of two clades which are different. To further evaluate the phenetic relationships within the genus we applied a principal component analysis (PCA) on data obtained from 481 individuals (Variables: V1–V17; see Table 4). The dis-

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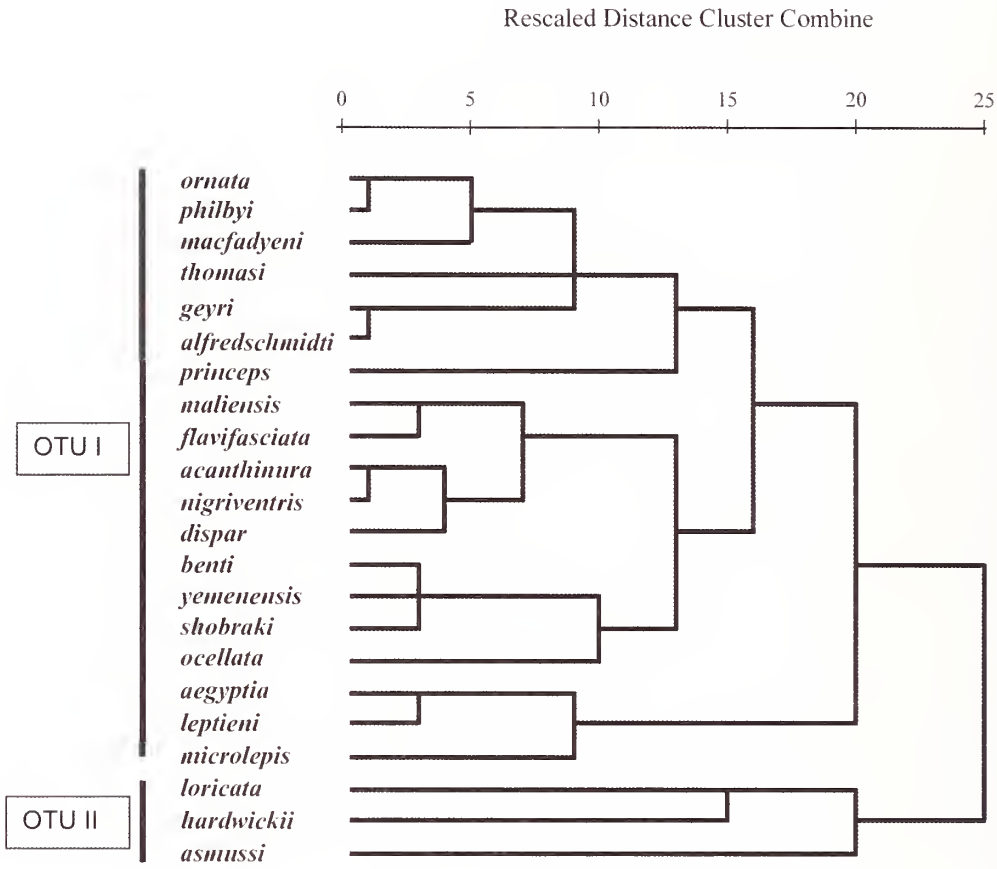

Fig. 3. Distance phenogram resulting from cluster analysis of average values of Variable V1–V18 (see Tab. 4) of the taxa of *Uromastyx* sensu lato (Hierarchical cluster using complete linkage, Tschebyscheff distances and *z*-transformation).

crepancy between the total number of specimens used in this study and the number of specimens subject to the statistical analysis is because of the elimination of incomplete datasets.

In the projection of the first two principal components all specimens of *hardwickii* cluster seperately as well as all specimens of *asmussi* and *loricata* respectively. Both clusters are clearly separated from all specimens of the remaining *Uromastyx* taxa (Fig. 4; for factor loadings on principal components see Table 5), and correspond to the clusters identified as OTU 1 and OTU II in the hierarchical cluster. OTU II contains two clearly separated subclusters with all *U. hardwickii* clustering together as well as *U. asmussi* and *U. loricata*. The finding of two phenetic clusters clearly outside the *Uromastyx* sensu stricto cluster as well as the identification of two well supported genetic clades raise the question of a polyphyletic origin of the genus *Uromastyx* sensu lato.

To evaluate the phenetic relationships and to discriminate the species or species groups within *Uromastyx* sensu stricto, data of all taxa (without *U. occidentalis*) were subject of six PCAs (Variables: V1–V15; see Table 6). Between the subsequent PCAs, data of taxa clustering outside the respective main clusters were removed. As a result of this procedure seven entities containing single species or phenetically similar taxa were recovered:

1. *benti, yemenensis, shobraki, princeps* (Fig. 5; for factor loadings on principal components see Table 7)

2. *ocellata* (Fig. 6; for factor loadings on principal components see Table 8)

3. *thomasi* (Fig. 7; for factor loadings on principal components see Table 9)

4. *aegyptia, microlepis, leptieni* (Fig. 8; for factor loadings on principal components see Table 10)

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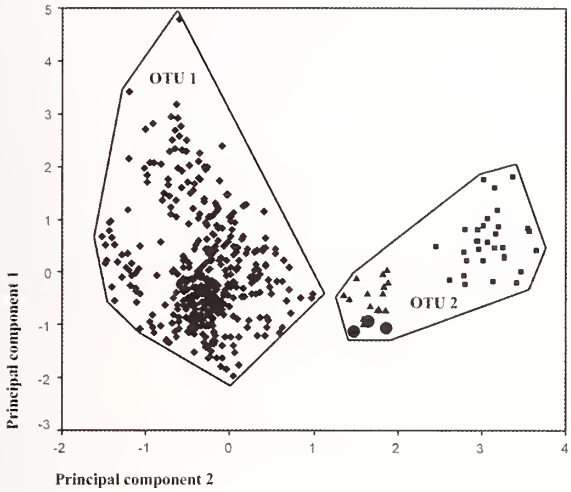

Fig. 4. Projection of the first two principal components from a PCA run on 481 individuals assignable to OTU 1 and OTU 2 (◆ = *Uromastyx* sensu stricto; ▲ = *Uromastyx loricata*;) ● = *Uromastyx asmussi*; ■ = *Uromastyx hardwickii*).

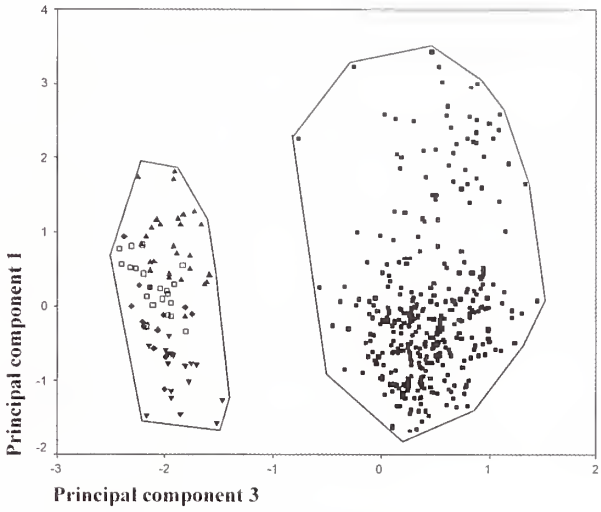

Fig. 5. Projection of the first and third principal component from a PCA run on 431 individuals assigned to *Uromastyx* sensu stricto (OTU 1) (◆ = *Uromastyx yemenensis*, ▲ = *Uromastyx princeps*; ▼ = *Uromastyx benti*; □ = *Uromastyx shobraki*; ■ = *Uromastyx* spp.).

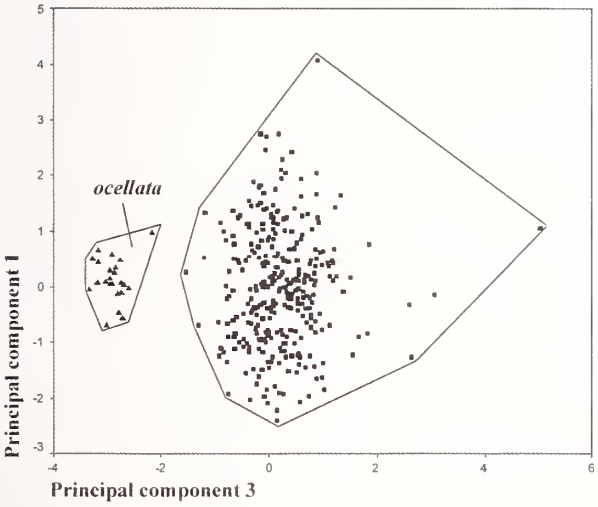

Fig. 6. Projection of the first and third principal component from a PCA run on 354 individuals assigned to *Uromastyx* sensu strico without *yemenensis*, *benti*, *shobraki* and *princeps* (■ = *Uromastyx* spp., ▲ = *Uromastyx ocellata*).

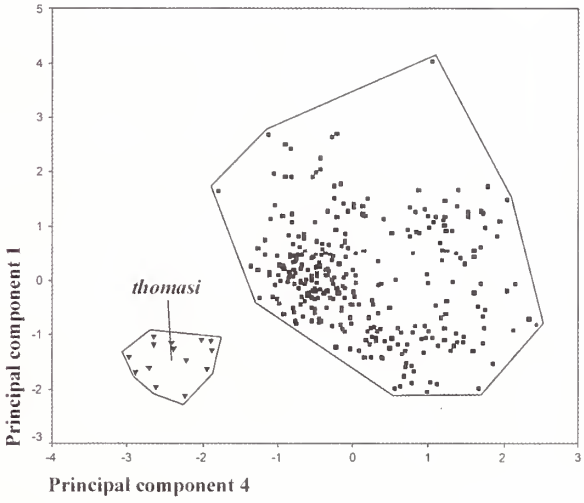

Fig. 7. Projection of the first and fourth principal component from a PCA run on 331 individuals assigned to *Uromastyx* sensu strico without *yemenensis*, *benti*, *shobraki*, *princeps* and *ocellata* (■ = *Uromastyx* spp.; ▼ = *Uromastyx thomasi*).

5. *dispar, flavifasciata, maliensis* (Fig. 9; for factor loadings on principal components see Table 11)

6. *acanthinura, nigriventris* (Fig. 10; for factor loadings on principal components see Table 12)

7. *alfredschmidti, geyri, ornata, philbyi, macfadyeni* (Fig. 10)

These seven clusters are based on external similarities and therefore do not exclusively reflect phylogenetic relationships but also identify phenetic similarities based on homoplasious character states. To evaluate phenetic relationships within the clades identified by genetic analysis, separate PCAs were applied to the data sets of the taxa.

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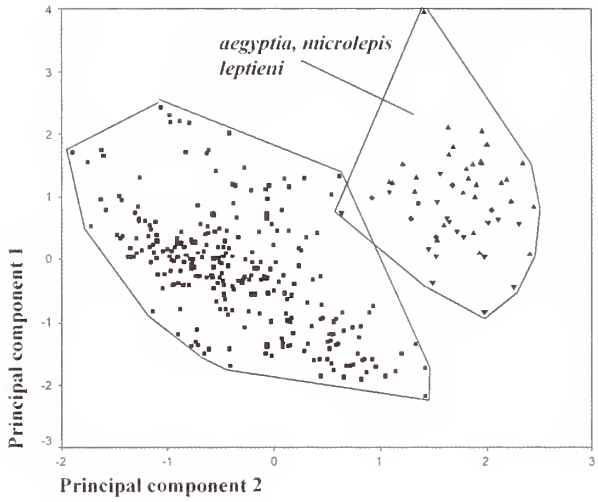

Fig. 8. Projection of the first two principal components from a PCA run on 317 individuals assigned to *Uromastyx* sensu stricto without *yemenensis*, *benti*, *shobraki*, *princeps*, *ocellata* and *thomasi* (■ = *Uromastyx* spp., ▲ = *Uromastyx a. microlepis*; ▼ = *Uromastyx a. aegyptia*; ◆ = *Uromastyx a. leptieni*).

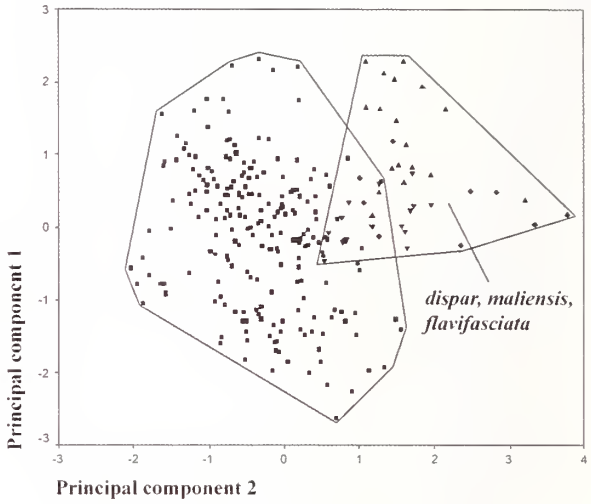

Fig. 9. Projection of the first two principal components from a PCA run on 265 individuals assigned to *Uromastyx* sensu stricto without *yemenensis*, *benti*, *shobraki*, *princeps*, *ocellata*, *thomasi*, *aegyptia*, *microlepis* and *leptieni* (■ = *Uromastyx* spp., ▲ = *Uromastyx dispar maliensis*; ◆ = *Uromastyx d. flavifasciata*; ▼ = *Uromastyx d. dispar*).

Uromastyx acanthinura group

The taxa of the *U. acanthinura* group cluster in three subsequent PCAs (PCA 5, 6 & 7). This indicates, that the morphology of the taxa of this group is to some degree different to the other species of the genus (see also discussion regarding cluster 7 also containing taxa not belonging to the *U. acanthinura* group).

PCAs carried out exclusively on the data of the *U. acanthinura* group revealed, that *U. geyri* and *U. alfredschmidti* cluster outside of the remaining taxa. Separation of *acanthinura*, *nigriventris*, *dispar*, *flavifasciata* and *maliensis* by means of PCA was not possible (data not shown; Variables: V1–V15).

Uromastyx aegyptia group

All taxa in this study belonging to this group cluster in one single PCA (PCA 4). Phenetical relationships within the taxa of the *U. aegyptia* group (excluding *U. occidentalis*) have already been assessed by Wilms & Böhme (2007). Analysis revealed that male specimens could be assigned according to the a priori specimen classification using cluster analysis and PCA. For females taxon discrimination was not possible.

Uromastyx ocellata group

The taxa of the *U. ocellata* group are included in several clusters of the previous PCAs (PCA 1, 2 & 7). This indicates, that some taxa of this group are readily distinguishable from other taxa of the genus (see also discussion regarding cluster 1 & 7 containing not only taxa belonging to the *U. ocellata* group).

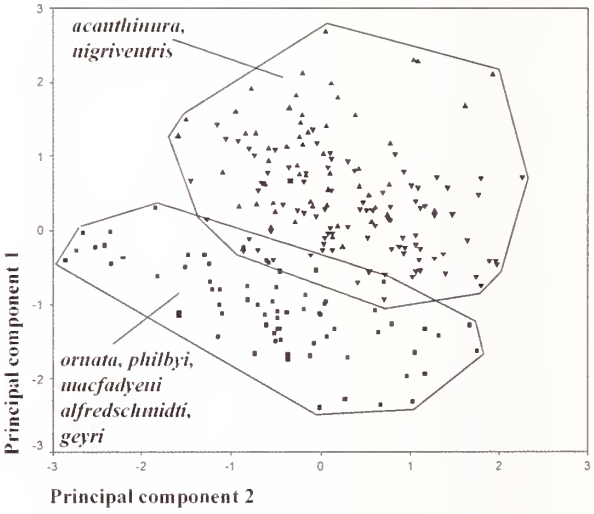

Fig. 10. Projection of the first two principal components from a PCA run on 223 individuals assigned to *Uromastyx* sensu stricto without *yemenensis*, *benti*, *shobraki*, *princeps*, *ocellata*, *thomasi*, *aegyptia*, *microlepis*, *leptieni*, *maliensis*, *dispar* and *flavifasciata* (■ = *Uromastyx* spp., ▲ = *Uromastyx acanthinura*; ▼ = *Uromastyx nigriventris*).

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A PCA carried out only on data of the specimens belonging to the *U. ocellata* group (data not shown) revealed, that two taxa cluster completely separate (*ocellata*, *benti*) while *shobraki* and *yemenensis* form a common cluster as well as *ornata* and *philbyi* (Variables: V1–V15).

***Uromastyx macfadyeni* / *Uromastyx princeps* clades**

Both species cluster in different PCAs (No. 1 & 7) and are clearly separated in the PCA carried out solely on data of both species (data not shown; variables: V1–V15).

***Uromastyx thomasi* group**

U. thomasi already clustered completely separate in one of the subsequent PCAs applied to data of the whole genus (PCA 3).

Results of the phylogenetic analysis of morphological data

A NJ analysis was carried out (tree not shown) and a MP heuristic parsimony analysis resulted in 254 shortest trees (L: 254, CI: 0.762, RI: 0.857, RC: 0.653) (not shown) whose 50% majority-rule consensus shows the following structure [numbers are bootstrap values (NJ/MP) for the following nodes; significant values in bold; values under 50 not shown *]:

(((((*acanthinura*,(((*aegyptia*, *microlepis*)**70**/56, *leptieni*)61/64, *occidentalis*)56/64, *alfredschmidti*,(*benti*, *macfadyeni*, *ocellata*,(*ornata*, *philbyi*)55/*, *shobraki*, *yemenensis*)53/**71**, *dispar*, *flavifasciata*, *geyri*, *maliensis*, *nigriventris*)56/*,(*princeps*, *thomasi*)**100/98**)**70/71**,(*asmussi*, *loricata*)**94**/*)53/*, *hardwickii*)**100/100**, *Leiolepis*)

Even though the resolution of the phylogenetic analysis of the morphological data is not surprisingly rather limited, the node separating *Leiolepis* from *Uromastyx* sensu lato is fully supported by bootstrap values (**100/100**), and more importantly the node separating *Uromastyx* sensu stricto from *U. hardwickii*, *U. loricata* and *U. asmussi* is also well supported in both analyses (**70/71**).

Synthesis and discussion of the morphological and genetic results

As pointed out by Amer & Kumazawa (2005) the relationship between *Leiolepis* and *Uromastyx* has been subject to scientific discussions. Based on morphology both genera possess autapomorphies supporting the monophyly of this clade within the Acrodontia and their position as the sister taxon to all remaining agamids (Moody 1980; Böhme 1982). Studies based on molecular data sets failed to support this monophyly (Macey et al. 1997, 2000) or did not place this clade as the sister taxon of the remaining agamids (Honda et al. 2000). We used members of the Agaminae (*Agama planiceps*, *A. impalearis*) and Amphibolurinae (*Tympanocryptis tetraporophora*) as outgroups in our analysis and found a weakly supported monophyly of the clade consisting of *Leiolepis* and *Uromastyx*. This result is consistent with the phylogeny established by Amer & Kumazawa (2005) also based on mtDNA.

Ananjeva et al. (2004, 2007) integrated morphological and molecular data and established a classification of agamid lizards by distinguishing six monophyletic lineages on subfamily level: Uromastycinae Theobald, 1868; Leiolepidinae Fitzinger, 1843; Amphibolurinae Wagler, 1830; Hydrosaurinae Kaup, 1828; Draconinae Fitzinger, 1826; Agaminae Spix, 1825. We follow this concept of Ananjeva et al. and regard the Leiolepidinae and Uromastycinae as separate lineages.

Our observations based on morphological and genetic data show a clear and well supported substructure within *Uromastyx* s.l. Both of these entities warrant recognition on genus level. For the clade comprising the taxa of the irano-turanian subregion (*hardwickii*, *asmussi*, *loricata*) the genus name *Saara* Gray, 1845 is available. We therefore resurrect *Saara* as the sister genus of *Uromastyx*. After the resurrection of the genus *Saara* for the species of the irano-turanian region, two genera are now placed within the Uromastycinae: *Saara* and *Uromastyx*. After the exclusion of the species of the genus *Saara*, *Uromastyx* is now monophyletic comprising 20 nominal taxa.

An early separation of *hardwickii* from the other species of the genus *Uromastyx* was already proposed by Joger (1986) based on immunological distances and Amer & Kumazawa (2005) based on molecular data. Joger (1986) furthermore established a close phylogenetic relationship between *hardwickii* and *loricata*. This author suggested that *Uromastyx* should be divided into several subgenera (one of them being the clade of *hardwickii* and *loricata*), but did not impose formal taxonomic changes with the exception of the resurrection of the name *Aporoscelis* for the two broad tailed species (*U. thomasi* and *U. princeps*). As Moody (1987) pointed out, applying this concept would have caused the genus *Uromastyx* to be paraphyletic. The separation between *Saara hardwickii* and the species of the Afro-Arabian radiation of *Uromastyx* was estimated at 25–29 Mya (Amer & Kumazawa 2005) which is in general accordance with the estimates made by Joger (1986). Within *Saara* a clear substructure is recognizable with *S. asmussi* and *S. loricata* forming sister clades which are themselves the sister taxa to *S. hardwickii*.

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The situation and relationships within *Uromastyx* are not as clear as in *Saara*. Genetically, we recognize five species groups within the genus of which four are at least partly supported by morphological data (*U. acanthinura* group, *U. aegyptia* group, *U. ocellata* group, *U. thomasi* group). The remaining group (cluster containing *U. princeps* and *U. macfadyeni*), feebly recognized on the basis of the molecular data set, is not supported by morphological data.

Differences in the composition of genetically based clusters and morphologically based groups might mainly be the result of a convergent evolution of the taxa involved due to similar ecological or climatic environments.

Well supported by morphological analysis are the *U. aegyptia* and the *U. thomasi* groups. While *U. thomasi* clusters completely separate in the PCA analysis, all taxa of the *U. aegyptia* group cluster together according to the genetic results (hierarchical cluster, PCA analysis, PAUP analysis of morphological data). It is therefore well established, that *U. thomasi* and the *U. aegyptia* group form phylogenetic entities of their own. This is especially remarkable for *U. thomasi*, because this species has in former studies been placed in a clade together with *U. princeps* (Joger 1986; Moody 1987; Wilms 2001) with which it also clusters in the PAUP analysis of morphological data (this study). The present study is the first including DNA samples of both broad tailed *Uromastyx* species and therefore recovers a biased morphological interpretation in the phylogenetic relationship of these two taxa. The overall similarity between *U. thomasi* and *U. princeps* is most possibly based on the extraordinary short tail in those taxa which was misinterpreted as an autapomorphy for this group instead of an independantly evolved analogous character state. From our point of view the phylogenetic affiliation of *U. princeps* and *U. macfadyeni* is probable, though this is not conclusive due to the low bootstrap values (PP: 0.77 / NJ: 51). Amer & Kumazawa (2005) found a sister group relationship of *U. macfadyeni* with species of the *U. acanthinura* clade (*U. geyri*, *U. acanthinura*, *U. dispar*), which we cannot confirm based on our own data. Nevertheless the relationships within the *U. acanthinura* group in this previous (Amer & Kumazawa 2005) and in the present study are in good accordance.

Within the North African *Uromastyx acanthinura* group seven taxa are recognized, of which all but *U. alfredschmidti* were available for genetic analysis. Based on 12S and 16S rRNA data *geyri* is the sister taxon of the clade comprising *acanthinura*, *nigriventris* and *U. dispar* ssp. As reported earlier *nigriventris* is the sister taxon of the two remaining taxa, which form themselves strongly supported clades.

Morphologically *acanthinura* and *nigriventris* as well as *dispar*, *flavifasciata* and *maliensis* form clusters in subsequent PCA analysis. These taxa cluster in the 5th and 6th PCA cycle respectively. All specimens of *geyri* and *alfredschmidti* remained in a cluster together with *ornata*, *philbyi* and *macfadyeni*, for which a further resolution was not possible based on the PCA methodology. It is evident, that the assingnment of *geyri* and *alfredschmidti* to the three taxa mentioned above is because of a superficial morphological similarity within the taxa in question, which is due to similar ecological adaptations (convergent evolution) and not due to phylogenetic relationships (all of them are predominantly rock dwelling species).

Another PCA was carried out exclusively on specimens belonging to the taxa of the *U. acanthinura* clade. In this PCA *geyri* and *alfredschmidti* clustered together and outside of the remaining taxa, with only a very small area of overlap between the respective clusters (data not shown). It was not possible to separate the remaining taxa with a further PCA.

On the basis of the morphological data we consider *dispar*, *flavifasciata* and *maliensis* as being closely related entities, as well as *geyri* and *alfredschmidti*. The taxa *acanthinura* and *nigriventris* show a certain morphological similarity, which led in the past to the conclusion to tread both taxa as subspecies of a single species (Wilms & Böhme 2001).

We suppose, that the *U. acanthinura* clade in North Africa represents a relatively recent radiation within the genus (see also Wilms 2001). This hypothesis is supported by the relatively low level of genetic difference within all taxa of this group, which is generally between 0.0 and 1.4 % difference in the 16S rRNA gene (within *Uromastyx*, only one further group shows a similarily low degree of separation: the *U. aegyptia* group) as well as the overall similarity concerning scalation characters. By including data for the 12S rRNA gene the resolution of taxa discrimination was significantly enhanced, resulting in genetic distances suitable to distinguish between the taxa involved. As has been shown earlier in this study, *acanthinura* as well as *nigriventris* exhibit a very low intraspecific genetic distance of 0.0–0.1 %, while *dispar* shows a respective distance up to 0.7 %. We have therefore assessed the internal distances within the nominal taxa *dispar*, *flavifasciata* and *maliensis*, which proved to be: *dispar* 0.0 %, *flavifasciata* 0.0–0.2 % and *maliensis* 0.0 (only one sequence available). The respective distances between those taxa are: *dispar-flavifaciata*: 0.53–0.74 %, *dispar-maliensis*: 0.58 %, *maliensis-flavifasciata*: 0.39–0.58 %. We therefore recognize *dispar*, *flavifasciata* and *maliensis* as valid taxa belonging to one species, *Uromastyx dispar*, but being differentated on subspecific level.

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To evaluate a further taxonomic problem, we have included several melanistic specimens of *flavifasciata* from northern Mauritania in this study. These animals have been described as *Uromastyx flavifasciata obscura* by MATEO et al. (1998), and the validity of this taxon was under debate ever since (WILMS & BÖHME 2001; GENIEZ et al. 2004). The genetic difference between these animals and typical *U. dispar flavifasciata* is 0.0–0.2 %. We therefore consider *obscura* to be synonymous with *flavifasciata* (see also WILMS & BÖHME 2001).

As a synthesis of our morphological and molecular data we consider five evolutionary entities within the *U. acanthinura* group as valid on specific level: *U. alfredschmidti*, *U. geyri*, *U. acanthinura*, *U. nigriventris* and *U. dispar*. This result is in general accordance with the results of AMER & KUMAZAWA (2005) and HARRIS et al. (2007).

The second group within the genus *Uromastyx* comprising several nominal taxa and only showing a weak morphological and genetic differentiation is the *Uromastyx aegyptia* group. Within this group four nominal taxa are known: *aegyptia*, *leptieni*, *microlepis* and *occidentalis*. We hypothesize that the origin of the *U. aegyptia* group is Africa and that the Arabian radiation of this group has only recently dispersed into the Arabian Peninsula. The clarification of the evolutionary scenario of the *U. aegyptia* group would require the incorporation of *U. occidentalis* in the genetic analysis and the resolution of the relationships between all identified species groups. A sister group relationship between the *U. acanthinura* and the *U. aegyptia* group as postulated on the basis of morphological data (MOODY 1987; WILMS 2001; this study) would bring the groups together, which represent the most recent evolutionary lineages.

Despite the overall similarity of the taxa of the *U. aegyptia* group, it is possible to differentiate between them on the basis of morphological characters (WILMS & BÖHME 2001, 2007). Genetically, they exhibit the following intertaxon distances: *aegyptia-microlepis*: 0.3–0.4 %, *microlepis-leptieni*: 0.3–0.6 % and *aegyptia-leptieni*: 0.7–0.9 %. These p-distances based on 12S and 16S rRNA are very low compared to those between *Uromastyx* species in general, but are similar to those shown by the taxa assigned to *U. dispar* as subspecies in the present study. We therefore recognize *Uromastyx aegyptia* as a polytypic species with three subspecies (*aegyptia*, *leptieni*, and *microlepis*). Because of the significant geographic distance between the Arabian *U. aegyptia* and the African *U. occidentalis* we suppose, that both are good species.

The results of the analysis of morphological as well as molecular data for the *U. ocellata* group have been published elswhere (WILMS & SCHMITZ 2007). This group consists of six taxa which represent five evolutionary entities: *benti*, *yemenensis*, *shobraki*, *ocellata*, *ornata*. In the context of the current data, we recognize the subspecies of *U. yemenensis* as valid at specific rank because of the intraspecific genetic distances which are similar between all taxa of the subclade comprising *benti*, *yemenensis* and *shobraki*.

4. TAXONOMY

DEFINITION AND RESURRECTION OF THE GENUS *SAARA* GRAY, 1845

1845 *Saara* Gray, Cat. Spec. Liz. Coll. brit. Mus.: 262. – Type species: *Uromastyx hardwickii* GRAY, 1827

Original definition: Head very short, broad, much arched. Body depressed, with a fold on each side of the back. Scales minute, equal. Tail short, broad, depressed; upper part with cross bands of compressed, conical scales, separated by other rings of granular and smooth square scales; beneath covered with square, smooth, imbricate scales. Femoral pores distinct (GRAY 1845).

Diagnosis: Acrodont dentition, with the premaxillary bone forming in adult specimens a sharp, tooth- like structure replacing the incisive teeth. Tail scalation arranged in distinct whorls, which are separated by 1–6 rows of intercalary scales dorsally.

Species: *Saara asmussi, S. hardwickii, S. loricata.*

Distribution: The species of the genus *Saara* are distributed in eastern Iraq, Iran, Afganistan, Pakistan and northwestern India.

Taxonomy: As shown in the present study, *Saara hardwickii* represents most probably a polytypic species, whose taxa are genetically distinct. Further study on the taxonomy of *Saara hardwickii* is required to evaluate the distribution and morphological characters of the taxa involved.

SYNOPSIS OF THE SPECIES OF THE GENUS *SAARA* GRAY, 1845

***Saara asmussi* (Strauch, 1863) new comb.**
[Common name: Persian Spiny-tailed Lizard]

Centrotrachelus asmussi STRAUCH, 1863; Bull. Acad. Sci. St. Pétersbourg, 6: 479.

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Uromastix asmussi – Boulenger 1885; Cat. Liz. brit. Mus., 1: 409.

Uromastyx asmussi – Mertens 1956; Jh. Ver. vaterl. Naturk. Württemb., 111: 93.

Holotype: ZISP 3029 (Zoological Museum, Academy of Sciences, Russian Academy of Sciences, St. Petersburg), male, Seri-Tschah (Eastern Persia), coll. Keyzerling, 1858–1859.

Differential diagnosis: The species *asmussi* belongs to the genus *Saara*. This taxon is distinguished from *Saara hardwickii* by having 1–2 rows of unkeeled intercalary scales separating each tail whorl dorsally (2–6 keeled intercalary scales in *S. hardwickii*). *S. asmussi* is distinguished from *S. loricata* in having fewer preanofemoral-pores (8–13 in *S. asmussi* vs. 14–20 in *S. loricata*).

Subspecies: None

Description: Maximum total length 475 mm, maximum SVL 265 mm. 170–201 scales around mid-body, 94–103 scales between gular- and inguinal fold, 40–53 gular scales, 21–27 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–7 scales between supralabial and enlarged subocular scale. 25–30 scales around 5th whorl. 23–26 tail whorls. 11–13 scales beneath 4th left toe. 8–13 preanofemoral pores on either side.

Colouration: Head, shoulders and forelegs coloured light grey to blue. Hindlegs yellowish grey to blue. Tail dull grey-olive with yellowish spines or completely blue. Back light ocker yellow up to the tailroot; some tubercules on the back are coloured orange. The belly is yellowish white with dark spots on the breast. At low temperatures the back is blackgrey. For pictures of live animals see Anderson (1999).

Distribution: *Saara asmussi* lives in the dry areas of Iran, Afghanistan and Pakistan. In Iran the species lives in the following provinces: Esfehan, Kerman, Khorasan and Baluchistan-Sistan (Anderson 1974, 1999). In Pakistan the species is known from Baluchistan (Minton 1966, Kahn 1980). The presence in Afghanistan obviously is limited to the southern part of the country in the bordering area with Iran and Pakistan (for map see Anderson 1999 and Wilms 2001).

***Saara hardwickii* (Gray, 1827)**
[Common name: Indian Spiny-tailed Lizard]

Uromastix hardwickii Gray, 1827; in Hardwicke & Gray, Zool. J. 3: 219.

Uromastix griseus Cuvier, 1829; Règne animal. Ed. 2, 2: 34.

Uromastix reticulatus Cuvier, 1829; (nomen nudum; syn. fide Boulenger 1885), Règne animal, Ed. 2, 2: 34.

Uromastyx grisseus – Gray 1831; Gray (ex errore) in Griffith, Animal Kingdom of Cuvier 9 Synops. Spec.: 62.

Centrocercus griseus – Fitzinger 1843; (non *Centrocercus* Swainson 1831 = Aves), Syst. Rept. 1: 18, 86.

Uromastyx similis Fitzinger, 1843; (nomen nudum; syn. fide Boulenger 1885), Syst. Rept., 1: 86

Saara hardwickii – Gray 1845; Cat. Spec. Liz. Coll. brit. Mus.: 262.

Uromastyx hardwickii – Kahn 1980; Biologica 26 (1/2): 133.

Uromastyx hardwickii – Sharma 1992; Cobra, Madras Snake Park Trust 10: 8 (error typographicus).

Holotype: BMNH 1946.8.14.44, male, Plains of Kanouge, Hindustan, India, pres. General Hardwicke, without date.

Differential diagnosis: The species *hardwickii* is the type species of the genus *Saara*. This taxon is distinguished from *S. asmussi and S. loricata* by having 2–6 keeled intercalary scales separating each tail whorl dorsally (1–2 rows of unkeeled intercalary scales in *S. asmussi and S. loricata*).

Subspecies: None

Description: Maximum total length 438 mm, maximum SVL 233 mm. 190–275 scales around mid-body, 112–157 scales between gular- and inguinal fold, 32–46 gular scales, 24–42 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 6-9 scales between supralabial and enlarged subocular scale. 40–52 scales around 5th whorl. 28–39 whorls. 15–21 scales beneath 4th left toe. 12–19 preanofemoral pores on either side.

Colouration: The colouration of the back is yellow brown, with dark dots or with a vermiculation. The belly is whitish. The throat is scattered with dark dots. The front sides of the upper thighs on both sides show a black spot at the base of the frontlegs. The pattern of the juveniles consists of black dots, which are arranged in a regular way on the back. For pictures of live specimens see Wilms (2005).

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Distribution: *Saara hardwickii* is widely distributed in the dry areas of northwest India and Pakistan. In Afghanistan this species lives at least in the border area with Pakistan (near Jalalabad; WILMS 2001).

***Saara loricata* (Blanford, 1874) new comb.**
[Common name: Iraqi Spiny-tailed Lizard]

Centrotrachelus loricatus Blanford, 1874; Proc. zool. Soc. London, 1874: 660.

Centrotrachelus asmussi – MURRAY 1884; Ann. Mag. Nat. Hist. 14 (Ser.5): 101.

Uromastix loricatus – BOULENGER 1885; Cat. Liz. brit. Mus., 1: 409.

Uromastix costatus Müller, 1885; Verh. natforsch. Ges. Wien 7: 292 & 713 (syn. fide BOULENGER, Zool. Rec. 1885).

Uromastyx asmussi loricatus – MERTENS 1956; Jh. Ver. vaterl. Naturk. Württemb., 111: 93.

Uromastyx loricatus – CLARK, CLARK & ANDERSON 1966; Occ. Pap. Calif. Acad. Sci. 55: 6.

Centrotrachelis loricatus – HAAS & WERNER 1969; Bull. Mus. Comp. Zool., 138 (6): 341.

Uromastyx loricata – WILMS 1995; Dornschwanzagamen: 95.

Holotype: BMNH 1946.8.11.59, female, Bushir, Iraq, pres. P.L. Sclater, without date.

Differential diagnosis: This taxon is distinguished from *Saara hardwickii* by having 1–2 rows of unkeeled intercalary scales separating each tail whorl dorsally (2–6 keeled intercalary scales in *S. hardwickii*). *S. loricata* is distinguished from *S. asmussi* in having more preanofemoralpores (8–13 in *S. asmussi* vs. 15–20 in *S. loricata*).

Subspecies: None

Description: Maximum total length 520 mm, maximum SVL 290 mm. 183–234 scales around mid-body, 101–110 scales between gular- and inguinal fold, 32–45 gular scales, 24–36 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–8 scales between supralabial and enlarged subocular scale. 23–33 scales around 5th whorl. 22–26 tail whorls. 11–13 scales beneath 4th left toe. 15–20 preanofemoral pores on each side.

Colouration: Head, limbs, back and tail brown, yellow-grey or crème coloured with small intermixed brown dots. Back sometimes vividly red coloured. The belly is yellow brown or yellowish white (KALAF 1959; HAAS & WERNER 1969). For pictures of live animals see ANDERSON (1999).

Distribution: *Saara loricata* lives in the arid areas of Iraq and southwest Iran. In Iran the following provinces are inhabitated: Kurdestan-Kermanshah, Kuzestan-Lorestan and Fars (ANDERSON 1974).

DEFINITION OF THE GENUS *UROMASTYX* MERREM, 1820

1820 *Uromastyx* MERREM, Tent. Syst: 56. – Type species (fide FITZINGER 1843): *Stellio spinipes* Daudin = *Uromastyx aegyptia* (ForsskÅl)

Original definition: Cauda squamis magnis crassis aculeatis verticillata (Tail annulated by large, thick and spiny scales) (MERREM 1820).

Diagnosis: Acrodont dentition, with the premaxillary bone forming in adult specimens a sharp, tooth- like structure replacing the incisive teeth. Tail scalation arranged in distinct whorls, which are not separated by intercalary scales dorsally.

Species: *Uromastyx acanthinura, U. aegyptia, U. alfredschmidti, U. benti, U. dispar, U. geyri, U. nigriventris, U. ornata, U. ocellata, U. occidentalis, U. princeps, U. macfadyeni, U. shobraki, U. thomasi, U. yemenensis.*

Distribution: The species of the genus *Uromastyx* are distributed in all North African countries bordering the Sahara desert (Algeria, Chad, Egypt, Libya, Mali, Mauritania, Morocco, Niger, Sudan, and Tunesia) as well as in Ethiopia, Eritrea, Djibouti and Somalia in Africa and in all countries on the Arabian Peninsula. In the north *Uromastyx* occures in Israel, Jordan, Syria, Iraq and to the east on a narrow stripe along the Arabian Gulf in Iran (up to the city of Bandar Abbas).

Taxonomy: Within the genus *Uromastyx* several taxonomic problems remain unresolved. Further studies should focus on the phylogenetic relationships between and within the different species groups (eg. *U. o. ornata* and *U. o. philbyi*) as well as on the evaluation of the taxonomic placement of *U. princeps*, *U. macfadyeni*, *U. alfredschmidti* and *U. occidentalis* within the genus.

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SYNOPSIS OF THE SPECIES OF THE GENUS *UROMASTYX* MERREM, 1820

***Uromastyx acanthinura* Bell, 1825**
[Common name: North African Spiny-tailed Lizard]

Uromastyx acanthinurus Bell, 1825; Zool. J., 1:457.

Uromastix mutabilis – FISCHER 1885; Zool. Garten 26: 272.

Uromastix acanthinurus – BOULENGER 1885; Cat. Liz. Brit. Mus. Vol. 1: 406.

Uromastix acanthinurus nigerrimus – HARTERT, 1913; Novitat. Zool. Tring 20: 79.

Uromastyx acanthinurus acanthinurus – MERTENS 1962; Senckenberg. biol. 43: 426.

Uromastyx acanthinura acanthinura – WILMS 1995; Dornschwanzagamen: 57.

Holotype: OUM 7845 (Oxford University Museum of Natural History), N. Africa (brought by Capt. Lyon RN), Bell & Hope Collection.

Differential diagnosis: *U. acanthinura* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (50.27–74.42 % of SVL in *U. acanthinura* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and from *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row in *U. acanthinura*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia*, 297–301 in *U. occidentalis* vs. 146–195 in *U. acanthinura*), from *U. geyri* and *U. alfredschmidti* by the shorter tail (50.27–74.42 % of SVL in *U. acanthinura* vs. 65.45–98.06 % in *U. geyri* and 79.31–87.26 % in *U. alfredschmidti*). Diagnostic characters between *U. acanthinura* and the subspecies of *U. dispar* are: Lower number of scales around midbody [145–195 (mean. 165.6) in *U. acanthinura* vs. 187–227 (mean: 205.0) in *U. d. dispar*]; lower number of ventrals [74–96 (mean. 83.1) in *U. acanthinura* vs. 88–118 (mean: 104.5) in *U. d. flavifasciata*] and lower number of subdigital scales [9–15 (mean: 12.7) in *U. acanthinura* vs. 15–18 (mean: 16.4) in *U. d. maliensis*]. *U. acanthinura* is differentiated from *U. nigriventris* by being much less colourful and lacking red, green and citreous colouration.

Subspecies: None

Description: Maximum total length 430 mm, maximum SVL 253 mm. 146–195 scales around midbody, 74–96 scales between gular- and inguinal fold, 25–45 gular scales, 22–38 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–8 scales between supralabial and enlarged subocular scale. 26–32 scales around 5th whorl. 16–20 tail whorls. 9–15 scales beneath 4th left toe. 10–16 preanofemoral pores on each side.

Colouration: Pattern and colouration of *U. acanthinura* is not very variable. There is a sexual dimorphism with males being black with white or yellowish dots and females being beige to silvergrey with small dark spots. For pictures of live specimens see SCHLEICH et al. (1996) and WILMS (2005).

Distribution: *U. acanthinura* lives at the northern edge of the Sahara, but penetrades deep into the central Sahara along wadis or along plateaus and mountain chains. Geographically it occurs in the dry areas of eastern Algeria, Tunesia and northwest Libya. For detailed discussion of the distribution of this taxon and for a distribution map see WILMS (2005). Further studies are needed to assess the geographic distribution of *U. acanthinura* and *U. nigriventris* in the area between the Great Ergs (Grande Erg Occidental and Grande Erg Oriental).

***Uromastyx aegyptia* Forsskål, 1775**
[Common names: Egyptian Spiny–tailed Lizard]

Differential diagnosis: *U. aegyptia* is distinguished from *U. thomasi* and *U. princeps* by the longer tail (60.18–102.83 % of SVL in *U. aegyptia* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and from *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–8 whorls forming a continuous scale row in *U. aegyptia*; from the species of the *U. acanthinura* group by more scales around midbody (238–322 in *U. aegyptia* vs. 142–231 in the species of the *U. acanthinura* group). *U. aegyptia* is distinguished from *U. occidentalis* by having preanofemoral pores.

Subspecies: We recognize three of the closely related taxa within the *U. aegyptia* clade as subspecies of one single species: *U. aegyptia aegyptia, U. a. microlepis and U. a. leptieni*. The phylogenetic relationship of the nominal species *U. occidentalis* requires further studies based on new material.

***Uromastyx aegyptia aegyptia* (Forsskål, 1775)**
Lacerta aegyptia Forsskål, 1775; Descr. Anim. Itin. orient.: 13.

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Lacerta harbai Forsskal, 1775; Descr. Anim. Itin. orient.: 9 (? syn. fide MERREM 1820).

Stellio spinipes Daudin, 1802; Hist. nat. gén. part. Rept. 4: 31.

Uromastyx spinipes – MERREM 1820; Tent. Syst. Amph.: 56.

Lacerta herbai – MERREM 1820; Tent. Syst. Amph.: 56 (nomen substitutum pro *Lacerta harbai* Forsskål, 1775).

Mastigura spinipes – FLEMING 1822; Philos. Zool., 2: 277.

Uromastix spinipes – BOULENGER 1885; Cat. Liz. brit. Mus. 1: 407.

Uromastix aegyptius – ANDERSON 1896; Contrib. Herpetol. Arabia: 79, 85.

Uromastyx aegyptia – FLOWER 1933; Proc. zool. Soc. London 1933: 779.

Uromastyx aegyptius – WERNER 1982; Herp. Comun.,Wildl. Res. Rep. 13: 155.

Uromastyx aegyptius aegyptius – ARNOLD 1987; Proc. Symp. Fauna Zoogeogr. Middle East. 28: 249.

Uromastyx aegyptia – SCHÄTTI & GASPARETTI 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx aegyptia aegyptia – WILMS 1995; Dornschwanzagamen: 71.

Neotype: ZFMK 44216, adult male, Suez at the road to Cairo, Egypt, coll. I. REHAK, VIII. 1982 (designated by WILMS & BÖHME 2000 a).

Differential diagnosis: The nominotypic subspecies is distinguished from *U. a. microlepis* by having enlarged tubercular scales scattered over the scalation of the flanks and by lower scale counts. It is distinguished from *U. a. leptieni* by a different juvenile colour pattern and a higher number of ventrals (see WILMS & BÖHME 2000 a).

Description: Maximum total length exceeding 700 mm. 247–322 scales around midbody, 126–158 scales between gular- and inguinal fold, 33–59 gular scales, 24–31 scales from the mid of the lower end of the ear opening to the mental scale. On both sides 4–7 scales between supralabial and enlarged subocular scale. 29–46 scales around 5th whorl. 20–23 tail whorls. 16–20 scales beneath 4th left toe. 14–20 preanofemoral pores on either side.

Colouration: *U. aegyptia* has the ability of a physiological colour change. At high temperatures the animals show a light brown to light grey coloration with a black throat and small black dots on the neck. Some individuals have an entirely black to dark blue colouration of the head. At low temperatures the animals show a dark grey, nearly black, colouration. Juveniles have characteristic transverse rows of yellow to orange ocelli on their back. The main colouration of the body is greyish brown. For pictures of live specimens see WILMS (2005).

Distribution: The nominotypic subspecies inhabits nothern Egypt east of the river Nile, the Sinai Peninsula, Palestina and extreme northwestern Saudi Arabia (Wadi Sawawin / Jabal as Sinfa). The border between the ranges of the taxa *aegyptia* and *microlepis* is obviously east of Wadi Araba in Palestina and Jordan and east of Wadi Sawawin in the Jabal as Sinfa region of Saudi Arabia.

***Uromastyx aegyptia microlepis* Blanford, 1874**

Uromastix microlepis Blanford, 1874; Proc. zool. Soc. London, 1874.

Uromastyx microlepis – SCHMIDT 1939; Field Mus. nat. Hist. Zool. 24: 59.

Uromastyx aegyptius – SCHMIDT 1941; Field Mus. nat. Hist. Zool. 24 (16): 162.

Uromastyx aegyptius microlepis – MERTENS 1956; Jh. Ver. vaterl. Naturk. Württemb., 111: 93.

Uromastix aegyptius – KEVORK & AL-UTHMAN 1972; Bull. Iraq Nat. Hist. Mus. 5 (2): 26.

Uromastyx aegyptius – MOODY 1987; Proc. 4th General Meeting of the Societas Europaea Herpetologica: 287.

Uromastyx aegyptia – SCHÄTTI & GASPARETTI 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx aegyptia microlepis – WILMS 1995; Dornschwanzagamen: 72.

Lectotype: BMNH 1946.8.14.55, adult male, Basrah, Iraq, leg. Capt. Phillips, without date (designated by WILMS & BÖHME 2000 a).

Differential diagnosis: *Uromastyx a. microlepis* is distinguished from *U. a. aegyptia* by lacking enlarged tubercular scales scattered over the scalation of the flanks and by smaller scales. It is distinguished from *U. a. leptieni* by a different juvenile colour pattern and a higher number of ventrals (see WILMS & BÖHME 2000 a).

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Description: Maximum total length exceeding 700 mm. 255–391 scales around mid-body, 149–193 scales between gular- and inguinal fold, 38–65 gular scales, 27–49 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–8 scales between supralabial and enlarged subocular scale. 30–43 scales around 5th whorl. 20–24 tail whorls.14–23 scales beneath 4th left toe. 13–21 preanofemoral pores on either side.

Colouration: *U. aegyptia microlepis* has the ability of physiological colour change. At high temperatures the animals show a light brown to yellow or greenish coloration with a black throat and small black dots on the neck and dorsum. Some individuals have an entirely black to dark blue colouration of the head. At low temperatures the animals show a dark grey, nearly black, colouration. For pictures of live specimens see Wilms (2005) and Sindalco & Jeremčenko (2008).

Juveniles have characteristic transverse rows of yellow to orange ocellae on their back. The main colouration of the body is greyish brown.

Distribution: *Uromastyx aegyptia microlepis* lives in the deserts and semideserts of Arabia (Saudi Arabia, Yemen, Oman, United Arab Emirates, Qatar, Kuwait), in Jordan, Syria, Iraq and coastal Iran.

***Uromastyx aegyptia leptieni* Wilms & Böhme, 2000 new status**

Uromastyx leptieni Wilms & Böhme, 2000; Herpetozoa 13(3/4): 142.

Uromastyx leptiens – Harris, Vaconcelos & Brito 2007; Amphibia-Reptilia 28 (2007): 1 (error typographicus).

Holotype: ZFMK 52398, adult female, Wadi Siji, United Arab Emirates (UAE), coll. R. Leptien, VI. 1983.

Differential diagnosis: *Uromastyx a. leptieni* is distinguished from *aegyptia* and *microlepis* by a different juvenile colour pattern and a lower number of ventrals (see Wilms & Böhme 2000 a).

Description: Maximum total length 675 mm. 238–294 scales around mid-body, 112–130 scales between gular- and inguinal fold, 40–47 gular scales, 30–37 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–7 scales between supralabial and enlarged subocular scale. 32–37 scales around 5th whorl. 22–24 tail whorls. 17–21 scales beneath 4th left toe. 12–19 preanofemoral pores on either side.

Colouration: Main colour olive-beige with small dark dots. Neck, head and throat black. In some specimens the throat is marbled with black and orange. Ventral part of the front-legs, chest and belly marbled with grey. Ventral parts of the hind legs and first half of the tail grey.

Colouration of juveniles red brown to dark brown with a dark brown to black net-like pattern. For pictures of live specimens see Wilms (2005) and Wilms & Böhme (2007).

Distribution: *Uromastyx aegyptia leptieni* is known from east of the Hajar al-Gharbi mountains in northern Oman (from the vicinity of Muscat up to the Musandam peninsular), and from north-eastern United Arab Emirates. The westernmost locality is near Abu Dhabi Airport (24° 27' N 54°38'E). For detailed distribution maps for the taxa assigned here to the species *Uromastyx aegyptia* on subspecific level see Wilms & Böhme (2007).

***Uromastyx alfredschmidti* Wilms & Böhme, 2001**
[Common name: Schmidt's Spiny-tailed Lizard]

Uromastyx acanthinurus – Joger 1981; Bonn. Zool. Beitr. 32 (3–4): 323.

Uromastyx alfredschmidti Wilms & Böhme, 2001; Zool. Abh. 51 (1): 95.

Holotype: ZFMK 24643, adult male, Tassili N'Ajjer, Tamrit Plateau (1600 m), approx. 30 km northeast Djanet, Algeria, leg. Dr. G. Wangorsch, 22.07.1974.

Differential diagnosis: *U. alfredschmidti* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (79.31–87.26 % of SVL in *U. alfredschmidti* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–3 whorls forming a continuous scale row in *U. alfredschmidti*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia*, 297–301 in *U. occidentalis* vs. 138–202 in *U. alfredschmidti*), from *U. acanthinura*, *U. nigriventris* and *U. dispar* by its longer tail (79.31–87.26 % of SVL in *U. alfredschmidti* vs. 50.27–74.42 in *U. acanthinura*, 47.83–70 % in *U. dispar* and 43.48–75.14 % in *U. nigriventris*). From *U. geyri* it is distinguished by differences in the scalation of the flanks (enlarged triangular and imbricate scales in *U. alfredschmidti* vs. enlarged tubercular scales in *U. geyri*), as well as the complete black colouration of adult males in *U. alfredschmidti*.

Subspecies: None

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Description: Maximum total length 429 mm, maximum SVL 230 mm. 138–202 scales around midbody, 68–94 scales between gular- and inguinal fold, 26–42 gular scales, 17–36 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–6 scales between supralabial and enlarged subocular scale. 28–32 scales around 5th whorl. 21–24 tail whorls. 12–15 scales beneath 4th left toe. 13–21 preanofemoral pores on each side.

Colouration: Adult males are entirely black. One female from the type-series has a lightbrown colour, with throat and rear part of the abdomen being ivory-coloured with a light brown reticulation. The top of the tail is coloured dark brown. Adult females can also be totally black. For pictures of live specimens see Wilms (2005) and Sindalco & Jeremčenko (2008).

Distribution: *U. alfredschmidt* is restricted to the Tamrit plateau, the Hoggar Mountains in southern Algeria and the Akkakus region in southwestern Libya (for distribution map see Wilms & Böhme 2001)

***Uromastyx benti* (Anderson, 1894)**
[Common name: Yemeni Spiny-tailed Lizard]

Aporoscelis benti Anderson, 1894; Ann. Mag. nat. Hist., London, (6) 14: 376.

Uromastix (*Aporoscelis*) *benti* – Anderson 1896; Contrib. Herpetol. Arabia: 33.

Uromastix simonyi Steindachner, 1899; Anz. Akad. Wiss. Wien. math. naturwiss. Kl., 36: 143

Uromastyx benti – Parker 1938; Ann. Mag. Nat. Hist. (11) 1: 486.

Aporoscelis benti – Schmidt 1939; Field Mus. nat. Hist. Zool. 24: 59.

Uromastix philbyi – Haas & Battersby 1959; Copeia 1959: 202 (syn. fide Arnold 1986).

Uromastyx thomasi – Al-Badry & Al-Safadi 1982; Proc. Egypt. Acad. Sci 34: 66 (syn. fide Schätti 1989).

Uromastyx (*Aporoscelis*) *benti* – Joger 1987; Proc. Symp. Fauna Zoogeogr. Middle East. 28: 260.

Uromastyx ocellata benti – Schätti & Gasparetti, 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – Schätti & Desvoignes 1999; The Herpetofauna of southern Yemen and the Sokotra Archipelago: 39.

Lectotype: BMNH 1946.8.11.72, adult male, Wadi Hadramaut, Yemen, leg. Dr. J. Anderson, without date (designated by Wilms & Böhme 2000 b).

Differential diagnosis: *Uromastyx benti* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group and *U. macfadyeni*) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. ocellata*, *U. ornata* and *U. macfadyeni* the species differs in lacking femoral- and preanalpores.

Uromastyx benti differs from *U. shobraki* and *U. yemenensis* in having larger scales around midbody (188.92 +/- 13.22 in *U. shobraki*, 197.44 +/- 20.9463 in *U. yemenensis* vs. 160.05 +/- 8.98 in *U. benti*) and larger ventrals (86.64 +/- 4.88 in *U. shobraki*, 88.25 +/- 6.98 in *U. yemenensis* vs. 74 +/- 4.02 in *U. benti*), but also in significant genetic differences.

Subspecies: None

Description: Maximum total length 360 mm, maximum SVL 196 mm. 143–187 scales around midbody, 66–86 scales between gular- and inguinal fold, 23–33 gular scales, 19–27 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–7 scales between supralabial and enlarged subocular scale. 28–38 scales around 5th whorl. 22–26 tail whorls. 11–15 scales beneath 4th left toe. No preanofemoral pores.

Colouration: Ground colour of the males back, tail and hind legs yellowish brown. Tail without distinct pattern, hind legs with a turquoise and orange colouration. Back with a pattern consisting of dark brown lines and dots, as well as 7–9 rows of ocellae (ivory coloured with dark brown edges); Dorsal side of the front legs anthracite coloured with orange and green colour elements. Hands yellowish brown. Head orange, dark brown and black marbled. Underside of the head anthracite coloured with some orange dots. Ventral parts of forelegs and chest marbled with grey. Belly with narrow grey/anthracite crossbands. The females are much paler in colouration, with a yellowish brown ground colour and a pattern of small dark brown lines and dots. For pictures of live specimens see Wilms & Böhme (2007) and Sindalco & Jeremčenko (2008).

Distribution: *Uromastyx benti* occurs in southern and southeastern Yemen, from the vicinity of Azzan eastwards to the Hadramaut Valley and along the coast of the Arabian Sea. In the Sultanate of Oman this species is only known from the vicinity of Mirbat in south-western Oman (Seufer et al. 1998, Wilms & Hulbert 2000).

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***Uromastyx dispar* Heyden, 1827**
[Common name: Southern Saharan Spiny-tailed Lizard]

Differential diagnosis: *U. dispar* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (43.83–70 % of SVL in *U. dispar* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row in *U. dispar*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia*, 297–301 in *U. occidentalis* vs. 164–231 in *U. dispar*), from *U. geyri* and *U. alfredschmidti* by the shorter tail (43.83–70 % of SVL in *U. dispar* vs. 65.45–98.06 % in *U. geyri* and 79.31–87.26 % in *U. alfredschmidti*). Diagnostic characters between *U. acanthinura*, *U. nigriventris* and the subspecies of *U. dispar* are: Lower number of scales around midbody [145–195 (mean. 165.6) in *U. acanthinura*, 139–208 (mean: 170.63) in *U. nigriventris* vs. 187–227 (mean: 205) in *U. d. dispar*]; lower number of ventrals [74–96 (mean. 83.1) in *U. acanthinura*, 66–99 (mean: 83.98) in *U. nigriventris* vs. 88–118 (mean: 104.5) in *U. d. flavifasciata*] and lower number of subdigital scales [9–15 (mean: 12.7) in *U. acanthinura*, 9–17 (mean: 13.15) in *U. nigriventris* vs. 15–18 (mean: 16.4) in *U. d. maliensis*]. For a detailed discussion of the differences between *acanthinura*, *nigriventris*, *dispar*, *flavifasciata* and *maliensis* see WILMS & BÖHME (2001).

Subspecies: We recognize three of the closely related taxa within the *U. acanthinura* clade as subspecies of *U. dispar*: *U. d. dispar*, *U. d. flavifasciata* and *U. d. maliensis*.

***Uromastyx dispar dispar* Heyden, 1827**
Uromastyx dispar Heyden, 1827; Atl. Reise nördl. Afr. Rept.: 5.

Uromastix acanthinurus – WAKE & KLUGE 1961; Contr. Sci. No. 40: 11.

Uromastyx acanthinurus dispar – MERTENS 1962; Senckenb. biol. 43: 430.

Holotype: SMF 10417, female, Desert near Ambukol and Dongola, Sudan, coll. E. Rüppel, 1826.

Differential diagnosis: Discrimination between the subspecies of *U. dispar* is possible only by means of colouration of adult males. Adult *U. d. dispar* males are distinguished from adult *U. d. flavifasciata* males by lacking transversal stripes on the animals back and from adult *U. d. maliensis* males by the less pronounced black colouration of the body.

Description: Maximum total length 376 mm, maximum SVL 231 mm. 187–227 scales around midbody, 79–103 scales between gular- and inguinal fold, 30–43 gular scales, 24–33 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–8 scales between supralabial and enlarged subocular scale. 30–36 scales around 5th whorl. 16–21 tail whorls. 12–18 scales beneath 4th left toe. 11–18 preanofemoral pores on each side.

Colouration: Adult males of *U. d. dispar* show a black colouration of limbs, heads and tails. Dorsal colouration is yellow or yellowish green. Females are sand coloured with small black dots and occasionally 4–5 grey bars at the flanks. For pictures of live specimens see WILMS et al. (2003) and WILMS (2005).

Distribution: *U. dispar dispar* is found in the desert areas west of the Nile in Sudan and in the Tibesti and Ennedi mountains in Chad. The northernmost locality is Wadi Halfa at the border beween Sudan and Egypt. This taxon has not been found in Egypt yet (contra SALEH 1997). In the Ennedi Mountains, *U. d. dispar* is known from Fada, while it is known from Bardai and Zouar in the Tibesti Mountains. Between the Ennedi and Tibesti this taxon is known from Ouniaga/Erdi. The westernmost location is Zouar (western Chad).

***Uromastyx dispar flavifasciata* Mertens, 1962**
Uromastyx acanthinurus flavifasciatus Mertens, 1962; Senckenb. biol. 43: 427.

Uromastyx acanthinura acanthinura – WILMS 1995; Dornschwanzagamen: 57.

Uromastyx acanthinura flavifasciata – SCHLEICH, KÄSTLE & KABISCH 1996; Amph. & Rept.of North Africa: 309.

Uromastyx flavifasciata flavifasciata – MATEO, GENIEZ, LÓPEZ-JURADO & BONS 1998; Rev. Esp. Herp. 12: 104.

Uromastyx flavifasciata obscura MATEO, GENIEZ, LÓPEZ-JURADO & BONS, 1998; Rev. Esp. Herp. 12: 104.

Uromastyx dispar flavifasciata – WILMS & BÖHME 2001; Zool. Abh. 51 (1): 88.

Uromastyx flavifasciata – GENIEZ, MATEO, GENIEZ & PETHER 2004; Amph. & Rept. of the Western Sahara: 94.

Holotype: SMF 58032, male, approx. 50 km north of Dakar, Senegal (For the reliability of the type locality see BÖHME 1978), coll. N. Heidrich, 01.11.1961.

Differential diagnosis: Adult *U. d. flavifasciata* males can be distinguished from *U. d. dispar* and *U. d. maliensis*

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males by their black body colouration with 5–7 wide, clearly-defined yellow, white or red dorsal crossbands. Occasionally these crossbands can be reduced or be even completely absent.

Description: Maximum total length 455 mm, maximum SVL 280 mm. 164–231 scales around midbody, 88–118 scales between gular- and inguinal fold, 37–48 gular scales, 27–36 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–6 scales between supralabial and enlarged subocular scale. 31–37 scales around 5th whorl. 19–21 tail whorls. 14–18 scales beneath 4th left toe. 13–17 preanofemoral pores on each side.

Colouration: Adult males of *Uromastyx dispar flavifasciata* show black body colouration with 5–7 wide, clearly-defined yellow, white or red dorsal crossbands, which can occassionally, be absent. Females are sand colored with small black dots and ocelli at their backs. For pictures of live specimens see Wilms et al. (2003) and Wilms (2005).

Distribution: *Uromastyx dispar flavifasciata* lives in the Western Sahara south of 28° northern latitude, in Mauritania and in southwestern Algeria.

***Uromastyx dispar maliensis* Joger & Lambert, 1996**
Uromastix acanthinurus – Andersson 1935; K. Vet. O. Vitterh. Samh. Handl. Ser. B. 4 (10): 9.

Uromastyx acanthinurus – Papenfuss 1969; Wasman Jour. Biol. 27 (2): 286.

Uromastyx sp. – Joger 1986; Studies in Herpetology: 187.

Uromastyx maliensis Joger & Lambert, 1996; J. Afr. Zool. 110 (1): 24.

Uromastyx dispar maliensis – Wilms & Böhme 2001; Zool. Abh. 51 (1): 89.

Holotype: HLMD RA 1545, female, 40 km southeast of Gao, Mali, coll. H. Rudolf, without date.

Differential diagnosis: Adult *Uromastyx dispar maliensis* males differ from adult *dispar* males by the more pronounced black colouration of the body and from adult *flavifasciata* males by lacking transversal crossbands on the dorsum.

Description: Maximum total length 383 mm, maximum SVL 232 mm. 177–224 scales around midbody, 86–112 scales between gular- and inguinal fold, 34–46 gular scales, 30–40 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–9 scales between supralabial and enlarged subocular scale. 30–38 scales around 5th whorl. 16–20 whorls. 15–18 scales beneath 4th left toe. 11–17 preanofemoral pores on each side.

Colouration: Dorsal colouration in adult male *maliensis* consists of yellow ocelli on a dark ground colour. The ocelli may merge partially, though they never form crossbands. Adult females are brownish black with a beige-yellow to yellow dorsal coloration, which may have dark brown to brownish black vermiculation or ocelli. For pictures of live specimens see Joger & Gray (1997), Wilms & Müller (1998) and Wilms (2005).

Distribution: *U. dispar maliensis* lives in northwestern Mali, in the Tilemsi Valley, on the edge of the Adrar des Iforas and in southwestern Algeria (Taoudrart in Tanezrouft). *U. dispar maliensis* und *U. geyri* occur sympatrically in the region of the Adrar des Iforas (Joger & Lambert 1996). The northernmost locality of *U. d. maliensis* is Gara Djenoum / Hoggar Mountains (Wilms & Böhme 2001).

***Uromastyx geyri* Müller, 1922**
[Common name: Geyr's Spiny-tailed Lizard]

Uromastix temporalis Valenciennes, 1854; C. R. Acad. Sci. 39: 89.

Uromastix acanthinurus nigerimmus – Geyr von Schweppenburg 1917; J. Ornith. 65 (3): 286 (error typographicus).

Uromastix geyri Müller, 1922; Naturwiss. Beobachter 63: 193.

Uromastyx acanthinurus geyri – Mertens 1962; Senckenb. biol. 43: 430.

Uromastyx geyri – Joger 1981; Bonn. zool. Beitr. 32 (3–4): 324.

Uromastyx acanthinura geyri – Wilms 1995; Dornschwanzagamen: 61.

Uromastyx (*acanthinura*) *geyri* – Joger & Lambert 1996; Jour. Afr. Zool. 100(1): 24.

Neotype: ZFMK 9230 (designated by Müller 1951), male, Gara Djenoum, Ahaggar Mts. Algeria, S Algeria, coll. Frhr. Hans Geyr von Schweppenburg, 10 March 1914.

Differential diagnosis: *U. geyri* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (65.45–98.06 % of SVL in *U. geyri* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the

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species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row in *U. geyri*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia,* 297–301 in *U. occidentalis* vs. 142–196 in *U. geyri*), from *U. acanthinura, U. nigriventris* and *U. dispar* by its longer tail (65.45–98.06 % of SVL in *U. geyri* vs. 50.27–74.42 in *U. acanthinura*, 47.83–70 % in *U. dispar* and 43.48–75.14 % in *U. nigriventris*). From *U. alfredschmidti* it is distinguished by differences in the scalation of the flanks (enlarged triangular and imbricate scales in *U. alfredschmidti* vs. enlarged tubercular scales in *U. geyri*), as well as the complete black colouration of adult males in *U. alfredschmidti*.

Subspecies: None

Description: Maximum total length 355 mm, maximum SVL 193 mm. 142–196 scales around midbody, 69–93 scales between gular– and inguinal fold, 22–40 gular scales, 19–28 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–4 scales between supralabial and enlarged subocular scale. 23–32 scales around 5th whorl. 20–23 tail whorls. 13–17 scales beneath 4th left toe. 13–20 preanofemoral pores on each side.

Colouration: *Uromastyx geyri* shows only a limited variability. The animals are either beautifully vermilion red or shiny yellow. The pattern consists of brown to black ornaments, which form a non continuous reticulated pattern, and of transversal rows of eyed-like dots. For pictures of live specimens see Löhr (2004) and Wilms (2005).

Distribution: Endemic to the Hoggar- and Air mountains, to the Adrar des Iforas in northeastern Mali and southern Algeria as well as to the Tassili N'Ajjer in the vicinity of Amguid. For a distribution map of the species see Wilms (2005).

***Uromastyx macfadyeni* Parker, 1932**
[Common name: Macfadyen's Spiny-tailed Lizard]

Uromastix ocellatus – Tornier 1905; Zool. Jahrb. Syst., 22 (4): 372 (syn. fide Parker 1932).

Uromastix ocellatus – Neumann 1905; Zool. Jahrb. Syst., 22 (4): 392 (syn. fide Parker 1932).

Uromastix macfadyeni Parker, 1932; Proc. zool. Soc. London, 1932: 353.

Uromastyx macfadyeni – Lanza 1983; Monit. zool. ital. 8: 208.

Uromastyx ocellata macfadyeni – Lanza 1988; Biogeographia 14: 420.

Uromastyx ocellata ocellata – Schätti & Gasperetti 1994; Fauna of Saudi Arabia 14: 369.

Holotype: BMNH 1946.8.14.54, male, near Berbara British Somaliland, Somalia, pres. & coll. V. S. Bryan, without date.

Differential diagnosis: *Uromastyx macfadyeni* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. benti*, *U. shobraki* and *U. yemenensis* the species differs in possessing preanofemoralpores and from *U. ocellata* in having enlarged scales on the anterior margin of the ear opening. From *U. ornata* it is distinguished by a different ratio between tail width at the 5th tail whorl and between 4th and 5th whorl (tail width between the 4th and 5th whorl equivalent to 63–79 % of maximum tail width at the 5th whorl in *U. ornata* vs. tail width between the 4th and 5th whorl equivalent to 56–62 % of maximum tail width at 5th whorl in *U. macfadyeni*).

Subspecies: None

Description: Maximum total length 221 mm, maximum SVL 120 mm. 157–182 scales around midbody, 78–93 scales between gular- and inguinal fold, 29–32 gular scales, 22–27 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–4 scales between supralabial and enlarged subocular scale. 23–26 scales around 5th whorl. 22–23 tail whorls. 14–16 scales beneath 4th left toe. 13–15 preanofemoral pores on each side.

Colouration: Males have an either yellowish, greenish or bluish ground colour, dorsally with a brown or black net-like pattern. The inner areas of these patterns are brightly yellow, brown or bluish. Belly blue or green, partially white. Females are much paler in colouration.

Distribution: *Uromastyx macfadyeni* is known only from the area between Berbera and Heis (20 miles west of Mait) on the Gulf of Aden (Somalia).

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***Uromastyx nigriventris* Rothschild & Hartert, 1912 new status**
[Common name: Moroccan Spiny-tailed Lizard]

Uromastix acanthinurus nigriventris Rothschild & Hartert, 1912; Novitat. Zool. 18: 468.

Uromastyx acanthinurus werneri Müller, 1922; Naturwissenschaftlicher Beobachter 63: 201.

Uromastyx acanthinurus var. *pluriscutata* Fejérváry, 1927; Ann. Mag. Nat. Hist. 20 (9): 514.

Uromastyx acanthinurus acanthinurus – Bons & Geniez 1996; Amphibiens et Reptiles du Maroc: 126

Holotype: BMNH 1969.2074, male, Tilrhempt between Laghouat and Ghardaia, Algeria, coll. W. Rothschild and E. Hartert, without date (for remarks see Wilms & Böhme 2001).

Differential diagnosis: *U. nigriventris* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (43.48–75.14 % of SVL in *U. nigriventris* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row in *U. nigriventris*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia,* 297–301 in *U. occidentalis* vs. 139–208 in *U. nigriventris*), from *U. geyri* and *U. alfredschmidti* by the shorter tail (43.48–75.14 % of SVL in *U. nigriventris* vs. 65.45–98.06 % in *U. geyri* and 79.31–87.26 % in *U. alfredschmidti*). Diagnostic characters between *U. nigriventris* and the subspecies of *U. dispar* are: lower number of scales around midbody [139–208 (mean: 170.63) in *U. nigriventris* vs. 187–227 (mean: 205) in *U. d. dispar*]; lower number of ventrals [66–99 (mean: 83.98) in *U. nigriventris* vs. 88–118 (mean: 104.5) in *U. d. flavifasciata*] and lower number of subdigital scales [9–17 (mean: 13.15) in *U. nigriventris* vs. 15–18 (mean: 16.4) in *U. d. maliensis*]. *U. nigriventris* is differentiated from *U. acanthinura* by being much more colourful, with vividly red, green and citreous coloured specimens.

Subspecies: None

Description: Maximum total length 415 mm, maximum SVL 250 mm. 139–208 scales around midbody, 66–99 scales between gular- and inguinal fold, 26–46 gular scales, 22–35 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–6 scales between supralabial and enlarged subocular scale. 25–36 scales around 5th whorl. 16–21 tail whorls. 9–17 scales beneath 4th left toe. 11–18 preanofemoral pores on each side.

Colouration: In *Uromastyx nigriventris* colouration is very variable, with red, yellow, green and orange coloured specimens. Old adult males show frequently a black colouration of head and belly. For pictures of live specimens see Wilms (2005).

Distribution: *Uromastyx nigriventris* is widespread in Morocco east and south of the Atlas Mountain Chain. In western Algeria it ranges in the Sahara Atlas and in the regions northwest, northeast and southwest of the Great Western Erg. In Morocco the southern distribution limits for this taxon are Oued Draa (Draa-valley) and Djebel Ouarkziz (see also discussion of the distribution of this taxon in Wilms & Böhme 2001).

***Uromastyx ornata* Heyden, 1827**
[Common name: Ornate Spiny-tailed lizard]

Differential diagnosis: *Uromastyx ornata* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group and *U. macfadyeni*) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. benti*, *U. shobraki* and *U. yemenensis* the species differs in possessing preanofemoralpores and from *U. ocellata* in having enlarged scales on the anterior margin of the ear opening. From *U. macfadyeni* it is distinguished by a different ratio between tail width at the 5th tail whorl and between 4th and 5th whorl (tail width between the 4th and 5th whorl equivalent to 63–79 % of maximum tail width at the 5th whorl in *U. ornata* vs. tail width between the 4th and 5th whorl equivalent to 56–62 % of maximum tail width at 5th whorl in *U. macfadyeni*).

Subspecies: Based on the high morphological and genetical similarity between *ornata* and *philbyi* we consider both taxa to be conspecific and assign them as subspecies to *Uromastyx ornata*: *U. ornata ornata* and *U. ornata philbyi*.

***Uromastyx ornata ornata* Heyden, 1827**
Uromastyx ornatus Heyden, 1827; Atlas Reise nördl. Afr., Rept.: 1.

Uromastix ornatus – Anderson 1896; Contrib. Herpetol. Arabia: 79.

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Uromastix oronatus – Farag & Banaja 1980; Bull. Fac. Sci. K.A.U. 4: 12 (error typographicus).

Uromastyx ocellatus ornatus – Arnold 1986; Fauna of Saudi Arabia 8: 393.

Uromastyx ocellata ornata – Lanza 1988; Biogeographia 14: 420.

Uromastyx ocellata ornata – Schätti & Gasparetti 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – Schätti & Desvoignes 1999; The Herpetofauna of south. Yemen and the Sokotra Archipelago: 39.

Holotype: SMF 10403, Mohila = Al Muwaylih, Saudi Arabia, leg. E. Rüppell, 1828.

Differential diagnosis: *Uromastyx o. ornata* is distinguished from *U. o. philbyi* by its narrower tail (ratio tail length divided by maximum tail width at the 5th whorl is 3.61–5.3 in *ornata* vs. 3.03–3.96 in *philbyi*).

Description: Maximum total length 368 mm, maximum SVL 196 mm (BMNH 97.10.28.199). 149–185 scales around mid–body, 75–99 scales between gular- and inguinal fold, 22–31 gular scales, 21–27 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–5 scales between supralabial and enlarged subocular scale. 19–25 scales around 5th whorl. 20–23 tail whorls. 11–15 scales beneath 4th left toe. 7–14 preanofemoral pores on each side.

Colouration: *U. ornata* is a very variable species. Colour of the males is green, blue or red, with a irregularly reddish brown net-like pattern and yellow spots on the back. Sometimes yellow cross-bands are present. Ventrum with dark pattern. Females are not as colourful as males. They are light brown with dark brown spots and sometimes light yellow or light red spots. Belly without pattern, yellowish or white. For pictures of live specimens see Wilms et al. (2002), Wilms (2005) and Wilms & Böhme (2007).

Distribution: For discussion and map of the distribution range see Wilms & Böhme (2007).

***Uromastyx ornata philbyi* Parker, 1938**

Uromastyx philbyi Parker, 1938; Ann. Mag. nat. Hist. (11) 1: 484.

Uromastyx ocellatus philbyi – Arnold 1986; Fauna of Saudi Arabia 8: 416.

Uromastyx ornatus philbyi – Arnold 1987; Proc. Symp. Fauna Zoogeogr. Middle East. 28: 249.

Uromastyx ocellata philbyi – Schätti & Gasparetti 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – Schätti & Desvoignes 1999; The Herpetofauna of southern Yemen and the Sokotra Archipelago: 39.

Holotype: BMNH 1946.8.14.65 (former number: BMNH 1938.2.1.1), male, between Makkah and Shabwa, southern Hejaz, between Mountains and Rub al Khali, Saudi Arabia, coll. H. St. J. B. Philby, without date.

Differential diagnosis: see under *U. o. ornata*.

Description: Maximum total length 341 mm, maximum SVL 205 mm (MZUF 27906). 138–193 scales around midbody, 69–96 scales between gular- and inguinal fold, 17–31 gular scales, 18–22 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–5 scales between supralabial and enlarged subocular scale. 22–29 scales around 5th whorl. 17–22 tail whorls. 11–14 scales beneath 4th left toe. 7–14 preanofemoral pores on each side.

Colouration: Similar to *Uromastyx o. ornata*. For pictures of live specimens see Wilms (2007 b).

Distribution: For discussion and map of the distribution areas of this taxon see Wilms & Böhme (2007).

***Uromastyx ocellata* Lichtenstein, 1823**
[Common name: Eyed Spiny-tailed Lizard]

Uromastyx ocellatus Lichtenstein, 1823; Verz. Doubl. zool. Mus. k. Univ. Berlin: 107.

Uromastix ornatus – Boulenger 1885; Cat. Liz. Brit. Mus.,1: 406.

Uromastix ocellatus – Anderson 1898; Zool. Egypt, 1 Rept. Batr.: 127.

Uromastyx ocellata ocellata – Lanza 1988; Biogeographia 14: 420.

Syntypes: ZMB 809, Nubia; ZMB 811–13, Nubia; ZMB 810, Syria; all specimens leg. Hemprich & Ehrenberg. After Denzer et al. (1997), ZMB 811–13 are lost which we cannot confirm at least for ZMB 811.

Differential diagnosis: *Uromastyx ocellata* is distinguished from *U. thomasi* and *U. princeps* by the signifi-

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cantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group and *U. macfadyeni*) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. benti*, *U. shobraki* and *U. yemenensis* the species differs in possessing preanofemoralpores and from *U. ornata* and *U. macfadyeni* in lacking enlarged scales on the anterior margin of the ear opening.

Subspecies: None

Description: Maximum total length 276 mm, maximum SVL 174 mm. 189–256 scales around midbody, 95–113 scales between gular- and inguinal fold, 29–42 gular scales, 23–33 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–6 scales between supralabial and enlarged subocular scale. 24–39 scales around 5th whorl. 22–29 tail whorls. 14–19 scales beneath 4th left toe. 12–17 preanofemoral pores on each side.

Colouration: Showing a distinctive sexual dichromatism. Ground colour of males either beautifully red with a black vermiculation, olive green with red dots or red with green dots. On the back 7–8 transversal rows of yellow or white, black edged ocellae. Sides of the neck, throat and breast light green or lively blue coloured. The belly is monochromatic yellow or white. Females are by far not as lively coloured as the males, with an either pale brownish, green, redish or grey groundcolour. For pictures of live specimens see Wilms (2005) and Frahm (2006).

Distribution: This species occures in the dry areas west of the red sea in the following countries: Somalia (Borama district), Djibouti, Eritrea, Sudan and southeastern Egypt, where the southernmost locality is in the Borama district (northwestern Somalia) and the northernmost in the Wadi Gul'an (Egypt). According to Largen & Spawls (2006) this species lives also in Ethiopia near the border to Somalia.

***Uromastyx occidentalis* Mateo, Geniez, López-Jurado & Bons, 1998**
[Common name: Western Giant Spiny-tailed Lizard]

Uromastyx occidentalis Mateo, Geniez, López-Jurado & Bons, 1998

Holotype: DB.ULPGC-5 (Departamento de Biología, Universidad de Las Palmas de Gran Canaria), Aagtel Agmumuit, between Yeloua and Mades (Adrar Souttouf, Western Sahara) (21° 52'N, 15° 31'W), coll. M. Hasi, 25. June 1995.

Differential diagnosis: *U. occidentalis* is distinguished from *U. thomasi* and *U. princeps* by the longer tail; from the species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. less than 7 whorls forming a continuous scale row in *U. occidentalis*; from the species of the *U. acanthinura* group by more scales around midbody (297–301 in *U. occidentalis* vs. 142–231 in the species of the *U. acanthinura* group). *U. occidentalis* is distinguished from *U. aegyptia* by lacking preanofemoral pores.

Subspecies: None

Description: Maximum total length 536 mm, maximum SVL 228 mm. 297–301 scales around midbody, 121–122 scales between gular- and inguinal fold. On both sides 7 scales between supralabial and enlarged subocular scale. 23 whorls. No preanofemoral pores.

Colouration: Colouration in life not known. For picture of the holotype see Mateo et al. (1998) and Wilms (2005).

Distribution: Known only from the type locality and from Udei Sfa (45 km west of Maatal Laj, 22°22'N 15°32'W; Geniez et al. 2004).

***Uromastyx princeps* O'Shaughnessy, 1880**
[Common name: Princely Spiny-tailed Lizard]

Uromastix princeps O'Shaughnessy, 1880; Proc. zool. Soc. London, 1880: 445.

Aporoscelis princeps – Boulenger 1885; Cat. Liz. Brit. Mus.,1: 410.

Uromastix princeps scorteccii – Cherchi 1954; Atti. Soc. ital. Sci. Nat. Milano, 93: 540.

Uromastyx princeps – Lanza 1983; Monitore zool. ital. (new Series) Suppl. 18: 208

Uromastyx scortecci – Moody 1987; Proc. 4th General Meeting of the Societas Europaea Herpetologica: 286.

Holotype: BMNH 1946.814.56, male, Zanzibar, coll. Sir J. Kirk, without date (see comments on type locality in Wilms 2001).

Differential diagnosis: With the exception of *Uromastyx thomasi*, *U. princeps* is distinguished from all other taxa in the genus by its significantly shorter tail. From *U. thomasi* it is distinguished by the absence of preanofemoral pores.

Subspecies: None

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Description: Maximum total length 265 mm, maximum SVL 180 mm. 150–226 scales around mid–body, 77–128 scales between gular- and inguinal fold, 28–43 gular scales, 22–34 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 2–5 scales between supralabial and enlarged subocular scale. 20–27 scales around 5th whorl. 9–14 tail whorls. 14–18 scales beneath 4th left toe. No preanofemoral pores.

Colouration: This species displays a pronounced sexual dimorphism. The ground colour of the body is olive grey to green with small brown markings. Males have a yellowish red to green dorsum with small, scattered black spots. The venter is yellowish with blue grey marbling in the area of the chest and throat. The tail is yellow green or red in colour. Females are grey brown dorsally with a light red shimmer and small black spots. The venter is immaculate white. For pictures of live specimens see Wilms & Hulbert (1995) and Wilms (2005).

Distribution: *Uromastyx princeps* is found in the Somalian provinces of Sanaag, Bari, Nogal and Mudug.

***Uromastyx shobraki* Wilms & Schmitz, 2007 new status**
[Common name: Shobrak's Spiny-tailed Lizard]

Uromastyx ocellata benti – Schätti & Gasparetti 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – Schätti & Desvoignes 1999; The Herpetofauna of southern Yemen and the Sokotra Archipelago: 39.

Uromastyx yemenensis shobraki Wilms & Schmitz, 2007; Zootaxa 1394: 16.

Holotype: ZFMK 48681, adult male, Mafraq Mocca (Mafraq al-Mukha), km 13.5, Republic of Yemen, leg. B. Schätti, 5.–6.IV.1988.

Differential diagnosis: *Uromastyx shobraki* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. ocellata*, *U. ornata* and *U. macfadyeni* the species differs in lacking femoral- and preanal-pores.

Uromastyx shobraki differs from *U. benti* in having smaler scales around midbody (188.92 +/- 13.22 in *U. shobraki* vs. 160.05 +/- 8.98 in *U. benti*) and smaller ventrals (86.64 +/-4.88 in *U. shobraki* vs. 74 +/-4.02 in *U. benti*). *U. shobraki* is differentiated from *U. yemenensis* not only by its larger maximum size (393 mm in *U. shobraki* vs. 337 mm in *U. yemenensis*) but also in different colour pattern and in significant genetic differences.

Subspecies: None

Description: Maximum total length 393 mm, maximum SVL 208 mm. 163–207 scales around midbody, 79–97 scales between gular- and inguinal fold, 25–33 gular scales, 23–31 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–5 scales between supralabial and enlarged subocular scale. 32–39 scales around 5th whorl. 24–27 tail whorls. 15–17 scales beneath 4th left toe. No preanofemoral pores.

Colouration: In preserved specimens dorsal surface of head, body and hindlimbs dark brown, tail lighter. Light brown roundish dots (diameter 4–5 scales) are present on the dorsum, tending to form transverse rows. In addition, irregular light brown dots are present on the whole dorsum. Colour of the hands not different to the colour of the forearm. Head dark brown, with light brown pattern. Ventral side yellowish brown. Ventral side of head and chest marbled with anthracite and dark brown. For a picture of a live specimen see Wilms & Böhme (2007).

Distribution: South-western Yemen. For a map of the distribution area see Wilms & Böhme (2007).

***Uromastyx thomasi* Parker, 1930**
[Common name: Omani Spiny-tailed Lizard]

Uromastix thomasi Parker, 1930; Ann. Mag. nat. Hist., London, (10) 6: 595.

Uromastyx thomasi – Arnold 1980; J. Oman Stud. Spec. Rep. No. 2: 293.

Holotype: BMNH 1946.8.14.43 (former number: BMNH 1930.6.30.2), male, Bu Ju'ay, Rub al Khali, Dhofar, Oman, coll. B. Thomas, without date.

Differential diagnosis: With the exception of *Uromastyx princeps*, *U. thomasi* is distinguished from all other taxa in the genus by its significantly shorter tail. From *U. princeps* it is distinguished by the presence of preanofemoral pores.

Subspecies: None

Description: Maximum total length approx. 24 cm, maximum SVL approx. 19 cm. 125–150 scales around midbody, 72–100 scales between gular- and inguinal fold,

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25–36 gular scales between a hypothetical line between the anterior margins of the ears and the mental scale, 19–25 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 2–4 scales between supralabial and enlarged subocular scale. 28–34 scales around 5th whorl. 11–13 whorls. 13–18 scales beneath 4th left toe. 12–19 preanofemoral pores each side.

Colouration: Yellowish green with a dark net-like pattern. A broad red vertebral-stripe runs from the neck to the first half of the tail. In some specimens an orange to red colouration of the head can occur. Ventral side yellowish or white. Neck and sides of the head of the juveniles striped (black and white). Colouration of the upper side of the body black with 6 lighter transversal bands. Between those bands yellowish to orange coloured ocellae. Tail above brown with some large black spots. Belly and throat white. Ventral side of the tail white with black dots. For pictures of live specimens see Wilms et al. (2002)

Distribution: *Uromastyx thomasi* lives in coastal Oman (for map see Wilms & Böhme 2007).

***Uromastyx yemenensis* Wilms & Schmitz, 2007**
[Common name: South Arabian Spiny-tailed Lizard]

Uromastyx ocellata benti – Schätti & Gasparetti 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – Schätti & Desvoignes 1999; The Herpetofauna of southern Yemen andthe Sokotra Archipelago: 39.

Uromastyx y. yemenensis Wilms & Schmitz, 2007; Zootaxa 1394: 12.

Holotype: ZFMK 47861, adult male, Abyan Governorate, vicinity of Lodar (= Lawdar), Republic of Yemen, leg. I. Haikal, don. 1985.

Differential diagnosis: *Uromastyx yemenensis* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. ocellata*, *U. ornata* and *U. macfadyeni* the species differs in lacking femoral– and preanalpores.

Uromastyx yemenensis differs from *U. benti* in having smaler scales around midbody (197.44 +/-20.9463 in *U. yemenensis* vs. 160.05 +/- 8.98 in *U. benti*) and smaler ventralia (88.25 +/-6.98 in *U. yemenensis* vs. 74 +/-4.02 in *U. benti*). *U. yemenensis* is differentiated from *U. shobraki* not only by its smaller maximum size (393 mm in *U. shobraki* vs. 337 mm in *U. yemenensis*) but also in different colour pattern and significant genetic differences.

Subspecies: None

Description: Maximum total length 337 mm, maximum SVL 185 mm. 146–227 scales around midbody, 73–100 scales between gular- and inguinal fold, 25–40 gular scales, 22–30 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–6 scales between supralabial and enlarged subocular scale. 33–40 scales around 5th whorl. 23–27 tail whorls. 12–18 scales beneath 4th left toe. No preanofemoral pores.

Colouration: Ground colour of the males back, tail and hind legs yellowish brown. Tail without distinct pattern, hind legs with very small dark brown dots. Back with a pattern consisting of dark brown lines and dots; five distinct cross bands without or with very few pattern on the back. Dorsal side of the front legs anthracite coloured. Hands yellowish brown. Head yellowish brown, dark brown marbled. Underside of the head anthracite coloured with some yellowish brown dots. Ventral parts of forelegs and chest marbled with grey. Belly with narrow grey/anthracite crossbands. The females are much paler in colouration. With a yellowish brown ground colour with a pattern of small dark brown lines and dots. Five pale cross bands on the back. The ground colour of the ventral side is a light yellowish brown.

Distribution: South-western Yemen. For a map of the distribution area see Wilms & Böhme (2007).

KEY TO THE SPECIES OF THE GENERA *SAARA* Gray, 1845 AND *UROMASTYX* Merrem, 1820

1 a – Tail whorls separated dorsally by 1–6 continuous rows of intercalary scales.....*Saara*

b –Tail whorls without dorsal intercalary scales .....*Uromastyx*

***Saara* Gray, 1845**

1 a –Tail with 29–36 primary whorls; 2–6 rows of keeled intercalary scales between whorls on dorsal surface of tail; dorsal scalation interspersed with irregular, only slightly enlarged, tubercular scales.....*S. hardwickii*

b –Tail with less than 28 primary whorls; 1–2 rows of unkeeled intercalary scales between tail whorls on dorsal surface of tail; dorsal scalation with transverse rows of conspicuously enlarged tubercular scales 2

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2 a – Slightly enlarged scales at front edge of ear opening; 8–13 preanofemoral pores on either side; 7–10 scales in a transverse row on the dorsal surface of the tail base..... *S. asmussi*

b –Without enlarged scales at the front edge of the ear opening; 15–20 preanofemoral pores on either side; 12 scales in a transverse row on the dorsal surface of the tail base..... .....*S. loricata*

***Uromastyx* Merrem, 1820**

1 a – Without preanofemoral pores 2

b – With preanofemoral 6

2 a – Tail short, approx. 35–53 % of SVL; 9–14 whorls ....*U. princeps*

b – Tail long, approx. 71–94 % of SVL; 22–27 whorls 3

3 a – Body scales small, approx. 297–301 scales around midbody; 121–122 scales between gular and inguinal fold ..... *U. occidentalis*

b – Body scales larger, approx. 143–227 scales at midbody; 66–100 scales between gular and inguinal fold 4

4 a – 143–187 scales around midbody (average 160.05 +/- 8.98), 66–86 ventral scales .....*U. benti*

b – 163–227 scales around midbody (average 192.53 +/- 16.63), 79–97 ventral scales 5

5 a – Ground colour light brown with five distinct crossbands on the back .....*U. yemenensis*

b – Ground colour dark brown with light brown dots tending to form transverse rows on the back .....*U. shobraki*

6 a – Tail short, approx. 25–35 % of SVL, from above disk-shaped ..... *U. thomasi*

b – Tail long, approx. 48–103 % of SVL, from above elongated 7

7 a – The last 12–21 tail whorls formed of continuous scale rows 8

b – The last 2–5 tail whorls formed of continuous scales rows 10

8 a – Anterior margin of ear opening without enlarged scales ..... *U. ocellata*

b – Anterior margin of ear opening with enlarged scales 9

9 a – 17–29 (very rarely 31) gular scales; tail width between the 4th and 5th whorl equivalent to 63–79 % of maximum tail width at the 5th whorl ..... *U. ornata*

b – 29–32 gulars; tail width between the 4th and 5th whorl equivalent to 56–62 % of maximum tail width at 5th whorl .....*U. macfadyeni*

10a – 238–391 scales at midbody, 112–193 ventrals between gular and inguinal fold ..... *U. aegyptia*

b – 138–227 scales at midbody, 68–112 ventrals between gular and inguinal fold 11

11 a – Tail with 20–24 whorls; tail length in adult specimens approx. 70–98 % of SVL 12

b – Tail with 16–21 whorls; tail length approx. 48–75 % of SVL 13

12 a – Several transverse rows of enlarged scales along the flanks; max. total length 35.5 cm; never completely black coloured ..... *U. geyri*

b – Flank scalation imbricate with enlarged triangular scales; max. total length 42.9 cm; adult males and occasionally females completely black.....*U. alfredschmidti*

13 a – 79–118 ventrals between gular and inguinal fold; 164–231 scales at midbody; 30–38 scales around 5th whorl ..... *U. dispar*

b – 66–99 ventrals between gular and inguinal fold; 139–208 scales at midbody; 25–36 scales form 5th whorl 14

14 a – Adult males black with ivory coloured or yellowish dots, adult females beige to silvergrey with small dark spots..... *U. acanthinura*

b – Colouration very variable, with red, yellow, green and orange coloured specimens. Old adult males show frequently a black colouration of head and belly .....*U. nigriventris*

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Appendix I.

Table 1. Character matrix for thirteen polarized characters (Outgroup *Leiolepis* and all twenty-three taxa in this study). For character coding see Appendix III.

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M
acanthinura	1	0	0	0	1	0	0	0	0	1	1	0	1
aegyptia	1	0	1	1	1	0	1	0	0	1	0	0	1
alfredschmidti	1	0	0	0	1	0	0	0	0	1	0	0	1
asmussi	1	0	0	0	1	0	0	0	0	2	0	1	0
benti	1	0	0	0	1	0	0	0	1	1	0	0	1
dispar	1	0	0	0	1	0	0	0	0	1	1	0	1
flavifasciata	1	0	0	0	1	0	0	0	0	1	1	0	1
geyri	1	0	0	0	1	0	0	0	0	1	0	0	1
hardwickii	0	0	0	1	0	0	0	0	0	2	0	1	0
leptieni	1	0	1	0	1	0	1	0	0	1	0	0	1
loricata	1	0	0	0	1	0	0	0	0	2	0	1	0
macfadyeni	1	0	0	0	1	0	0	0	1	1	1	0	1
maliensis	1	0	0	0	1	0	0	0	0	1	1	0	1
microlepis	1	0	1	1	1	0	1	0	0	1	0	0	1
nigriventris	1	0	0	0	1	0	0	0	0	1	1	0	1
occidentalis	1	0	1	–	–	–	0	0	0	–	–	0	1
ocellata	1	0	0	0	1	0	0	0	1	1	0	0	1
ornata	1	1	0	0	1	0	0	0	1	1	0	0	1
philbyi	1	1	0	0	1	0	0	0	1	1	1	0	1
princeps	2	0	0	0	1	1	0	1	0	0	2	0	1
shobraki	1	0	0	0	1	0	0	0	1	1	0	0	1
thomasi	2	0	0	0	1	1	0	1	0	0	2	0	1
yemenensis	1	0	0	0	1	0	0	0	1	1	0	0	1
Leiolepis	0	0	0	0	0	0	0	0	0	0	0	0	0

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Table 2. List of samples used for genetic analysis (geographic origin, locality and GenBank accession numbers).

Species	Geographic origin	Locality	Voucher	GenBank Accession No.
Tympanocryptis tetraporophora E105.13	Australia	Mount Olga	ZFMK 83840	EF081041 (16s)
Saara asmussi E107.5	Iran	30 km north of Bampur, direction to Zahedan (Pakistan)	NMP6V 73519	FJ639585 (16s)
Saara loricata E107.3	Iran	Chahak, approx. 15 km north of Bandar-e-Genaveh, Province Busheer	ZFMK 87396	FJ639586 (16s)
Saara hardwickii E111.17	unknown	unknown	ZFMK 83797	FJ639587 (16s)
Saara hardwickii E111.18	unknown	unknown	ZFMK 83795	FJ639588 (16s)
Saara hardwickii E111.19	unknown	unknown	ZFMK 83794	FJ639589 (16s)
Saara hardwickii E111.20	unknown	unknown	ZFMK 83796	FJ639590 (16s)
Saara hardwickii E112.2	unknown	unknown	No Voucher	FJ639591 (16s)
Uromastyx acanthinura E105.21	Tunesia	unknown	ZFMK 83816	FJ639630 (12s) FJ639592 (16s)
Uromastyx acanthinura E105.22	Tunesia	unknown	ZFMK 83817	FJ639631 (12s) FJ639593 (16s)
Uromastyx acanthinura E105.23	Tunesia	unknown	ZFMK 83818	FJ639632 (12s) FJ639594 (16s)
Uromastyx acanthinura E107.15	Tunesia	unknown	No Voucher	FJ639633 (12s) FJ639595 (16s)
Uromastyx nigriventris E106.4	Morocco	unknown	ZFMK 83820	FJ639634 (12s) FJ639596 (16s)
Uromastyx nigriventris E106.5	Morocco	Guelmim	ZFMK 83819	FJ639635 (12s) FJ639597 (16s)
Uromastyx nigriventris E107.14	Morocco	Guelmim	ZFMK 84438	FJ639636 (12s) FJ639598 (16s)
Uromastyx dispar dispar E106.2	Chad	Zouar, Tibesti Mountains	ZFMK 84800	FJ639637 (12s) FJ639599 (16s)
Uromastyx dispar dispar E110.19	Chad	Zouar, Tibesti Mountains	ZFMK 84437	FJ639638 (12s) FJ639600 (16s)
Uromastyx dispar flavifasciata E105.15	Mauritania	Captive bred; father from vicinity of Atar, mother from vicinity of Akjoujt	ZFMK 85163	FJ639639 (12s) FJ639605 (16s)
Uromastyx dispar flavifasciata E105.27	Mauritania	Captive bred; father from vicinity of Atar, mother from vicinity of Akjoujt	ZFMK 83824	FJ639640 (12s) FJ639601 (16s)
Uromastyx dispar flavifasciata E106.22	Mauritania	Atar	ZFMK 73500	FJ639641 (12s) FJ639602 (16s)
Uromastyx dispar flavifasciata E110.8	Algeria	Tindouf	ZFMK 84261	FJ639642 (12s) FJ639603 (16s)
Uromastyx dispar flavifasciata E110.9	Algeria	Tindouf	ZFMK 84262	FJ639643 (12s) FJ639604 (16s)
Uromastyx dispar flavifasciata (*obscura*- phenotype) E111.21	Mauritania	Vicinity of Atar	ZFMK 86473	FJ639644 (12s) FJ639606 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E111.22	Mauritania	northern Mauritania	ZFMK 86474	FJ639645 (12s) FJ639610 (16s)
Uromastyx dispar flavifasciata (*obscura*- phenotype) E133.2	Mauritania	33 km southwest of Choum, (21.0036°N/13.1347°W)	No Voucher	FJ639648 (12s) FJ639607 (16s)

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Species	Geographic origin	Locality	Voucher	GenBank Accession No.
Uromastyx dispar flavifasciata (*obscura*- phenotype) E133.3	Mauritania	Track Aghmakoum - El Beyed (21°28'23" N/11° 33' 24" W)	No Voucher	FJ639649 (12s) FJ639608 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.6	Mauritania	south of Choum at 21.0027°N/13.1636°W	No Voucher	FJ639650 (12s) FJ639612 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.7	Mauritania	south of Choum at 21.0027°N/13.1636°W	No Voucher	FJ639651 (12s) FJ639613 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.8	Mauritania	33 km southwest of Choum (21.0043°N/13.1324°W)	No Voucher	FJ639652 (12s) FJ639614 (16s)
Uromastyx dispar flavifasciata (*obscura*- phenotype) E133.9	Mauritania	26 km northwest of Atar (20.7462°N/13.1293°W)	No Voucher	FJ639653 (12s) FJ639609 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.10	Mauritania	track Atar - Choum (21.0003°N / 13.1598°W)	No Voucher	FJ639646 (12s) FJ639615 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.11	Mauritania	26 km northwest of Atar (20.7432°N/13.1183°W)	No Voucher	FJ639647 (12s) FJ639611 (16s)
Uromastyx dispar maliensis E106.26	Mali	unknown	ZFMK 71647	FJ639616 (16s)
Uromastyx geyri E105.24	Niger	Kafadek, near Agadez	ZFMK 83821	FJ639654 (12s) FJ639617 (16s)
Uromastyx geyri E105.25	Niger	Kafadek, near Agadez	ZFMK 83822	FJ639655 (12s) FJ639618 (16s)
Uromastyx aegyptia aegyptia E106.21	Egypt	Sinai Peninsula	ZFMK 83792	FJ639656 (12s) FJ639619 (16s)
Uromastyx aegyptia microlepis E117.7	Saudi Arabia	Mahazat as Sayd	ZFMK 86573	FJ639658 (12s) FJ639620 (16s)
Uromastyx aegyptia microlepis E117.11	Saudi Arabia	Mahazat as Sayd	ZFMK 86567	FJ639657 (12s) FJ639621 (16s)
Uromastyx aegyptia leptieni E106.27	United Arab Emirates	Rimah / Al-Kaznah	No Voucher	FJ639659 (12s) FJ639622 (16s)
Uromastyx aegyptia leptieni E.110.14	United Arab Emirates	Wadi Siji	ZFMK 52398 Holotype	FJ639660 (12s) FJ639623 (16s)
Uromastyx benti E106.3	Oman	Dhofar, vicinity of Mirbat	ZFMK 83801	EF081054 (16s)
Uromastyx benti E111.2	Oman	Dhofar, vicinity of Mirbat	ZFMK 73681	EF081055 (16s)
Uromastyx benti E111.4	Oman	Dhofar, vicinity of Mirbat	ZFMK 83347	EF081056 (16s)
Uromastyx benti E111.13	Oman	Dhofar, vicinity of Mirbat	ZFMK 73680	EF081057 (16s)
Uromastyx yemenensis E111.12	Yemen	Abian, southern Yemen	ZFMK 47861 Holotype	EF081058 (16s)
Uromastyx yemenensis E106.18	Yemen	unknown	ZFMK 83805	EF081059 (16s)
Uromastyx yemenensis E106.19	Yemen	unknown	ZFMK 83806	EF081060 (16s)
Uromastyx yemenensis E106.20	Yemen	unknown	ZFMK 83807	EF081061 (16s)
Uromastyx shobraki E111.1	Yemen	Mocca, northern Yemen	ZFMK 73677	EF081065 (16s)
Uromastyx shobraki E111.3	Yemen	Mocca, northern Yemen	ZFMK 73676	EF081066 (16s)
Uromastyx shobraki E111.6	Yemen	Between Mafraq and Mocca, northern Yemen	ZFMK 48681 Holotype	EF081067 (16s)
Uromastyx shobraki E111.7	Yemen	Mocca, northern Yemen	ZFMK 73675	EF081068 (16s)
Uromastyx macfadyeni E112.1	Somalia	unknown	ZFMK 84441	EF081042 (16s)

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Species	Geographic origin	Locality	Voucher	GenBank Accession No.
Uromastyx macfadyeni E112.3	Somalia	unknown	ZFMK 84440	EF081043 (16s)
Uromastyx ocellata E106.6	Sudan	unknown	ZFMK 83798	EF081044 (16s)
Uromastyx ocellata E106.7	Sudan	unknown	ZFMK 83799	EF081045 (16s)
Uromastyx ornata ornata E106.11	Egypt	Sinai Peninsula	ZFMK 83815	EF081051 (16s)
Uromastyx ornata ornata E106.8	Egypt	Sinai Peninsula	ZFMK 83812	FJ639629 (12s) EF081052 (16s)
Uromastyx ornata ornata E106.9	Egypt	Sinai Peninsula	ZFMK 83813	EF081053 (16s)
Uromastyx ornata philbyi E110.20	Saudi Arabia	19°05'N 41°50'E, Tihama	ZFMK 84442	EF081046 (16s)
Uromastyx princeps E106.24	Somalia	Bossasso	ZFMK 58985	FJ639624 (16s)
Uromastyx princeps E106.25	Somalia	Bossasso	ZFMK 58048	FJ639625 (16s)
Uromastyx thomasi E105.4	Oman	Vicinity of Ras Hilf, Masirah Island	ZFMK 83830	FJ639626 (16s)
Uromastyx thomasi E105.11	Oman	Vicinity of Ras Hilf, Masirah Island	ZFMK 83837	FJ639627 (16s)
Uromastyx thomasi E105.12	Oman	Vicinity of Ras Hilf, Masirah Island	ZFMK 83838	FJ639628 (16s)

Table 3. Variables used to calculate the distance phenogram (Fig. 3); for definition of appreviations see "Material and Methods".

Variable	**V1**	**V2**	**V3**	**V4**	**V5**	**V6**	**V7**	**V8**	**V9**
Definition	W	SD	G	MBS	V	SW	PP left	PP right	LS left
Variable	**V10**	**V11**	**V12**	**V13**	**V14**	**V15**	**V16**	**V17**	**V18**
Definition	LS right	SO left	SO right	HS left	HS right	ES * PES	IS	TF	TD

Table 4. Definition of variables used for the PCA separating OTU I and OTU II; for definition of abbreviations see "Material and Methods".

Variable	**V1**	**V2**	**V3**	**V4**	**V5**	**V6**	**V7**	**V8**	**V9**
Definition	W	SD	G	MBS	V	SW	PP left	PP right	LS left
Variable	**V10**	**V11**	**V12**	**V13**	**V14**	**V15**	**V16**	**V17**	
Definition	LS right	SO left	SO right	HS left	HS right	ES * PES	IS	TD	

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Table 5. Factor loading on the first four principal components (PC) from a correlation matrix of V1–V17 for individuals of OTU I and OTU II.

Variable	PC 1	PC 2	PC 3	PC 4
V1	- 0.066	0.293	- 0.092	0.073
V2	0.189	- 0.062	- 0.159	0.041
V3	0.194	- 0.147	0.089	- 0.040
V4	0.199	- 0.092	- 0.009	- 0.050
V5	0.176	- 0.066	0.021	- 0.031
V6	0.022	0.205	- 0.133	0.157
V7	- 0.050	- 0.021	0.456	- 0.017
V8	- 0.050	- 0.018	0.458	- 0.027
V9	- 0.033	0.022	- 0.031	0.462
V10	- 0.035	0.029	- 0.014	0.458
V11	0.045	0.131	0.017	0.022
V12	0.064	0.115	- 0.011	0.050
V13	0.162	- 0.035	0.016	- 0.023
V14	0.167	- 0.050	0.022	- 0.026
V15	0.129	0.068	- 0.153	- 0.042
V16	- 0.116	0.324	0.033	- 0.016
V17	- 0.128	0.264	0.166	- 0.206
Eigenvalues	7,264	2,512	1,959	1,560
Accumulated percent of trace	42,731	57,508	69,031	78,207

Table 6. Definition of variables used for the PCA separating species and species groups within *Uromastyx* (Figs 5–10); for definition of abbreviations see "Material and Methods".

Variable	V1	V2	V3	V4	V5	V6	V7	
Definition	W	SD	G	MBS	V	SW	PP left	
Variable	**V8**	**V9**	**V10**	**V11**	**V12**	**V13**	**V14**	**V15**
Definition	PP right	LS left	LS right	SO left	SO right	HS left	HS right	ES * PES

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Table 7. Factor loading on the first four principal components (PC) from a correlation matrix of V1–V15 for 431 individuals of *Uromastyx*.

Variable	PC 1	PC 2	PC 3	PC 4	PC 5
V1	0.274	- 0.216	0.598	0.246	0.581
V2	0.630	- 0.311	- 0.265	0.433	- 1.898E-02
V3	0.850	7.232E-02	- 0.219	9.518E-02	- 0.168
V4	0.841	- 0.148	- 0.133	0.346	7.417E-02
V5	0.824	- 6.121E-02	- 0.234	0.365	2.631E-02
V6	0.622	- 0.105	0.475	0.148	9.023E-02
V7	0.433	0.715	- 0.314	- 0.134	0.403
V8	0.439	0.702	- 0.316	- 0.137	0.419
V9	0.147	0.753	0.402	0.261	- 0.295
V10	0.166	0.785	0.358	0.239	- 0.288
V11	0.742	-2.223E-02	0.308	- 0.430	8.690E-02
V12	0.755	-1.883E-02	0.281	- 0.439	- 4.109E-02
V13	0.857	- 5.430E-02	- 8.995E-02	- 0.220	- 0.253
V14	0.852	- 3.638E-02	- 9.704E-02	- 0.200	- 0.273
V15	0.649	- 0.488	0.115	- 8.413E-02	6.694E-03
Eigenvalues	6.399	2.615	1.466	1.166	1.037
Accumulated percent of trace	42.662	60.097	69.870	77.646	84.560

Table 8. Factor loading on the first three principal components (PC) from a correlation matrix of V1–V15 for 354 individuals of *Uromastyx*.

Variable	PC 1	PC 2	PC 3
V1	0.337	- 0.403	- 0.427
V2	0.728	- 5.468E-02	- 0.354
V3	0.884	0.147	1.143E-02
V4	0.872	- 2.405E-02	- 0.240
V5	0.860	4.975E-02	- 0.246
V6	0.757	0.105	2.198E-02
V7	0.603	0.500	- 0.418
V8	0.611	0.442	- 0.446
V9	6.418E-02	0.831	0.311
V10	7.056E-02	0.835	0.323
V11	0.715	- 0.282	0.449
V12	0.724	- 0.228	0.504
V13	0.848	- 7.847E-02	0.314
V14	0.852	-4.002E-02	0.308
V15	0.715	- 0.381	8.754E-02
Eigenvalues	7.238	2.318	1.658
Accumulated percent of trace	48.250	63.706	74.756

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Table 9. Factor loading on the first four principal components (PC) from a correlation matrix of V1–V15 for 331 individuals of *Uromastyx*.

Variable	PC 1	PC 2	PC 3	PC 4
V1	0.363	0.221	4.585E-02	0.809
V2	0.727	0.130	- 0.320	0.144
V3	0.894	5.650E-02	- 1.491E-02	- 6.992E-02
V4	0.874	0.117	- 0.139	0.289
V5	0.861	0.150	- 0.167	0.235
V6	0.765	- 1.862E-02	- 0.121	- 0.329
V7	0.630	0.532	- 0.327	- 0.247
V8	0.626	0.520	- 0.335	- 0.256
V9	0.193	0.607	0.664	- 5.942E-02
V10	0.211	0.599	0.653	- 6.505E-02
V11	0.711	- 0.462	0.288	- 6.479E-03
V12	0.724	- 0.496	0.260	- 3.671E-02
V13	0.850	- 0.282	0.130	- 0.121
V14	0.855	- 0.245	0.146	- 0.104
V15	0.749	- 0.280	0.145	3.519E-02
Eigenvalues	7.463	2.064	1.462	1.089
Accumulated percent of trace	49.751	63.512	73.262	80.523

Table 10. Factor loading on the first three principal components (PC) from a correlation matrix of V1–V7 & V10–V15 for 317 individuals of *Uromastyx* (because V8 & V9 are coding for preanofemorapores, it is justified to exclude these variables in the PCAs dealing exclusively with species possessing preanofemoralpores).

Variable	PC 1	PC 2	PC 3
V1	0.271	0.620	- 0.564
V2	0.766	0.213	- 0.369
V3	0.879	9.939E-02	1.397E-02
V4	0.852	0.249	- 0.281
V5	0.849	0.265	- 0.270
V6	0.786	- 5.101E-02	4.997E-02
V7	0.137	0.684	0.601
V10	0.162	0.695	0.581
V11	0.751	- 0.359	0.234
V12	0.764	- 0.406	0.226
V13	0.870	- 0.202	0.148
V14	0.873	- 0.161	0.158
V15	0.768	- 0.164	8.008E-02
Eigenvalues	6.799	1.912	1.468
Accumulated percent of trace	52.301	67.010	78.299

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Table 11. Factor loading on the first three principal components (PC) from a correlation matrix of V1–V7 & V10–V15 for 265 individuals of *Uromastyx* (because V8 & V9 are coding for preanofemorapores, it is justified to exclude these variables in the PCAs dealing exclusively with species possessing preanofemoralpores).

Variable	PC 1	PC 2	PC 3
V1	- 0.289	0.578	- 0.458
V2	0.486	0.328	- 0.502
V3	0.774	0.190	0.127
V4	0.677	0.310	- 0.328
V5	0.704	0.352	- 0.309
V6	0.757	0.151	4.432E-02
V7	- 5.536E-02	0.618	0.619
V10	- 3.002E-02	0.684	0.576
V11	0.716	- 0.397	0.239
V12	0.764	- 0.384	0.210
V13	0.895	- 2.617E-02	9.960E-02
V14	0.890	1.378E-02	0.130
V15	0.747	- 8.992E-02	- 8.770E-02
Eigenvalues	5.694	1.884	1.534
Accumulated percent of trace	43.804	58.295	70.092

Table 12. Factor loading on the first three principal components (PC) from a correlation matrix of V1–V7 & V10–V15 for 223 individuals of *Uromastyx* (because V8 & V9 are coding for preanofemorapore, it is justified to exclude these variables in the PCAs dealing exclusively with species possessing preanofemoralpores).

Variable	PC 1	PC 2	PC 3
V1	- 0.554	0.490	- 0.118
V2	- 9.640E-02	0.494	- 0.325
V3	0.743	0.315	- 0.112
V4	0.396	0.515	- 0.282
V5	0.417	0.529	- 0.308
V6	0.662	0.239	- 4.877E-02
V7	0.140	0.497	0.741
V10	0.110	0.580	0.680
V11	0.656	- 0.491	0.209
V12	0.707	- 0.495	0.147
V13	0.866	4.393E-02	- 0.100
V14	0.876	8.752E-02	- 9.225E-02
V15	0.563	- 0.131	1.228E-02
Eigenvalues	4.434	2.283	1.405
Accumulated percent of trace	34.108	51.667	62.473

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Appendix II.

List of examined specimens

***Saara asmussi* (Strauch, 1863)**

MHNP 1989.3005, unknown; ZFMK 7925, Afghanistan, Seistan, 50 km east Seranj; BMNH 1964.279, Pakistan, Kharan / Balutschistan; BMNH 74.11.239, Iran, near Rigan / Narmashir; BMNH 79.8.15.18, Afghanistan, Ghorak; BMNH 79.8.15.30, Afghanistan, Ghorak.

***Saara hardwickii* (Gray, 1827)**

NMW 21175, Pakistan, Sindh; NMW 21167:1, India, Katchh; NMW 21167:2, India, Katch; NMW 21167:3, India Katchh; NMW 21173, unknown, foothills of the western Himalaya; NMW 21169:1, Pakistan, Sindh; NMW 21169:2, Pakistan, Sindh; NMW 21169:3, Pakistan, Sindh; NMW 15121:2, India, Katchh; NMW 19981:2, Pakistan, Karachi; NMW 19981:3, Pakistan, Karachi; NMW 19981:4, Pakistan, Karachi; NMW 19981:5, Pakistan, Karachi; MHNP 1962.726, Pakistan, Gizri; MHNP 1962.727, Pakistan, Gizri; MHNP 1962.728, Pakistan, Gizri; ZSM 327/79, Pakistan, Uthal; ZSM 20/1912, Pakistan, Habb; ZSM 7/1912, Pakistan, Wajara; ZSM 7/1912, Pakistan, Wajara; ZFMK 21453, Pakistan, Mokran coast; ZFMK 8616, Afghanistan, Nimla to Djalalabad; ZFMK 21454, Pakistan, Mokran coast; ZFMK 21455, Pakistan, Mokran coast; ZFMK 22103, Pakistan, Mokran coast; BMNH 1933.4.1.23, India, Thar Parkar/Rajputana; BMNH 1933.4.1.24, India, Thar Parkar/Rajputana; BMNH 91.9.11.9, Pakistan, Sindh; BMNH 60.3.19.1006, India, Goojerat; BMNH 1973.447, Pakistan, Karachi; BMNH 1946.8.14.44, India, Plains of Kanouge/Hindustan; BMNH 98.12.22.10, Pakistan, Karachi.

***Saara loricata* (Blanford, 1874)**

NMW 21177, Iran, Bushir; NMW 21179:1, Iran, Bushir; NMW 21179:2, Iran, Bushir; ZSM 2/1966, Iraq, Chankin / southeast Bagdad; ZFMK 22072, Iran, Ahwaz; ZFMK 44906, Iraq, Kirkuk; ZFMK 40594, Iraq, Kirkuk; ZFMK 40593, Iraq, Kirkuk; ZFMK 40592, Iraq, Kirkuk; ZFMK 40591, Iraq, Kirkuk; ZFMK 40590, Iraq, Kirkuk; BMNH 1933.4.1.25, Iran, Bushir; BMNH 87.9.22.19, Iran, Bushir; BMNH 1905.10.14.21, Iran, 30 mls northwest Ahwaz.

***Uromastyx acanthinura* Bell, 1825**

BMNH 1907.4.6.14, Algeria, Biskra; BMNH 1907.4.6.15, Algeria, Biskra; BMNH 1912.11.9.4.6., Algeria, Fort Miribel; BMNH 1912.11.9.50, Paratype of *Uromastix acanthinurus nigerrimus*, Algeria, Oued Mya; BMNH 1912.11.9.51, Paratype of *Uromastix acanthinurus nigerrimus*, Algeria, Ain Guettara; BMNH 1938.7.5.10, Algeria, Biskra; BMNH 1938.7.5.11, Algeria, Bistra; BMNH 1938.7.5.12, Algeria, Bistra; BMNH 1938.7.5.13, Algeria, Biskra; BMNH 1964.2075, Libya, Ain Uif Jebel Nefrousa; BMNH 1969.2088, Algeria, Bistra; BMNH 1969.2090, Algeria, Bistra; BMNH 1969.2091, Algeria, Bistra; BMNH 1969.2106, Algeria, Touggourt; BMNH 1969.2107, Algeria, Touggourt; BMNH 1969.2108, Algeria, Touggourt; BMNH 71.4.16.52, Algeria, Bistra; BMNH 91.4.5.41, Algeria, Bistra; BMNH 91.4.5.42, Algeria, Biskra; BMNH 91.5.439, Tunesia, Duirat; BMNH 91.5.440, Tunesia, Duirat; BMNH 96.2.29.1, Tunesia; Duirat; MZUF 13757, Algeria, Touggourt (Tourghuf); MZUF 21666, Somalia, unreliable locality!; MZUF 25125, Tunesia, Tamerza/Gafsa; MZUF 25126, Tunesia, Tamerza/Gafsa; MZUF 743, Libya, Bu Ngem; MZUF 744, Libya, Cirenaica (Barqa), NMW 21192:1, Tunesia, Gafsa; NMW 21192:2, Tunesia, Gafsa; NMW 21192:3, Tunesia, Gafsa; NMW 21197:1, Algeria, Bistra; NMW 21198:1, Tunesia, Gafsa; NMW 21198:10, Tunesia, Gafsa; NMW 21198:2, Tunesia, Gafsa; NMW 21198:3, Tunesia, Gafsa; NMW 21198:4, Tunesia, Gafsa; NMW 21198:5, Tunesia, Gafsa; NMW 21198:6, Tunesia, Gafsa; NMW 21198:7, Tunesia, Gafsa; NMW 21198:8, Tunesia, Gafsa; NMW 21198:9, Tunesia, Gafsa; NMW 21202:1, Algeria, Biskra; NMW 21202:2, Algeria, Bistra; NMW 21207, Tunesia, Gafsa; NMW 21208, Tunesia, El Guietar; NMW 22116, Libya, Tripolis; SMNS 602:1, Algeria, Biskra; ZFMK 2707, Tunesia, Gabes (Quderef); ZFMK 2708, Tunesia, Gabes-Matmata; ZFMK 2709, Algeria, Biskra; ZFMK 2710, Algeria, Biskra; ZFMK 2711, Algeria, Biskra; ZFMK 2714, Algeria, Biskra; ZMH-R4507, Algeria, Biskra; ZMH-R4508, Algeria, Biskra; ZMH-R4509, Algeria, Biskra; ZSM 112/1983, Libya, south of Tripolis; ZSM 18/1968 (1), Libya, Jebel el Soda; ZSM 18/1968 (2), Libya, Jebel el Soda; ZSM 18/1968 (3), Libya, Jebel el Soda; ZSM 18/1968 (4), Libya, Jebel el Soda; ZSM 181/36, Libya, Jebel el Soda; ZSM 26/1951 (1), Tunesia, Nefta south of Tozeur; ZSM 26/1951 (2), Tunesia, Nefta south of Tozeur; ZSM 4/1963, Tunesia, El Hamma; ZSM 472/79, Libya, Gharian/Tripolis; ZSM 510/1978, Libya, Wadi Bundindin.

Uromastyx aegyptia

***Uromastyx aegyptia aegyptia* Forsskål, 1775**

BMNH 1908.6.9.6, Egypt, Tor / Sinai; BMNH 1951.1.2.55, Israel, Wadi Araba; BMNH 97.10.28.212, Egypt, Suez; BMNH 97.10.28.213, Egypt, Beltim Delta; MZUF 28899, Saudi Arabia, Sawawin; NMW 21182:1, Egypt, Cairo; NMW 21182:2, Egypt, Desert near Cairo; NMW 21183, Egypt, Suez; NMW 21187, Egypt, Cairo; NMW 21222, Egypt, Beltim; ZFMK 2703, Egypt, Lower Egypt; ZFMK 2704, Egypt, Lower Egypt; ZFMK 39073, Egypt, Suez; ZFMK 44216, Neotype of *Uromastyx aegyptia aegyptia*, Egypt, Suez; ZFMK 46502, Egypt; ZFMK 46504, Egypt; ZFMK 64405, Egypt, vicinity of Hurgharda; ZFMK 64406, Jordan, Wadi Araba.

***Uromastyx aegyptia microlepis* Blanford, 1874**

BMNH 1930.6.30.3, Yemen, Bin Khautar / Hadramaut; BMNH 1946.8.11.67, Iraq, Paralectotype of *Uromastyx microlepis*, Basrah; BMNH 1946.8.14.55, Lectotype of Uromastyx microlepis, Iraq, Basrah; BMNH 1950.1.4.71, Oman; BMNH 1950.1.5.4, Arabia, Miofa; BMNH 1952.1.3.51, Saudi Arabia, ElGaisuma-Turaif; BMNH 1953.1.8.50, Yemen, North of Jol / Hadramaut; BMNH 1970.2076; Saudi Arabia, Ruma; BMNH 1970.2481,

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Bahrain, Ras Al Barr; BMNH 1970.2482, Bahrain, Ras Al Barr; BMNH 1971.748, Bahrain; BMNH 1972.1259, United Arab Emirates, Al Hamran / Abu Dhabi; BMNH 1972.833, United Arab Emirates, near Bada Zaid / Abu Dhabi; BMNH 1978.2072, Kuwait; BMNH 1980.569, Oman, Jiddat al Harasis; BMNH 1982.1327, Saudi Arabia, Dib Dibah; BMNH 1982.1328, Saudi Arabia, Dib Dibah; BMNH 1985.880, Saudi Arabia, 30 km SE Ronya; BMNH 1986.435, Saudi Arabia, Shigree; BMNH 1988.214, Saudi Arabia, 26°56'N, 38°59'E; BMNH 1988.93, Saudi Arabia, Al Rawdah, north of Khobar; BMNH 1996.207, United Arab Emirates, Jebel Gaddah near Jebel Dannah; BMNH 85.7.11.11, Iraq, Fao; BMNH 88.12.6.8, Iraq, Fao; ZFMK 20267, Iraq, Basrah; ZFMK 21091, Iraq, Basrah; ZFMK 42413, Oman, 100 km from Muscat; ZFMK 42414, Oman, 100 km from Muscat; ZFMK 43648, Saudi Arabia, 100 km NO Riyadh; ZFMK 43649, Saudi Arabia, 100 km NO Riyadh; ZFMK 44907, Iraq, Kirkuk; ZFMK 44908, Iraq, Kirkuk; ZFMK 44909, Iraq, Kirkuk; ZFMK 44910, Iraq, Kirkuk; ZFMK 44911, Iraq, Kirkuk.

***Uromastyx aegyptia leptieni* Wilms & Böhme, 2000**

BMNH 1973.2039, United Arab Emirates, S Jebel Jayah; BMNH 1973.2040, United Arab Emirates, Jebel Ali SW Dubai; BMNH 1973.2041, United Arab Emirates, Tawi Bil Khabis 25km WSW Dayd; BMNH 1973.721, Oman, Munay; BMNH 1975.958, Oman, Rostaq 23°24'N 57°27'E; BMNH 85.II.7.4, Oman, Muscat; BMNH 85.II.7.5, Oman, Muscat; ZFMK 52398, Holotype *Uromastyx leptieni*, Wadi Siji.

***Uromastyx alfredschmidti* Wilms & Böhme, 2001**

MHNG 1515.77, Paratype of *Uromastyx alfredschmidti*, Algeria, Tassili n'Ajjers; MHNP 1961.261, Paratype of *Uromastyx alfredschmidti*, Algeria, Hoggar; MHNP 9905, Paratype of *Uromastyx alfredschmidti*, Algeria, Hoggar; NMW 8224:3, Paratype of *Uromastyx alfredschmidti*, Sahara; ZFMK 24643, Holotype of *Uromastyx alfredschmidti*, Algeria, Tassili n'Ajjers /30 km NO Djanet.

***Uromastyx benti* (Anderson, 1894)**

BMNH 1946.8.11.69, Paralectotype of *Uromastyx benti*, Yemen, Makulla, Hadramaut; BMNH 1946.8.11.70, Paralectotype of *Uromastyx benti*, Yemen, Makulla, Hadramaut; BMNH 1946.8.11.71, Paralectotype of *Uromastyx benti*, Yemen, Makulla, Hadramaut; BMNH 1946.8.11.72, Lectotype of *U. benti*, Yemen, Makulla, Hadramaut; BMNH 1953.1.8.52, Yemen, Hadramaut; BMNH 1956.1.7.26, Yemen, Wadi Abr/ Hadramaut; MHNP 1895.43, Paralectotype of *Uromastyx benti*, Yemen, Makulla, Hadramaut; MTKD 24589, Yemen, Makulla; NMW 16174, Yemen, Makulla; NMW 21213:1, Yemen, Makulla; NMW 21213:2, Yemen, Makulla; NMW 21213:3, Yemen, Makulla; NMW 21213:4, Yemen, Makulla; NMW 21213:5, Yemen, Makulla; NMW 21213:6, Yemen, Makulla; NMW 21213:7, Yemen, Makulla; NMW 21213:8, Yemen, Makulla; NMW 21213:9,Yemen, Makulla; NMW 21214:1, Syntype *Uromastyx simonyi*, Yemen, Assan; NMW 21214:2, Syntype *Uromastyx simonyi*, Yemen, Assan; ZFMK 73680, Oman, Mirbat; ZFMK 73681, Oman, Mirbat; ZFMK 83347, Oman, Mirbat; ZFMK 83801, Oman, Mirbat; ZMH R04513, Yemen, Makulla/Hadramaut.

Uromastyx dispar

***Uromastyx dispar dispar* Heyden, 1827**

BMNH 1900.9.12.1, Sudan, Wadi Halfa; BMNH 1913.9.16.15, Sudan, Dongola Provinz; BMNH 1954.1.6.9, Tchad, Tibesti; BMNH 1956.1.1.6, Tchad, S of Zouar; BMNH 1958. 1.3.95, Tchad, Central Tibesti; BMNH 1962.286, Tchad, Bardai; BMNH 1962.287, Tchad, Bardai; BMNH 1973.3348, Tchad, Central Tibesti; BMNH 1986.721, Tchad, Ounianga 19°4'N/20°36'E; GMNH 1952-9100(1), Tchad, Tibesti; GMNH 1952-9100(2), Tchad, Tibesti; MHNP 1974.328, Egypt, Ismailia; MNHP 1993.0692, Tchad, Tibesti; BMNH 1900.9.12.1, Sudan, Wadi Halfa; BMNH 1913.9.16.15, Sudan, Wadi Halfa; SMF10417, Lectotype of *Uromastyx dispar*, Desert near Ambukol; ZFMK 2706, Tchad, Fada; ZFMK 39900, Sudan, SE Debba direction of Khartoum; ZFMK 65600, Tchad, Zouar; ZFMK 65601, Tchad, Zouar; ZFMK 65602, Tchad, Zouar.

***Uromastyx dispar flavifasciata* Mertens, 1962**

BMNH 1969.476, Mauritania, Ouadane; BMNH 1969.477, Mauritania, Ouadane; MHNG 1515.74, Mauritania, Guelta Zemour/Rio de Oro; MHNG 1515.75, Mauritania, Chingetti; MHNG 1515.76, Mauritania, Bir Moghrein/Fort Tringuet; MHNP 1981.178, Mauritania, Richat, Adrar; MHNP 1986.2012, Algeria, Tindouf; MHNP 1993.1501, Mauritania, Atar, Ar bou M'rait; MNHP 1993.5808, Mauritania, Matmata; SMF 58032, Holotype of *Uromastyx acanthinurus flavifasciatus*, Mauritania; ZFMK 17597, Mauritania, Hamdoun; ZFMK 17598, Mauritania, Atar.

***Uromastyx dispar maliensis* Joger & Lambert, 1996**

BMNH 1933.11.18.1, Mali, Gao; BMNH 1933.11.18.2, Mali, Gao; BMNH 1934.1.1.1, Mali, Taberreshat/17°40'N/0°10'E; GNHM 1930.32-5744 RE1772, Paratype *Uromastyx maliensis*, Mali Ti-N-Zaouatene; HLMD RA 1545, Holotype *Uromastyx maliensis*, Mali 40km SE Gao; MHNP 1965.0144, Paratype *Uromastyx maliensis*, Algeria, Taoudrart/Hoggar; NMW 21211, Algeria, Tamanrasset; ZFMK 9232, Algeria, Ahaggar/Gara Djenoun; ZMH-R04529, Algeria, Tassili du Hoggar; 11 Specimens from the trade (Mali).

***Uromastyx geyri* Müller, 1922**

BMNH 1961.417, Niger, near Abangharit/Air; BMNH 1970.1755, Niger, Iferouhane/Air; BMNH 1978.2093, Algeria, Hoggar; BMNH 1978.2094, Algeria, Hoggar; BMNH 1979.402, Algeria, 15km ENE Tamanrasset 22°57'N/05°47'E; BMNH 1986.733, Niger, N of Agadez; MZUF 21013, Algeria, Tamanrasset; MZUF 21014, Algeria, Tamanrasset; MZUF 21015, Algeria, Tamanrasset; MZUF 21017, Algeria, In Ecker 180km N Tamanrasset; GNMH 1930.32-5744 Re1761; MHNG 1513.40, Niger, Tin Teloust/Air; MHNP 1932.128, Algeria, Tanezrouft; MHNP 1943.3, Algeria, Hoggar; MHNP 1974.1412, Algeria, Tefedest; MHNP 1990.4665, Niger, El Meki/Air; MNHP 8971, Niger, Telouess Tabelot; MNHP 8972, Niger, Telouess Tabelot; MTKD 25699, Niger, Agadez; MTKD 25700, Niger, Agadez; SMF 68765, Niger; SMF 68766, Niger; SMF 68767, Niger; ZFMK 9228, Algeria, Ahaggar/In Kelmet; NMW 21210, Algeria, Tamanrasset; NMW 21211, Algeria, Tamanrasset; NMW 22000, Algeria, Hoggar/Tamanrasset; NMW 23517:1, Algeria,

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Ideles/Hoggar; NMW 23517:2, Algeria, Ideles/Hoggar; NMW 25481, Algeria, Tit near Tamanrasset; ZFMK 20042, Algeria, Hoggar/between In Eker and In Amguel; ZFMK 20043, Niger, 20 km S Arlit/Air; ZFMK 36627, Niger, 30-40 km N Gougaran; ZFMK 36628, Niger, 30-40km N Gougaran; ZFMK 40628, Niger, near Gougaran; ZFMK 9226, Paratype of *Uromastyx geyri*, Algeria, upper Tahihaout; ZFMK 9227, Paratype of *Uromastyx geyri*, Algeria, Oued Ouhat; ZFMK 9229, Algeria, Tharemert-n-akh; ZFMK 9230, Neotype of *Uromastyx geyri*, Algeria, Gara Dienoum; ZFMK 9231, Algeria, Ahaggar/Gara Djenoum; ZMH-R04523, Algeria, Oasis Abalessa E of Tamanrasset; ZSM 4451, Paratype of *Uromastyx geyri*, Algeria, Tharemert-n-akh.

Uromastyx macfadyeni Parker, 1932

BMNH 1946.8.14.52, Paratype of *Uromastyx macfadyeni*, Somalia, Dagah Shabell 24mls SE Berbera; BMNH 1946.8.14.54, Holotype of *Uromastyx macfadyeni*, Somalia, near Berbera; BMNH 1956.1.6.55, Somalia, Heis 20 mls W Mait.

Uromastyx nigriventris Rothschild & Hartert, 1912

BMNH 1911.12.5.1, Paratype of *Uromastyx acanthinurus nigriventris*, Algeria, Ghardaia; BMNH 1911.12.5.2, Paratype of *Uromastyx acanthinurus nigriventris*, Algeria, Ghardaia; BMNH 1969.2073, Algeria, Laghouat; BMNH 1969.2074, Holotype of *Uromastyx acanthinurus nigriventris*, Algeria, Tilghempt between Laghouat and Ghardaia; BMNH 1969.2075; Algeria, Laghouat; BMNH 1969.2080, Algeria, Ain Sefra; BMNH 1969.2085, Algeria, Laghouat; BMNH 1969.2086, Algeria, Ghardaia; BMNH 1969.2087, Algeria, Laghouat; BMNH 1969.2099, Algeria, Oued N'ca; BMNH 1969.2100, Algeria, Oued N'ca; BMNH 1969.2103, Algeria, (Oued N'ca)/Oued Mya; BMNH 1969.2109, Algeria, El Hadadra between El Golea and Ghardaia; BMNH 1970. 223, Morocco, Foum el Hassane; BMNH 1970. 224, Morocco, Foum el Hassane; BMNH 1970.220, Morocco, 3 km N Tuizgui-Remz, Tarfaya; BMNH 1970.221, Morocco, 5 km E Bou Izakarn; BMNH 1972.2280, Morocco, 3 km NNW Quarzazate; BMNH 1972.2281, Morocco, 3km NNW Quarzazate; BMNH 1972.2282, Morocco, 3km NNW Quarzazate; BMNH 1972.2283, Morocco, 2 km N Douar Zednagain, 3km NNW Quarzazate; BMNH 1972.2284, Morocco, 2 km N Douar Zednagain, 3 km NNW Quarzazate; MZUF 21003, Algeria, Ghardaia; MZUF 21004, Algeria, Ghardaia; MZUF 21005, Algeria, Ghardaia; MZUF 21006, Algeria, Ghardaia; MZUF 21007, Algeria, Ghardaia; MZUF 21008, Algeria, Ghardaia; MZUF 21009, Algeria, Ghardaia; MZUF 21010, Algeria, Ghardaia; MZUF 21011, Algeria, Ghardaia; MZUF 21012, Algeria, Ghardaia; HLMD RA 1177, Morocco, SW Tizgui el Haratuine; HLMD RA 1178, Morocco, 2 km N Rich; MHNP 1927.0094, Morocco, Colomb-Bechar; MHNP 1950.204, Algeria, Beni Ounif; MHNP 1953.18, Algeria, Zerhaura Indigene Beni Abbes; MHNP 1961.249, Morocco, Assa-Aouinet Torkos; MHNP 1961.250, Morocco, vicinity Doirat; MHNP 1961.251, Morocco, Foum el Hassane; MHNP 1961.252, Morocco, Foum el Hassane; MHNP 1961.253, Morocco, 10 km S Guercif; MHNP 1961.255, Morocco, Guercif; MHNP 1961.256, Morocco, N Aouinet Torkos; MHNP 1961.257, Morocco, N Aouinet Torkos; MHNP 1961.258; Morocco, Aoinet Torkos; MHNP 1961.259, Morocco, Zagora – Tagounite; MHNP 1961.260, Morocco, Zagora – Tagounite; MHNP 1986.2013, Morocco, Bechar; MHNP 1986.2014, Morocco, Bechar; MHNP 1991.405, Morocco, Quarzazate; MHNP 1993.800, Morocco; MHNP 1994.1199, Algeria, Beni Ounif; MHNP 1994.1205, Algeria, Beni Ounif; MHNP 1994.1207, Algeria, Beni Ounif; MHNP 1994.1208, Algeria, Beni Ounif; MHNP 1994.1209, Algeria, Beni Ounif; MTKD 18981, Algeria, Ain Sefra; MTKD 20205, Morocco; Quarzazate; MTKD 27995, Algeria, Ain Sefra; NMW 14895, Algeria, Ain Sefra; NMW 14896:1, Algeria, Ain Sefra; NMW 14896:10, Algeria, Ain Sefra; NMW 14896:2, Algeria, Ain Sefra; NMW 14896:3, Algeria, Ain Sefra; NMW 14896:4, Algeria, Ain Sefra; NMW 14896:5, Algeria, Ain Sefra; NMW 14896:6, Algeria, Ain Sefra; NMW 14896:7, Algeria, Ain Sefra; NMW 14896:8, Algeria, Ain Sefra; NMW 14896:9, Algeria, Ain Sefra; NMW 21189:1, Algeria, Gardaia; NMW 21190:1, Morocco, Mazagan; NMW 21190:2, Morocco, Mazagan; NMW 21190:3, Morocco, Gus; NMW 21192:4, Algeria, Beni Abbes; NMW 21192:5, Algeria, Beni Abbes; NMW 21195:2, Algeria, Beni Mzab; NMW 21199:1, Morocco, Colomb-Bechar; NMW 21199:2, Morocco, Colomb-Bechar; NMW 21200, Morocco, Aouinet-Torkoz; NMW 21204:2, Algeria, Beni Ounif/Figuig; NMW 21205, Morocco, Colomb-Bechar; NMW 21209:1, Algeria, Beni Abbes; NMW 21209:2, Algeria, Beni Abbes; NMW 34024, Morocco, Erfoud; SMF 58031, Morocco, Oued Moulonya/36 km E Guercif; SMF 69077, Morocco, Bou Afra near Figuig; SMNS 593:1, Algeria, Ain Sefra; SMNS 598, Algeria, Oued N'za; SMNS 599, Algeria, Beni Ounif/Ouuf; SMNS 601:1, Algeria, Ain Sefra; ZFMK 18021, Algeria, S Ghardaia, Oued Sebseb; ZFMK 18022, Algeria, S Ghardaia, Oued Sebseb; ZFMK 2715, Algeria, Oued Mzab; ZFMK 2716, Algeria, Oued N'ca; ZFMK 2717, Algeria, Oued N'ca; ZFMK 2718, Algeria, Oued N'ca; ZFMK 2719, Algeria, Oued N'ca; ZFMK 2723, Morocco, Erfoud; ZFMK 2724, Morocco, Oujda; ZFMK 2725, Morocco, Oujda; ZFMK 2726, Morocco, Oujda; ZFMK 2727, Morocco, Oujda; ZFMK 2728, Morocco, Oujda; ZFMK 2729, Morocco, Oujda; ZFMK 30806, Morocco, 10 km W Tinerhir; ZFMK 41168, Algeria, Ain Sefra; ZFMK 41512, Morocco, Goulmima; ZFMK 45946, Morocco, Quarzazate; ZFMK 49661, Algeria, El Homr; ZFMK 49742, Morocco, 10-15 km NW Quarzazate; ZFMK 51077, Algeria, Ain Sefra; ZFMK 51078, Algeria, Ain Sefra; ZFMK 52356, Morocco, south of Quarzazate, Ait-Saon; ZFMK 59062, Morocco, Quarzazate; ZFMK 59063, Morocco, Quarzazate; ZFMK 59064, Morocco, Quarzazate; ZFMK 60598, Morocco, 89 km E Guelmim; ZFMK 60600, Morocco, 52 km S Guelmim; ZFMK 60602, Morocco, Erfoud; ZFMK 60603, Morocco, Erfoud; ZFMK 60605, Morocco, Erfoud; ZFMK 60606, Morocco, Erfoud; ZFMK 60607, Morocco, Erfoud; ZFMK 60608, Morocco; ZFMK 60609, Morocco, Erfoud; ZFMK 60610, Morocco, Erfoud; ZFMK 7459, Morocco, Tinerhir; ZFMK 7462, Morocco, Tinerhir; ZMH R 04527, Morocco, Erfoud; ZMH R04517, Morocco, Rissani near Erfoud; ZSM 186/1983, Algeria, Ain el Hadjadi 24 km south of Ain Sefra; ZSM 31/1981, Morocco, Tinerhir; ZSM 34/1981, Algeria, Ain Sefra; ZSM 44/1960, Morocco, Zagora; ZSM 58/1978 (1), Morocco, 25 km N Zagora; ZSM 58/1978 (2), Morocco, 25km N Zagora; ZSM 689/1979, Morocco, Ksar es Souk west of Boudenib; ZSM 8/1994, Morocco, Meski.

Uromastyx ornata

Uromastyx ornata ornata Heyden, 1827

BMNH 97.10.28.199, Egypt, Tor/ Sinai; MHNP 1909.176, Egypt, Mt. Sinai; MHNP 1909.177, Egypt, Mt. Sinai; MHNP 6954, Egypt; MHNP 6970, Egypt; NMW 21217, Egypt, Dahab; NMW 21219:1, Egypt, Sherm Scheikh; NMW 21219:2, Egypt,

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Sherm Scheikh; NMW 21219:3, Egypt, Sherm Scheikh; NMW 21219:4, Egypt, Sherm Scheikh; NMW 21220, Egypt, Tor; ZFMK 65174, Egypt, Wadi Feiran; ZFMK 65175, Egypt, Wadi Feiran; ZFMK 65607, Egypt; ZFMK 65609, Egypt, ZFMK 8576, Israel, Elath; ZMH R 04525, Egypt, Sinai; ZMH R 04526, Egypt, Sinai; SMF 10403, Holotype of *Uromastyx ornata*, Saudi Arabia, Mohila (Al Muwaylih).

***Uromastyx ornata philbyi* Parker, 1938**

BMNH 1946.8.11.60, Holotype of Uromastyx philbyi, Saudi Arabia, between Mecca and Shabwa; BMNH 1946.8.11.62, Paratype of *Uromastyx philbyi*, Saudi Arabia, between Mecca and Shabwa; BMNH 1946.8.11.63, Paratype of *Uromastyx philbyi*, Saudi Arabia, between Mecca and Shabwa; BMNH 1946.8.11.64. Paratype of *Uromastyx philbyi*, between Mecca and Shabwa; BMNH 1946.8.11.65, Paratype of *Uromastyx philbyi*, Saudi Arabia, between Mecca and Shabwa; BMNH 1946.8.11.66, Paratype of *Uromastyx philbyi*, Saudi Arabia, between Mecca and Shabwa; BMNH 1964.296, Saudi Arabia, Burayman 21°40'N 39°10'E; BMNH 1975.518, Saudi Arabia, Bazzah 22°00'N 39°30'E; BMNH 1975.519, Saudi Arabia, Burayman 21°39'N 39°13'E; BMNH 1976.1748, Saudi Arabia, Wadi Fatma; BMNH 1979.960, Saudi Arabia, Burayman 21°45'N 39°15'E; BMNH 1985.882, Saudi Arabia, Mecca by pass km 91 / 21°14'N 29°48'E; BMNH 1985.884, Saudi Arabia, Mecca by pass km115 / 21°15,5'N 39°55'E; BMNH 1986.434, Saudi Arabia, 21°14'N 39°55'E; BMNH 1986.436, Saudi Arabia, 16 km N of Jeddah; BMNH 1975.518, Saudi Arabia, Bazzah 22°N 39°30'E; BMNH 1980.55, Saudi Arabia, Jabal as Sinfa; MZUF 27884, Yemen, Ju Amlah 26 km NW Sa'dah; MZUF 27885, Yemen, Ju Amlah 26 km NW Sa'dah; MZUF 27906, Yemen, Ju Amlah 26 km NW Sa'dah; MZUF 28187, Yemen, Ju Amlah 26 km NW Sa'dah; MHNG 2457.33, Saudi Arabia, Jebel Hababa; MHNG 2457.34, Saudi Arabia, Jebel Hababa; MHNG 2457.35, Saudi Arabia, Wadi Sawawin; MHNG 2536.49, Saudi Arabia, Makkah by pass km 56; MHNP 4318, Saudi Arabia, Jeddah; ZFMK 84442, Saudi Arabia, 19°05'N 41°50'E.

***Uromastyx ocellata* Lichtenstein, 1823**

BMNH 1914.5.14.13, Sudan, Sinkat; BMNH 1927.8.13.38, Sudan, Merowe/Dongola; BMNH 1927.8.13.39, Sudan, Merowe/Dongola; BMNH 1937.12.5.117, Somalia, Borama District; BMNH 1937.12.5.118, Somalia, Borama District; BMNH 1937.12.5.119, Somalia, Borama District; BMNH 1937.12.5.121, Somalia, Borama District; BMNH 1937.12.5.122, Somalia, Borama District 42°45'N 10°45'E; BMNH 1937.12.5.123, Somalia, Borama District 42°45'N 10°45'E; BMNH 1937.12.5.124, Somalia, Borama District 42°55'E 10°55'N; BMNH 1937.12.5.125, Somalia, Borama District 42°55'E 10°55'N; BMNH 1937.12.5.127, Somalia, Borama District 43°E 11°N; BMNH 1937.12.5.128, Somalia, Borama District 43°E 11°N; BMNH 1937.12.5.130, Somalia, Borama District; BMNH 1953.17.63, Sudan, Tehamiyam; BMNH 1953.17.64, Sudan, Tehamiyam; BMNH 1953.17.65, Sudan, Tehamiyam; BMNH 97.10.28.202, Sudan, Suakim; BMNH 97.10.28.203, Sudan, Suakim; BMNH 97.10.28.204, Sudan, Suakim; BMNH 97.10.28.205, Sudan, Suakim; BMNH 97.10.28.206, Sudan, Suakim; BMNH 97.10.28.207, Sudan, Suakim; BMNH 97.10.28.208, Sudan, Suakim; BMNH 97.10.28.209, Sudan, Suakim; MHNP 1897.348, Egypt; MHNP 1897.349, Egypt; NMW 21215, Oasis Harar; NMW 21216, Sudan, Suakim; ZFMK 20822, Sudan, Suakin; ZFMK 38396, Sudan, 40 km W Suakim direction Sinkat; ZMB 811, Holotype of *Uromastyx ocellata*, Sudan, Nubia; ZSM 219/1976, Sudan, Dongola Province.

***Uromastyx princeps* O'Shaughnessy 1880**

BMNH 1931.7.20.270, Somalia, 11°5'N 49°0'E; BMNH 1931.7.20.272, Somalia, 8°54'N 48°54'E; BMNH 1931.7.20.273, Somalia, Buran District 10°13'N 48°46'E; BMNH 1931.7.20.274, Somalia, 10°22'N 49°0'E; BMNH 1931.7.20.275, Somalia, 10°42'N 49°E; BMNH 1946.814.56, Holotype of *Uromastyx princeps*, Zanzibar (unreliable Locality, Wilms 2001); BMNH 1956.1.3.9, Somalia, Wachderria 45mls E Mait; BMNH 1961.1655, Somalia, Candala/Migiurtina; BMNH 1961.1656, Somalia, Candala/Migiurtina; BMNH 1983.735, Somalia, 5°56'N 48°55'E; MZUF 23691, Somalia, Scusciuban; MZUF 10536, Somalia, District of Alula; MZUF 23673, Somalia, Bur Dagner; MZUF 23674, Somalia, Bur Dagner; MZUF 23675, Somalia, Meleden; MZUF 23676, Somalia, Sukorre; MZUF 23686, Somalia, Carin-Gié Bahaia; MZUF 23690, Somalia, Scusciuban; MZUF 23692, Somalia, Monti Carcar; MZUF 23693, Somalia, Scusciuban; MZUF 23694, Somalia, Scusciuban; MZUF 23695, Somalia, Scusciuban; MZUF 23696, Somalia, Scusciuban; MZUF 23782, Somalia, Passo del Didim S of Carin; MZUF 5497, Somalia, Valle di Run; MZUF 5623, Somalia, Valle di Run; MZUF 739, Somalia, Passo del Didim S of Carin; MHNP 1966.1071, Somalia, Candala; MHNP 1966.1072, Somalia, Candala; MHNP 5732, Yemen, Aden (unreliable Locality); MHNP 5831, Somalia, Bender Meraya; MHNP 5832, Somalia, Bender Meraya ; SMF 22931, Somalia, Benden Cassim Migiurtinia; ZFMK 58048, Somalia, Bossasa; ZFMK 58985, Somalia, Bossasa.

***Uromastyx shobraki* Wilms & Schmitz, 2007**

BMNH 1938.2.1.47, Country not reliably traceable, southern Hejaz; BMNH 1987.854, Yemen, Tihama Taiz; BMNH 1988.54, Yemen, Mafraq-Al Mokka km 13,5; BMNH 1988.55, Yemen, Mafraq-Al Mokka km 13,6; MZUF 33614, Yemen, Mafraq-Al Mokka km 13,6; MZUF 33615, Yemen, Mafraq-Al Mokka km 13,5; MHNG 2455.100, Paratype of *Uromastyx yemenensis shobraki*, Yemen, Mafraq-Al Mukha 13,5km; MHNG 2464.44, Yemen, Mafraq-Al Mokka km 13,5; MHNG 2496.55, Paratype of *Uromastyx yemenensis shobraki*, Yemen, between Mocca and Wadi Zabid; MHNG 2496.56, Paratype of *Uromastyx yemenensis shobraki*, Yemen, between Mocca and Wadi Zabid; MHNG 2527.92, Yemen, Wadi Zabid; MHNG 2538.47, Yemen, Wadi Zabid; MHNG 2542.13, Yemen, Wadi Zabid; MHNG 2542.14, Yemen, Wadi Zabid; MHNG 2553.56, Paratype of *Uromastyx yemenensis shobraki*, Yemen, Mafraq-Al Mokka km 1,5, MTKD 31624, Yemen, North Yemen; MTKD 32847, Yemen, North Yemen; ZFMK 48680, Paratype of *Uromastyx yemenensis shobraki*, Yemen, Mafraq-Al Mokka km 13,6; ZFMK 48681, Holotype of *Uromastyx yemenensis shobraki*, Yemen, Mafraq-Al Mokka km 13,5; ZFMK 55651, Yemen, North Yemen; ZFMK 55652, Yemen, North Yemen; ZFMK 58047, Yemen, North Yemen; ZFMK 60687,Yemen, North Yemen; ZFMK 73676, Yemen, Mafraq - al Mocca; ZFMK 73677, Yemen, Mafraq - al Mocca.

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***Uromastyx thomasi* Parker, 1930**

BMNH 1931.7.16.46, Oman, Wadi Hauf; BMNH 1946.8.14.43, Holotype of *Uromastyx thomasi*, Oman, BU'Juay; BMNH 1954.1.2.98, Oman, Ras Duggum; BMNH 1956.1.16.8, Bahrein (unreliable locality); BMNH 1971.1354, Oman, W of Bai; BMNH 1971.1355, Oman, W of Bai; BMNH 1973.2908, Oman, Masirah; BMNH 1975.1038, Oman, Masirah; BMNH 1977.335, Oman, Jiddat al Harasis 19°32'N 57°12'E; BMNH 1978.1322, Oman, Al Ajaiz; BMNH 1978.2249, Oman, near Haql 20°25'N 58°47'E; BMNH 1980.213, Oman, Thamarit 17°38'N 54°02'E; BMNH 1980.570, Oman, Jiddat al Harasis 19°32'N 57°13'E; BMNH 1982.1221, Oman, Masirah.

***Uromastyx yemenensis* Wilms & Schmitz, 2007**

BMNH 1946.8.11.68, Paralectotype *Uromastyx benti*, Yemen, Makulla Hadramaut (doubtful record); BMNH 1963.755, Yemen, Wadi Tiban west of Aden; BMNH 95.11.27.6, Yemen, Hills 50 km from Aden; BMNH 95.11.27.7, Yemen, Hills 50 km from Aden; BMNH 99.12.13.106, Yemen, between Mount Manif and Jimil / N. of Lahej; BMNH 99.12.13.51,Yemen, Yabian mountains, MTKD 24554, Yemen, Zingibar, Abyan-Gouvernement; MTKD 25441, Yemen, Amran/Aden; MTKD 26951, Yemen, Lawdar, Abyan-Gouvernement, MTKD 26952, Yemen, Lawdar, Abyan-Gouvernement; MTKD 28873, Yemen, Lawdar, Abyan-Gouvernement; MTKD 29475, Paratype of *Uromastyx yemenensis*, Yemen, Zingibar, Abyan-Gouvernement; MTKD 34675, Yemen, Abyan-Gouvernement; ZFMK 47860, Paratype of *Uromastyx yemenensis*, Yemen, Lawdar, Abyan-Gouvernement; ZFMK 47861, Holotype of *Uromastyx yemenensis*, Yemen, Lawdar, Abyan-Gouvernement; ZFMK 49036, Paratype of *Uromastyx yemenensis*, Yemen, Lawdar, Abyan-Gouvernement.

Appendix III.

Morphological character coding

(A) Number of tail worls

(0) = 29–36 Whorls

(1) = 15–28 Whorls

(2) = 9–13 Whorls

The taxon *hardwickii* has 29–36 primary tail whorls. In *Leiolepis* more than 100 scale rows are always present from the cloacal slit to the tip of the tail. Therefore the character state present in *hardwickii* is considered to be plesiomorphic (0).The majority of the taxa (with the exception of *princeps* and *thomasi*) have 15–28 primary tail whorls (1). The short tailed taxa *princeps* amd *thomasi* are considered to show a character state derived from state 1 (2).

(B) Number of gular scales

(0) = > 29.7

(1) = < 25.9

With the exception of *ornata* and *philbyi*, all taxa have an average count of more than 29.7 gular scales. In *Leiolepis* between 33–45 gular scales are present. Therefore high numbers of gular scales are considered to be the plesiomorphic character state (0). In *ornata* and *philbyi* average gulare scale counts are 25.9 and 22.6 respectively (1).

(C) Number of scales around midbody

(0) = 140–220

(1) = 265–319

With the exception of *aegyptia*, *microlepis*, *leptieni* and *occidentalis* all taxa have an average scale count of less than 220 scales around midbody. *Leiolepis* has between 165–211 scales around midbody. Low scale counts are therefore considered to be the plesiomorphic character state (0). The high scale counts present in the taxa of the *U. aegyptia* group are considered to be apomorphic (1).

(D) Number of ventral scales between gular and inguinal fold

(0) = < 121

(1) = > 121

With the exception of *aegyptia*, *microlepis*, *leptieni* and *hardwickii* all taxa have an average number of ventral scales of less than 121. *Leiolepis* either has less than 100 ventral scales. Low numbers of ventral scales are therefore considered to be the plesiomorphic character state (0), while high numbers of ventral scales are considered to by apomorphic (1).

(E) Number of scales around 5th tail whorl

(0) = 46.2

(1) = < 37

In average *hardwickii* has 46.2 scales around the 5th tail whorl (Range: 40–52). Average values of all remaining taxa are considerably lower (between an average of 22.8 and 36.7). In *Leiolepis* the respective value is 71–125 scales. A high number of scales is therefore considered to be the plesiomorphic character state (0). All remaining taxa have low numbers of scales and are therefore considered to show the apomorphc character state (1). Only in three taxa (*microlepis, yemenensis* and *shobraki*) single specimens might show values overlapping with the range of *hardwickii* (43 scales for *microlepis*, 40 scales for *shobraki* and *yemenensis*).

(F) Number of scales between subocularia and supralabialia

(0) = > 3.6

(1) = < 3.2

Most taxa have 3–9 scales between the subocularia and supralabialia. In *Leiolepis* 5–7 scales are present. A high scale count is therefore considered to be the plesiomorphic character state (0). Only two taxa (*princeps* and *thomasi*) show scale counts as low as two scales. In both taxa average scale counts are lower than in the remaining taxa (*princeps* 3.2 / *thomasi* 3.0). This character state is considered to be apomorphic (1). From the remaining taxa only *geyri* and *ornata* have less than four scales between subocularia and supralabialia (*ornata*: 3.7; *geyri*: 3.6).

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(G) Snout-vent-length (SVL)

(0) = < 28.0 cm

(1) = > 35.5 cm

Species of the genus *Leiolepis* can reach the following maximum snouth-vent-length: *belliana*: 16.6 cm; *reevesii*: 15.1cm; *peguensis*: 13.6 cm; *triploida*: 14.8 cm and *guttata*: 18.4 cm (PETERS 1971). Taxa of the genus *Uromastyx* reach a maximum SVL of: *acanthinura*: 25.3 cm; *nigriventris*: 24.0 cm; bei *aegyptia*: 40.0 cm; *asmussi*: 26.5 cm; *alfredschmidti*: 23.0 cm; *benti*: 19.6 cm; *yemenensis*: 18.5 cm; *shobraki*: 20.8 cm; *dispar*: 23.1 cm; *flavifasciata*: 28.0 cm; *maliensis*: 23.2 cm; *microlepis*: 35.5 cm; *macfadyeni*: 11.7 cm; *geyri*: 19.3 cm; *hardwickii*: 23.3 cm; *loricata*: 27.7 cm; *leptieni*: 37,5 cm (WILMS & BÖHME 2007); *ocellata*: 17.4 cm, *ornata:* 19.6 cm; *philbyi*: 19.2 cm; *princeps*: 15.4 cm and *thomasi*: 18.2 cm. A maximum SVL of less than 28 cm is considered to be the plesiomorphic character state (0), while a maximum SVL of 35.5 cm or more is considered to be the apomorphic character state (1). Because of the very limited knowledge on the maximum length of *Uromastyx occidentalis* and the supposed relationship of this species with the large growing taxa of *Uromastyx aegyptia* we assign apomorphic character state to this taxon.

(H) Tail length

(0) = > 52.6 % of SVL

(1) = < 42.9 % of SVL

The character „short tailed" in *princeps* and *thomasi* is considered to be apomorphic (1) because this character state is exceptional within the genus *Uromastyx* and all species of the outgroup possess long tails (0).

(I) Tail scalation

(0) = last 2–8 whorls consisting of continuous scale rows

(1) = last 12–21 whorls consisting of continuous scale rows

The members of the *Uromastyx ocellata* group (*ocellata*, *ornata*, *philbyi*, *benti*, *yemenensis*, *shobraki*) as well as *macfadyeni* show a very unique scalation of the tail, with the last 12–21 whorls consisting of continuous scale rows in which one dorsal scale row corresponds with one row ventrally (1). In all other taxa the character „continous scale row on the tail" is restricted only to the last 2–8 whorls. All other whorls in these taxa consist of one dorsal scale row with more than one corresponding scale rows ventrally. The latter character state is considered to be plesiomorphic (0), because it can easily be derived from the tail of a *Leiolepis* with its scalation consisting of small scales.

(J) Value of the quotient of head width and head length

(0) = 0.861–0.875

(1) = 0.897–0.952

(2) = 0.967–0.997

Within the genus *Leiolepis* this quotient values between 0.66–0.75. A low average value is considered to be a plesiomorphy. Therefore *princeps* (value: 0.875), *thomasi* (value: 0.874) and *yemenensis* (value: 0.861) possess the plesiomorphic character state (0), but which is not assigned to *yemenensis* for the phylogenetic analysis because of the proven relationship of *yemenensis* to the *ocellata* group within *Uromastyx* [*yemenensis*: (1)]. Most of the remaining taxa (exceptions *hardwickii*, *asmussi*, *loricata*) have average values for this quotient ranging between 0.897–0.952 which are considered to be the apomorphic character state (1). The relatively broad headed taxa *asmussi*, *loricata* and *hardwickii* posses values for this quotient rangeing between 0.967–0.997. This character state is considered to be different from (1) and is therefore assigned to (2).

(K) Value of the quotient of tail length and maximun with of the tail at the 5th whorl

(0) = 4.4–5.2

(1) = 3.4–3.9

(2) = 1.2–2.1

The average value of this quotient within most taxa is between 4.4 bis 5.2. In the genus *Leiolepis* the respective values are between 15 and 20, therefore higth values are considered to be plesiomorphic (0).

For *acanthinura*, *nigriventris*, *dispar*, *flavifasciata*, *maliensis*, *macfadyeni* and *philbyi* the average value is between 3.4 and 3.9. These character states are considered to be apomorphic (1). For the two short tailed taxa *thomasi* and *princeps* the values are 1.2 and 2.1 respectively. These character states are considered to be different to (1) and are therefore assigned to (2).

(L) Enlarged tubercular scales on the dorsum

(0) = tubercular scales absent

(1) = tubercular scales present

Leiolepis lacks enlarged tubercular scales on the dorsum. Within the taxa in question only *hardwickii*, *loricata* and *asmussi* possess enlarged tubercular scales. This character state is considered to be apomorphic (1).

(M) Intercalary scales between tail whorls dorsally

(0) = intercalary scales present

(1) = intercalary scales absent

In *Leiolepis* tail scalation is not arranged in whorls. Therefore the presence of intercalary scales is considered to be the plesiomorphic character state, because their presence is easily derived from a tail witch is consisting of small scales (0). The apomorphic character state shows a reduction and enlargement of scale rows on the tail (1).

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Zoologisch-Botanische Datenbank/Zoological-Botanical Database

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