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Out of Africa: Phylogeny and biogeography of the widespread genus *Acanthodactylus* (Reptilia: Lacertidae)

Karin Tamar[a,b,*], Salvador Carranza[c], Roberto Sindaco[d], Jiří Moravec[e], Jean-François Trape[f], Shai Meiri[a,b]

[a] *Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv 6997801, Israel*
[b] *The Steinhardt Museum of Natural History, Israel National Center for Biodiversity Studies, Tel Aviv University, Tel Aviv 6997801, Israel*
[c] *Institut de Biologia Evolutiva (CSIC-Universitat Pompeu Fabra), Passeig Maritím de la Barceloneta, 37-49, 08003 Barcelona, Spain*
[d] *Museo Civico de Storia Naturale, via San Francesco di Sales 188, I-10022 Carmagnola, Torino, Italy*
[e] *Department of Zoology, National Museum, Cirkusová 1740, 19300 Prague 9, Czech Republic*
[f] *Laboratoire de paludologie et zoologie médicale, Institut de Recherche pour le Développement, UMR MIVEGEC, B.P. 1386, Dakar, Senegal*

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ABSTRACT

Acanthodactylus lizards are among the most diverse and widespread diurnal reptiles in the arid regions spanning from North Africa across to western India. *Acanthodactylus* constitutes the most species-rich genus in the family Lacertidae, with over 40 recognized species inhabiting a wide variety of dry habitats. The genus has seldom undergone taxonomic revisions, and although there are a number of described species and species-groups, their boundaries, as well as their interspecific relationships, remain largely unresolved. We constructed a multilocus phylogeny, combining data from two mitochondrial (*12S*, *cytb*) and three nuclear (*MC1R*, *ACM4*, *c-mos*) markers for 302 individuals belonging to 36 known species, providing the first large-scale time-calibrated molecular phylogeny of the genus. We evaluated phylogenetic relationships between and within species-groups, and assessed *Acanthodactylus* biogeography across its known range. *Acanthodactylus* cladogenesis is estimated to have originated in Africa due to vicariance and dispersal events from the Oligocene onwards. Radiation started with the separation into three clades: the Western and *scutellatus* clades largely distributed in North Africa, and the Eastern clade occurring mostly in south-west Asia. Most *Acanthodactylus* species diverged during the Miocene, possibly as a result of regional geological instability and climatic changes. We support most of the current taxonomic classifications and phylogenetic relationships, and provide genetic validity for most species. We reveal a new distinct *blanfordii* species-group, suggest new phylogenetic positions (*A. hardyi*, *A. masirae*), and synonymize several species and subspecies (*A. lineomaculatus, A. boskianus khattensis* and *A. b. nigeriensis*) with their phylogenetically closely-related species. We recommend a thorough systematic revision of taxa, such as *A. guineensis*, *A. grandis, A. dumerilii*, *A. senegalensis* and the *pardalis* and *erythrurus* species-groups, which exhibit high levels of intraspecific variability, and clear evidence of phylogenetic complexity.

1. Introduction

The Old World genus *Acanthodactylus* Fitzinger, 1834 is the most species-rich genus in the family Lacertidae, comprising over 40 currently recognized species (Uetz and Hošek, 2016). These lizards are commonly known as fringe-fingered lizards due to their distinctive lateral finger scalation. *Acanthodactylus* is a member of the Saharo-Eurasian clade within the Eremiadini tribe (Mayer and Pavlicev, 2007), and along with its phylogenetically closest members (i.e., *Eremias, Mesalina*, *Ophisops*; Pyron et al., 2013), it inhabits mostly xeric habitats in North Africa and Asia (Sindaco and Jeremčenko, 2008). *Acanthodactylus* ranges from the Iberian Peninsula, across North Africa (including the Sahel) and the Arabian Peninsula towards western India, and northward to Cyprus and southern Turkey (Fig. 1; Salvador, 1982; Arnold, 1983; Schleich et al., 1996; Sindaco and Jeremčenko, 2008). *Acanthodactylus* are diurnal, ground-dwelling, medium-sized lizards, occurring in several climatic regions, from the Mediterranean ecoregion to the harsh desert environments of the Sahara and Arabia, occupying a wide array of arid ecosystems from open woodland, shrubland and savanna to sand dune deserts (Salvador, 1982; Arnold, 1983; Sindaco and Jeremčenko, 2008).

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* Corresponding author at: Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv 6997801, Israel.

E-mail address: karintmr@gmail.com (K. Tamar).

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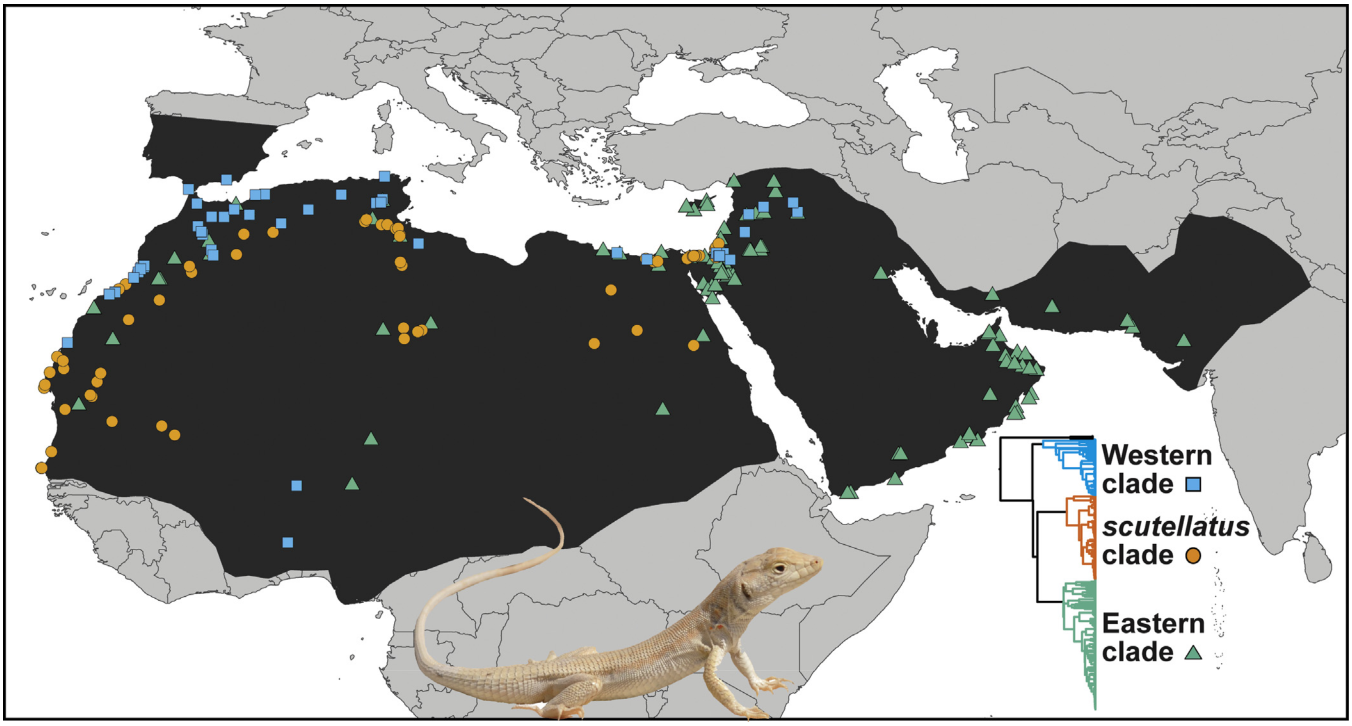

Fig. 1. Map illustrating the distributional range of *Acanthodactylus* (modified from Sindaco and Jeremčenko, 2008), including the phylogenetic tree with the three clades and the localities of each clade member.

Acanthodactylus is known among herpetologists as one of the most taxonomically complex genera. The genus is morphologically highly conservative, but some species have great intraspecific variability (e.g., *A. boskianus*; Salvador, 1982; Arnold, 1983). The taxonomy of this genus is unstable due to complex microevolution, great intraspecific variation (usually non-clinal; Schleich et al., 1996), and morphological convergence (Tamar et al., 2014). Consequently, the classification of many species remains unresolved and even ambiguous (e.g., *A. mechriguensis*; Nouira and Blanc, 1999; Fonseca et al., 2008).

The current systematic knowledge of *Acanthodactylus* is based on several revisions of its morphology, osteology, and hemipenial features (Boulenger, 1918; Salvador, 1982; Arnold, 1983; Harris and Arnold, 2000), as well as on phylogenetic studies (Harris and Arnold, 2000; Harris et al., 2004; Fonseca et al., 2008, 2009; Carretero et al., 2011; Heidari et al., 2014; Tamar et al., 2014). The first genus-level molecular phylogeny of *Acanthodactylus* sampled 15 species and divided the genus into three clades: Eastern, Western, and *scutellatus* (Harris and Arnold, 2000). The genus is further divided into species-groups based on gross morphological similarities among species (Salvador, 1982; Arnold, 1983; Harris and Arnold, 2000). Currently, *Acanthodactylus* species are divided into the following species-groups (hereafter 'groups') within the three clades: the Western clade comprises the *tristrami* group from the Middle East, and the *erythrurus* and *pardalis* groups occupying the Sub-Saharan region and the coastal areas of North Africa; the *scutellatus* clade corresponds to the *scutellatus* group solely, occurring mainly in the sandy areas of North Africa; and the Eastern clade is composed of the *micropholis*, *grandis*, *cantoris*, *opheodurus* and *boskianus* groups, mostly inhabiting south-west Asia. The group division within *Acanthodactylus* is frequently used today, although the actual number of groups is debated (Salvador, 1982; Arnold, 1983; Harris and Arnold, 2000), as is the assignment of some species to groups (e.g., *A. blanfordii* and *A. masirae* within the *cantoris* group; Harris and Arnold, 2000). Furthermore, clear systematic identifications within the groups are intricate (e.g., *A. schreiberi* and *A. boskianus* within the *boskianus* group; Tamar et al., 2014; *A. dumerilii* and *A. senegalensis* within the *scutellatus* group; Schleich et al., 1996; Crochet et al., 2003; Trape et al., 2012). The systematic classification is further obscured by the ambiguous boundaries and relationships among species and groups (Salvador, 1982; Arnold, 1983; Mellado and Olmedo, 1990; Harris and Arnold, 2000; Crochet et al., 2003; Harris et al., 2004; Fonseca et al., 2008, 2009; Tamar et al., 2014).

The widely-distributed, relatively species-rich *Acanthodactylus* genus provides an excellent model group to test biogeographic hypotheses and examine the processes that have resulted in its current diversification. However, an objective assessment of these hypotheses is complicated as there is no consensus regarding the evolutionary and biogeographical timeframe of the origin and diversification within the Eremiadini tribe and its Saharo-Eurasian clade, to which *Acanthodactylus* belongs. Several studies of the Lacertidae have suggested that the diversification within Eremiadini occurred during the Miocene, 17–19 million years ago (Mya), following the collision of Africa-Arabia and Eurasia, with the later recolonization of Asia (Arnold, 1989a, 2004; Mayer and Benyr, 1994; Harris et al., 1998; Arnold et al., 2007; Mayer and Pavlicev, 2007; Pavlicev and Mayer, 2009). Other authors, such as Wiens et al. (2006), Hipsley et al. (2009) and Zheng and Wiens (2016), have suggested much older dates, during the Eocene. In addition, several studies have hypothesized that *Acanthodactylus*, and its closest relatives within the Saharo-Eurasian clade (i.e., *Eremias, Mesalina, Ophisops*), originated in south-west Asia where most of their species occur, with multiple later invasions into Africa (Arnold, 1989b, 2004; Harris and Arnold, 2000; Mayer and Pavlicev, 2007; Hipsley et al., 2009).

A thorough examination of the phylogeny and phylogeography of *Acanthodactylus* will help to shed light on the complex systematics and biogeography of this genus. In this study we produce the first comprehensive, time-calibrated phylogeny of

Acanthodactylus, based on multilocus genetic data, in order to elucidate the biogeographical and evolutionary history and to clarify its systematics.

2. Material and methods

2.1. DNA extraction, amplification and sequence analysis

We analysed 302 specimens of *Acanthodactylus*, representing 36 recognizing species, from across its known distribution range (Figs. 1–4; Table S1). To enlarge the number of samples, additional sequences of eight species were retrieved from GenBank (sequences from Tamar et al., 2014). *Mesalina olivieri* and *M. guttulata* were used as outgroups based on previous publications (Harris et al., 1998; Fu, 2000; Mayer and Pavlicev, 2007; Kapli et al., 2011; Pyron et al., 2013). Codes, locations and GenBank accession numbers are listed in Table S1. Localities are shown in Figs. 2–4.

Genomic DNA was isolated from ethanol-preserved tissue samples using either the DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA) or the SpeedTools Tissue DNA Extraction kit (Biotools, Madrid, Spain). Individuals were sequenced for both strands of two mitochondrial gene fragments, the 12S ribosomal RNA (*12S*) and Cytochrome *b* (*cytb*), and three nuclear gene fragments: melano-cortin 1 receptor (*MC1R*), acetylcholinergic receptor M4 (*ACM4*) and oocyte maturation factor MOS (*c-mos*). Primers, PCR protocols and source references are listed in Table S2.

Chromatographs were edited using Geneious v.7.1.9 (Biomatter Ltd.). For the nuclear loci, *MC1R, ACM4* and *c-mos*, heterozygous positions were coded according to the IUPAC ambiguity codes. Coding gene fragments (*cytb, MC1R, ACM4, c-mos*) were translated into amino acids and no stop codons were observed, suggesting that the sequences are all functional and no pseudogenes were amplified. DNA sequences were aligned for each gene fragment independently using the online version of MAFFT v.7 (Katoh and Standley, 2013) with default parameters (Auto strategy, Gap opening penalty: 1.53, Offset value: 0.0). For the *12S* fragments we applied the Q-INS-i strategy, in which data on the secondary structure of the RNA are considered. Poorly aligned positions of *12S* were eliminated with G-blocks (Castresana, 2000) using low stringency options (Talavera and Castresana, 2007). Inter and intra-specific uncorrected *p*-distances with pairwise deletion of *12S* and *cytb*, and the number of variable (V) and parsimony informative (Pi) sites for the ingroup only, were calculated in MEGA v.5.2 (Tamura et al., 2011).

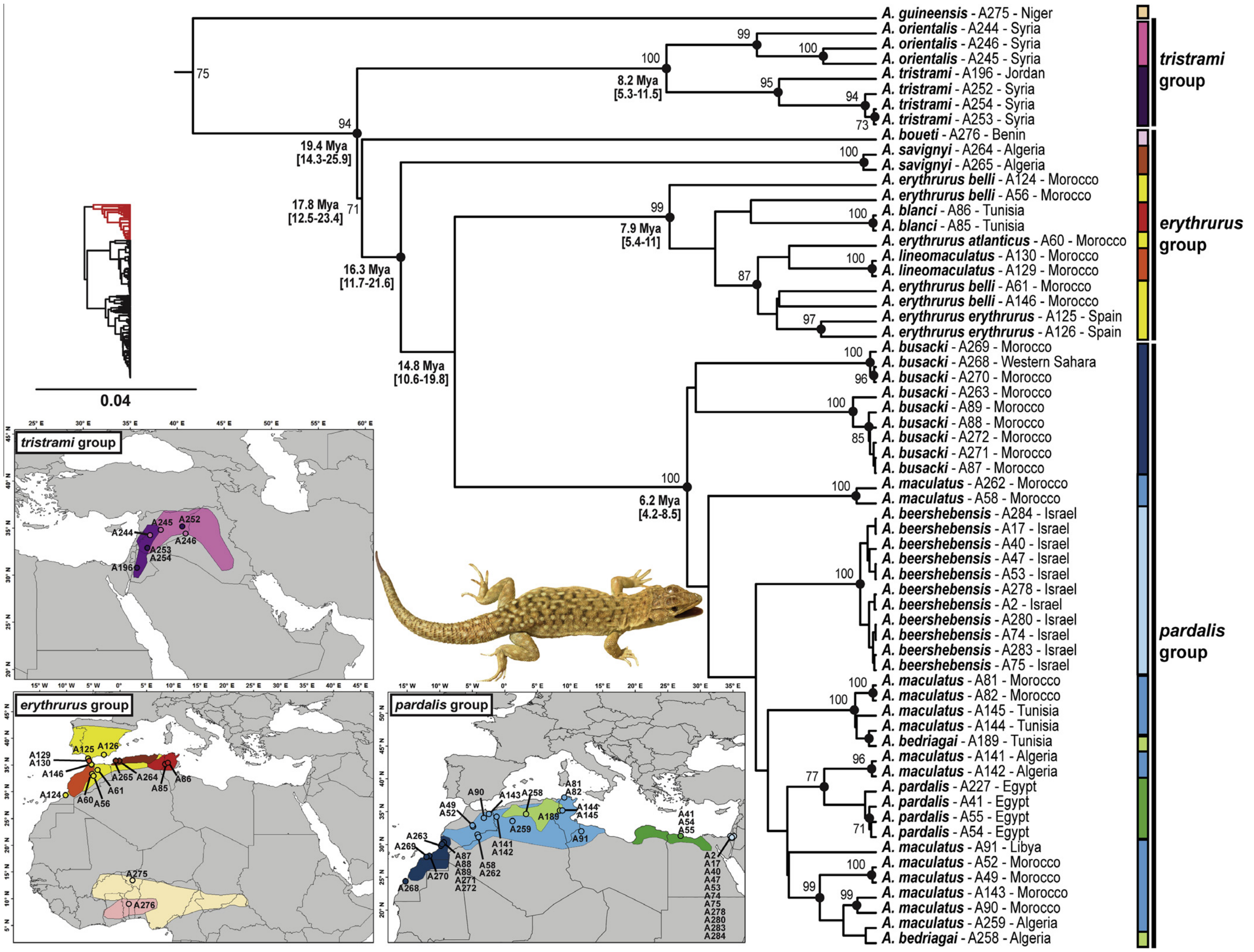

Fig. 2. The Western clade within *Acanthodactylus*, part of a Bayesian Inference tree inferred from the concatenated dataset (*12S, cytb, MC1R, ACM4, c-mos*). Distribution ranges of *Acanthodactylus* species were modified from Sindaco and Jeremčenko (2008). Codes next to each taxon refer to the locality in the distribution maps and country of origin (sample A227 is not shown). Data on all samples are given in Table S1. Maximum likelihood bootstrap support values (values ⩾ 70%) are indicated near the nodes and posterior probability in the Bayesian analysis is indicated by black dots on the nodes (values ⩾ 0.95). Age estimates obtained with BEAST are indicated near the relevant nodes and include the mean and, in parentheses, the 95% highest posterior densities (HPD).

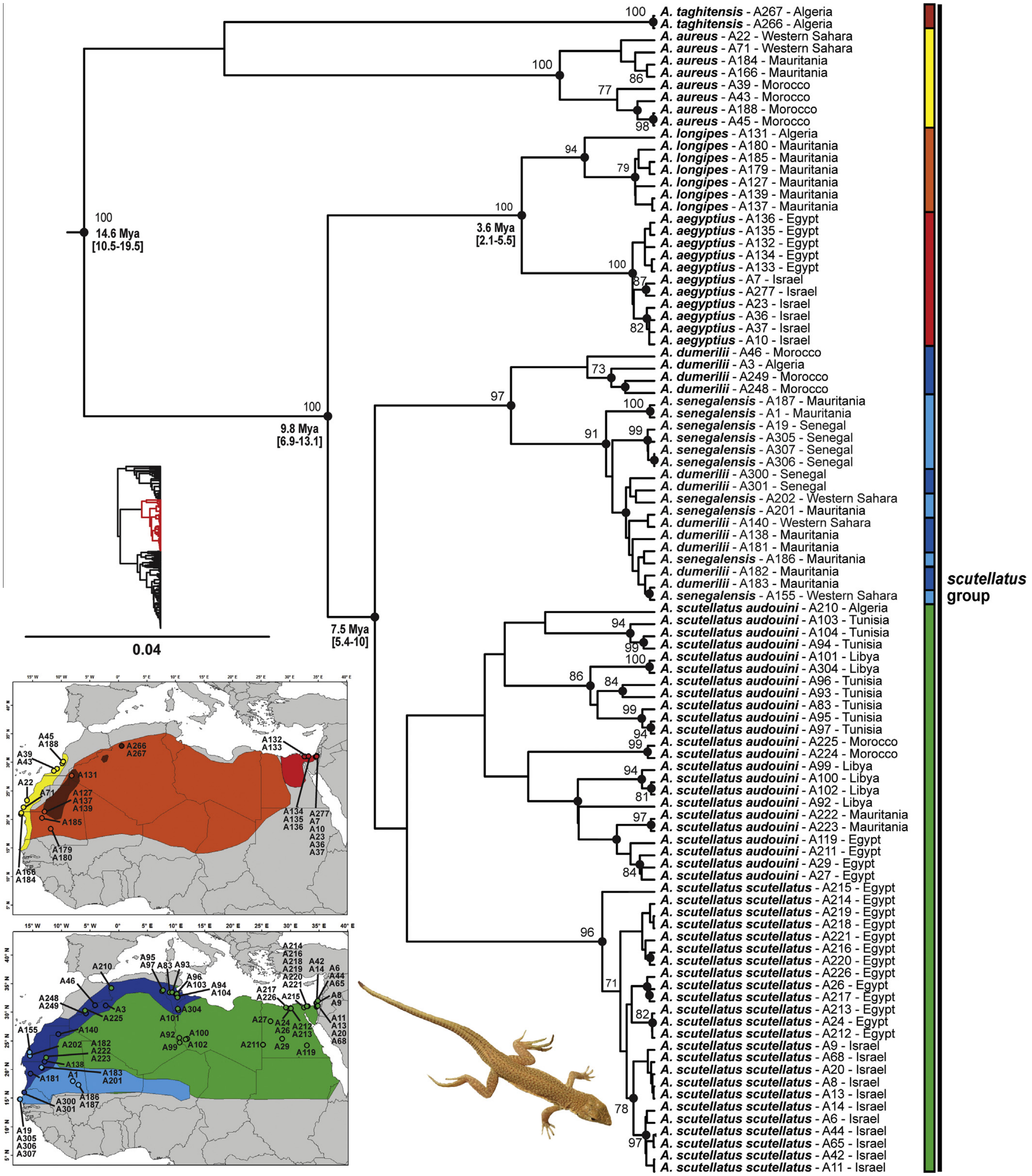

Fig. 3. The *scutellatus* clade within *Acanthodactylus*, part of a Bayesian Inference tree inferred from the concatenated dataset (*12S*, *cytb*, *MC1R*, *ACM4*, *c-mos*). Distribution ranges of *Acanthodactylus* species were modified from Sindaco and Jeremčenko (2008). Codes next to each taxon refer to the locality in the distribution maps and country of origin (sample A224 is not shown). Data on all samples are given in Table S1. Maximum likelihood bootstrap support values (values ⩾ 70%) are indicated near the nodes and posterior probability in the Bayesian analysis is indicated by black dots on the nodes (values ⩾ 0.95). Age estimates obtained with BEAST are indicated near the relevant nodes and include the mean and, in parentheses, the 95% highest posterior densities (HPD).

2.2. Phylogenetic analyses

We used PartitionFinder v.1.1.1 (Lanfear et al., 2012) to select the best-fit partitioning scheme and models of molecular evolution for the dataset, with the following parameters: linked branch length; models available in BEAST; AIC model selection; greedy search algorithm. Due to the large size of the dataset, to avoid over-parameterization, each of the five markers was set in the

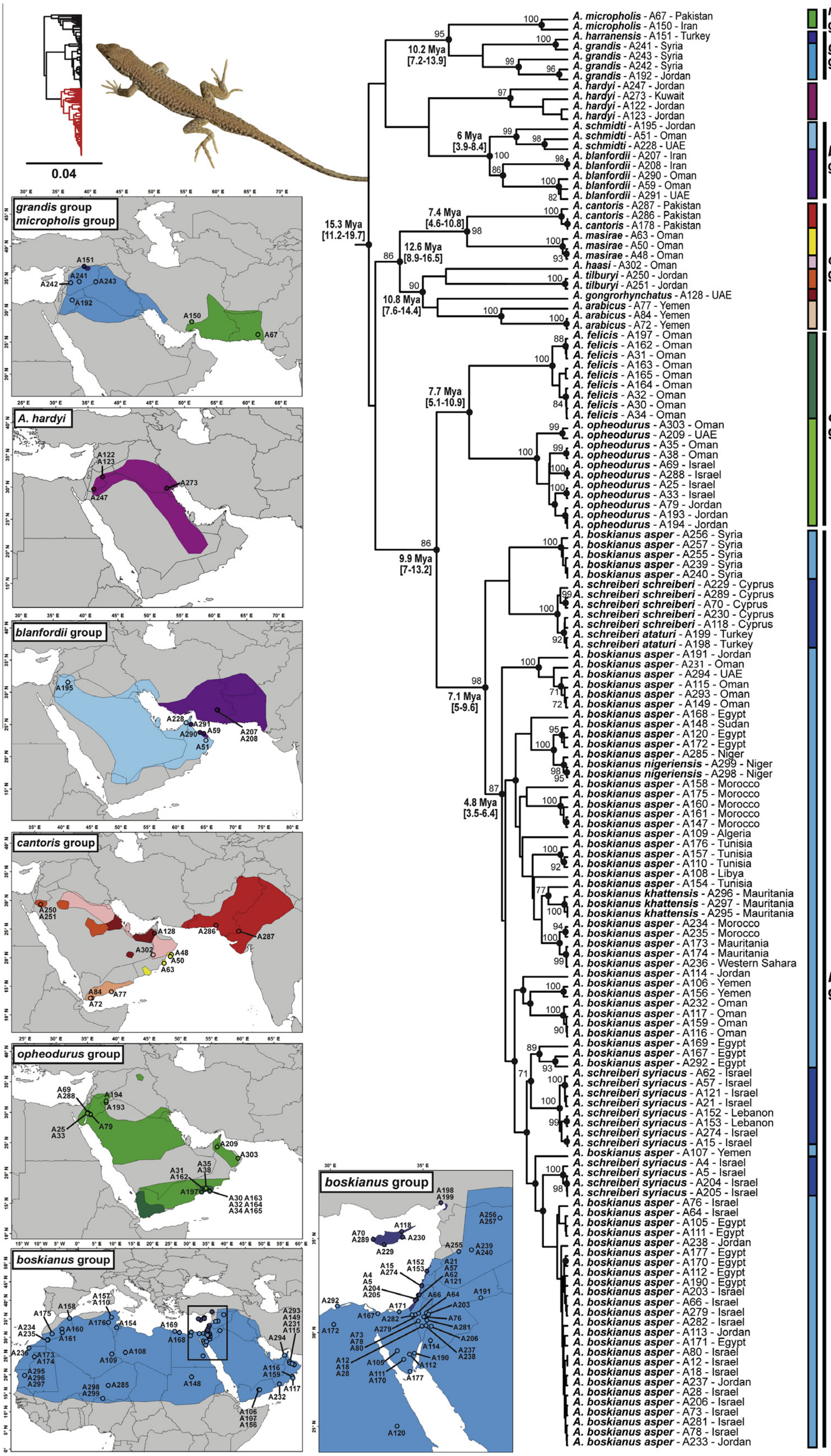

Fig. 4. The Eastern clade within *Acanthodactylus*, part of a Bayesian Inference tree inferred from the concatenated dataset (*12S*, *cytb*, *MC1R*, *ACM4*, *c-mos*). Distribution ranges of *Acanthodactylus* species were modified from Sindaco and Jeremčenko (2008). Codes next to each taxon refer to the locality in the distribution maps and country of origin (sample A178 is not shown). Data on all samples are given in Table S1. Maximum likelihood bootstrap support values (values ⩾ 70%) are indicated near the nodes and posterior probability in the Bayesian analysis is indicated by black dots on the nodes (values ⩾ 0.95). Age estimates obtained with BEAST are indicated near the relevant nodes and include the mean and, in parentheses, the 95% highest posterior densities (HPD).

input file as a distinct data block. A summary of DNA partitions and relevant models as determined by PartitionFinder is given in Table S3.

Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian Inference (BI) methods. Models, priors and parameter specifications applied are listed in Table S3. ML analyses were performed with RAxML v.7.4.2 (Stamatakis, 2006) as implemented in raxml GUI v.1.3 (Silvestro and Michalak, 2012) with a GTRGAMMA model of sequence evolution. All ML analyses were performed with 100 random addition replicates with parameters estimated independently for each partition. Nodal support was assessed by bootstrap analysis with 1000 pseudoreplications (Felsenstein, 1985). BI analyses were performed with BEAST v.1.8.0 (Drummond et al., 2012). For all analyses implemented in BEAST, the .xml file was modified to "Ambiguities = true" for the nuclear partitions to account for variability in the heterozygote positions, rather than treating them as missing data. Parameter values both for clock and substitution models were unlinked across partitions. All BEAST analyses were carried out in CIPRES Science Gateway (Miller et al., 2010). Convergence was assessed by confirming that all parameters had reached stationarity and had sufficient effective sample sizes (> 200) using TRACER v.1.6 (Rambaut et al., 2014). LogCombiner and TreeAnnotator (both available in the BEAST package) were used to combine the runs and produce the ultrametric tree after discarding 10% as burn-in. We treated alignment gaps as missing data, and the nuclear gene sequences were not phased. Nodes were considered strongly supported if they received ML bootstrap values $\geqslant 70\%$ and posterior probability (pp) support values $\geqslant 0.95$ (Wilcox et al., 2002; Huelsenbeck and Rannala, 2004).

In order to identify divergent lineages within *Acanthodactylus*, we performed the independent Generalized Mixed Yule-coalescent (GMYC) analysis (Pons et al., 2006). As this analysis relies on single locus data, we used a Bayesian concatenated mitochondrial phylogenetic tree including haplotypes only, reconstructed with BEAST v.1.8.0. Models, priors and parameters are specified in Table S3. We applied the single threshold algorithm implemented in the R "SPLITS" package (Species Limits by Threshold Statistics; Ezard et al., 2009) and compared to the null model (i.e., all individuals belong to a single species) using a log-likelihood ratio test.

2.3. Estimation of divergence times

Due to the lack of internal calibration points for *Acanthodactylus*, we used calibration points of other lacertids, *Gallotia* and *Podarcis,* as previously used in other lacertid phylogenies (e.g., Kaliontzopoulou et al., 2011; Carranza and Arnold, 2012; Kapli et al., 2013, 2015; Tamar et al., 2015). Divergence times were estimated in BEAST v.1.8.0 using the complete concatenated dataset (nuclear genes unphased). The dataset for this analysis included one representative of each independent GMYC entity of *Acanthodactylus* (in order to account for the deep lineages in the phylogeny; see Metallinou et al., 2015 for dataset strategy comparisons) and sequences of *Gallotia* and *Podarcis* (retrieved from GenBank; Table S1). The .xml file was manually modified to "Ambiguities = true" for the nuclear genes (*MC1R*, *ACM4*, *c-mos*). Models, priors and parameters are specified in Table S3.

One calibration coincides with the end of the Messinian Salinity Crisis (Normal distribution, mean 5.32, stdev 0.05) - the separation between *Podarcis pityusensis* and *Podarcis lilfordi* (endemic to the Balearic Islands; Brown et al., 2008), and between *Podarcis cretensis* and *Podarcis peloponnesiacus* (isolation of Crete from the Peloponnesus; Poulakakis et al., 2005). The other calibrations were based on the ages of the Canary Islands and the splits between the species of the Canary Islands' endemic genus *Gallotia* (Cox et al., 2010; Carranza and Arnold, 2012) as follows: (a) the split between *Gallotia* and *Psammodromus algirus* (age of the oldest islands Fuerteventura and Lanzarote; Normal distribution, mean 18, stdev 2); (b) the split between *G. galloti* and *G. caesaris* (age of La Gomera Island; Normal distribution, mean 6, stdev 3); (c) the split between *G. galloti palmae* and the ancestor of *G. g. galloti* and *G. g. eisentrauti* (age of La Palma Island; Normal distribution, mean 1, stdev 0.5); and (d) the splits between *G. gomerana* and *G. simonyi machadoi* and between *G. caesaris caesaris* and *G. c. gomerae* (age of El Hierro Island; Normal distribution, mean 0.8, stdev 0.2).

2.4. Ancestral area reconstruction

In order to identify the phylogeographic history and reconstruct the ancestral origin of *Acanthodactylus,* we used the Bayesian Stochastic Search Variable Selection (BSSVS; Lemey et al., 2009) of the discrete phylogeographic model as implemented in BEAST v.1.8.0. We used the complete concatenated dataset with one representative of each independent GMYC entity (Table S1; ingroup only; nuclear genes unphased). For a temporal frame we applied the average sequence evolution rates of *12S* and *cytb* mitochondrial regions (as estimated in Carranza and Arnold, 2012) also to cross-check the divergence time estimations. These rates were extracted from a fully calibrated phylogeny of the lacertid genus *Gallotia* from the Canary Islands and the divergence between *Podarcis pityusensis* and *P. lilfordi* from the Balearic Islands (for a full account of the specific calibration points see Carranza and Arnold, 2012). These rates had been implemented in other lacertid phylogenies, such as Tamar et al. (2014) and Bellati et al. (2015). We assigned the phylogeographic traits according to two discrete geographic regions, corresponding to the main areas from which *Acanthodactylus* was suggested to originate (Arnold, 1983, 1989a; Harris and Arnold, 2000) – Africa (including the Iberian Peninsula) and south-west Asia (including Cyprus and the Sinai and Arabian Peninsulas). Models, prior settings and parameters are listed in Table S3.

3. Results

3.1. Taxon sampling, genetic data and phylogenetic analyses

The dataset for the phylogenetic analyses comprised 302 individuals of 36 known species (Table S1). The dataset totalling 2404 bp comprised mitochondrial gene fragments of *12S* (~385 bp; V = 176; Pi = 154) and *cytb* (405 bp; V = 217; Pi = 200), and nuclear gene fragments of *MC1R* (663 bp; V = 100; Pi = 73), *ACM4* (429 bp; V = 76; Pi = 44) and *c-mos* (522 bp; V = 104; Pi = 80). The uncorrected *p*-distances of the *12S* and *cytb* mitochondrial gene fragments between and within each species are summarized in Table S4.

The results of the phylogenetic analyses of the complete and mitochondrial datasets, using ML and BI methods, produced very similar topologies, differing primarily at the less supported nodes (Figs. 2–4 and S1–S2). The level of genetic variability within *Acanthodactylus* is very high, as reflected in both the genetic distances (Table S4) and the results of the GMYC analysis with the single threshold approach (Fig. S3; based on the concatenated mitochondrial haplotype dataset). The latter analysis recovered three clades and 111 different entities, probably due to incomplete geographic sampling (Talavera et al., 2013). The result of the likelihood ratio test was significant ($p < 0.0001$), indicating that the null model (i.e., single population) could be rejected.

3.2. Phylogenetic relationships and genetic diversity within *Acanthodactylus*

The phylogenetic results reveal three clearly distinct clades within *Acanthodactylus*. Within them, ten groups are defined, though not all relationships among groups or species are equally supported (Figs. 1–4 and S1–S3). The three clades in our study correspond to the clades shown in Harris and Arnold (2000), we thus retain the names they coined: Western, *scutellatus* and Eastern. The phylogenetic results reveal that the Western clade is sister to a clade composed of the *scutellatus* and Eastern clades (ML support only for the mitochondrial tree; Figs. S1–S2).

The Western clade (Fig. 2 and S1–S2) incorporated one well-defined lineage representing *A. guineensis*, and three groups, *tristrami*, *erythrurus*, and *pardalis*, though the phylogenetic relationships within the clade are not well supported. *Acanthodactylus guineensis,* a Sub-Saharan member, is represented by mitochondrial gene fragments only (the nuclear gene fragments failed to amplify properly). This species is recovered as sister to the remaining species of the clade, genetically very distant from the other species of the group, clade, and genus (*p*-distance *12S*: 11.7–17.6%; *cytb*: 17.4–25.1%). The phylogenetic position of *A. guineensis* within the genus is not stable. According to the phylogenetic analyses of the complete and mitochondrial datasets, it is situated within the Western clade (Figs. 2 and S1–S3), whereas in the BI dating analysis it is sister to the entire genus (Fig. S4). The *tristrami* group, represented by *A. orientalis* and *A. tristrami*, is monophyletic. The *erythrurus* group is paraphyletic. The phylogenetic positions of *A. savignyi* from Algeria and the Sub-Saharan *A. boueti* are not well supported and they are highly genetically distant from the remaining members of the group (Table S4). The remaining species of the *erythrurus* group form a well-supported clade, in which *A. blanci* and *A. lineomaculatus* are nested within *A. erythrurus*, making the latter paraphyletic (*A. blanci* is not nested in the ML analysis; Fig. S1). The relationships within the *pardalis* group are very complex. Two species of this group, *A. beershebensis* and *A. pardalis*, are monophyletic, whereas *A. bedriagai* and *A. maculatus* are paraphyletic and exhibit high genetic diversity (Table S4). *Acanthodactylus busacki* is paraphyletic in the ML analyses of the complete and mitochondrial datasets (Figs. S1–S2) with no support for monophyly in the BI analysis (Fig. 2).

The *scutellatus* clade (Figs. 3 and S1–S2) is composed solely of the *scutellatus* group, represented by seven species. *Acanthodactylus taghitensis A. aureus, A. longipes* and *A. aegyptius* are monophyletic. Both *A. aegyptius* and *A. longipes* form a distinct, strongly supported, lineage. Although monophyly of the nominate species *A. scutellatus* is recovered, the bootstrap and pp support values are low. This species is divided into two reciprocally monophyletic lineages corresponding to its two subspecies, *A. s. scutellatus* and *A. s. audouini*. Both *A. dumerilii* and *A. senegalensis* are paraphyletic in respect to one another and form a monophyletic lineage. Within this lineage they form two geographic clusters, a northern cluster from Algeria and Morocco and a southern cluster from Western Sahara southwards.

The Eastern clade (Figs. 4 and S1–S2) comprises 16 species representing six well-supported monophyletic groups. The *micropholis* group (*A. micropholis*) is sister to the *grandis* group. *Acanthodactylus grandis* is paraphyletic with respect to *A. harranensis* and is highly diverse genetically (*p*-distance *12S*: 6.1%; *cytb*: 14.6%). A distinct lineage is composed of the sister species *A. blanfordii* and *A. schmidti*. The phylogenetic position of *A. hardyi* is not supported in either the ML or the BI analyses, but it forms a well-supported monophyletic lineage. The *cantoris* group is composed of six species: *A. cantoris, A. masirae, A. haasi, A. gongrorhynchatus, A. tilburyi*, and *A. arabicus,* though the phylogenetic relationships among the species are mostly not supported. *Acanthodactylus cantoris* and *A. masirae* are sister species, while the remaining species form a distinct clade. The *opheodurus* and *boskianus* are sister groups. The two species representing the *opheodurus* group, *A. opheodurus* and *A. felicis*, are reciprocally monophyletic. Although the monophyly of the *opheodurus* group is recovered, in the ML analyses the bootstrap support values are low (Figs. S1–S2). The two members of the *boskianus* group, *A. schreiberi* and *A. boskianus*, are both paraphyletic as the former species is nested entirely within the latter. The two Sahelian subspecies of *A. boskianus*, *A. b. nigeriensis* and *A. b. khattensis*, are also nested within the third widespread subspecies, *A. b. asper*.

3.3. Estimation of divergence times

The divergence time estimations (Fig. S4) are presented in Figs. 2–4 at the relevant nodes. *Acanthodactylus guineensis* is recovered as a sister taxon to *Acanthodactylus* in the BI dating analysis (Fig. S4), contradictory to its position within the Western clade based on the phylogenetic analyses of the complete and mitochondrial datasets (Figs. 2 and S1–S2). Our results indicate that diversification within *Acanthodactylus* originated during the Oligocene around 30–33 Mya (95% highest posterior density, HPD: 22.2–45.3 Mya). The Eastern and *scutellatus* clades separated approximately 27 Mya (95% HPD: 20–35.8 Mya). Further radiation within the genus occurred from the Miocene onwards.

3.4. Ancestral area reconstruction

The results of the discrete phylogeographic analyses using the BSSVS model, within a temporal framework of evolutionary rates, are presented in Fig. 5. The two dating approaches (i.e., geological calibration points and evolution rates) resulted in almost identical dates (Figs. 2–5). *Acanthodactylus* most likely originated in Africa (83% probability). The origin of both the Western and *scutellatus* clades is probably also African (91% and 99% probability, respectively), whereas the Eastern clade colonized south-west Asia from Africa (82% probability at the split between the *scutellatus* and the Eastern clades) and radiated there extensively. Subsequent splits within the genus imply dispersal from Africa to Arabia and *vice versa*.

4. Discussion

4.1. Systematics of the genus Acanthodactylus

Our study constitutes the first large-scale time-calibrated phylogenetic study of *Acanthodactylus*. Our results are mostly congruent with the current taxonomic classifications, with some systematic discrepancies. The molecular results confirm that *Acanthodactylus* is composed of three well-supported clades: the Western, *scutellatus,* and Eastern clades (Harris and Arnold, 2000; Figs. 1 and S1–S2).

4.1.1. The Western clade

This clade comprises one deeply-separated lineage represented by *A. guineensis* and three defined groups, containing mostly North African species (Figs. 2 and S1–S2). *Acanthodactylus guineensis* was originally described within the genus *Eremias* (Boulenger, 1887) and was later assigned to *Acanthodactylus,* within the *erythrurus* group (Salvador, 1982; Arnold, 1983). Its phylogenetic position within the genus, however, is not resolved. Salvador (1982) noted that *A. guineensis* diversification from the *erythrurus* group must have taken place before the separation of the morphologically similar Sub-Saharan species *A. boueti*. This, however, is in contrast to their phylogenetic affinity hypothesized by Fonseca et al. (2009). Our results, based solely on mitochondrial data of *A. guineensis*, accord with Salvador (1982), but also bring into question its phylogenetic position within the genus as well as within the group. The extremely high genetic distance from the other species sug-

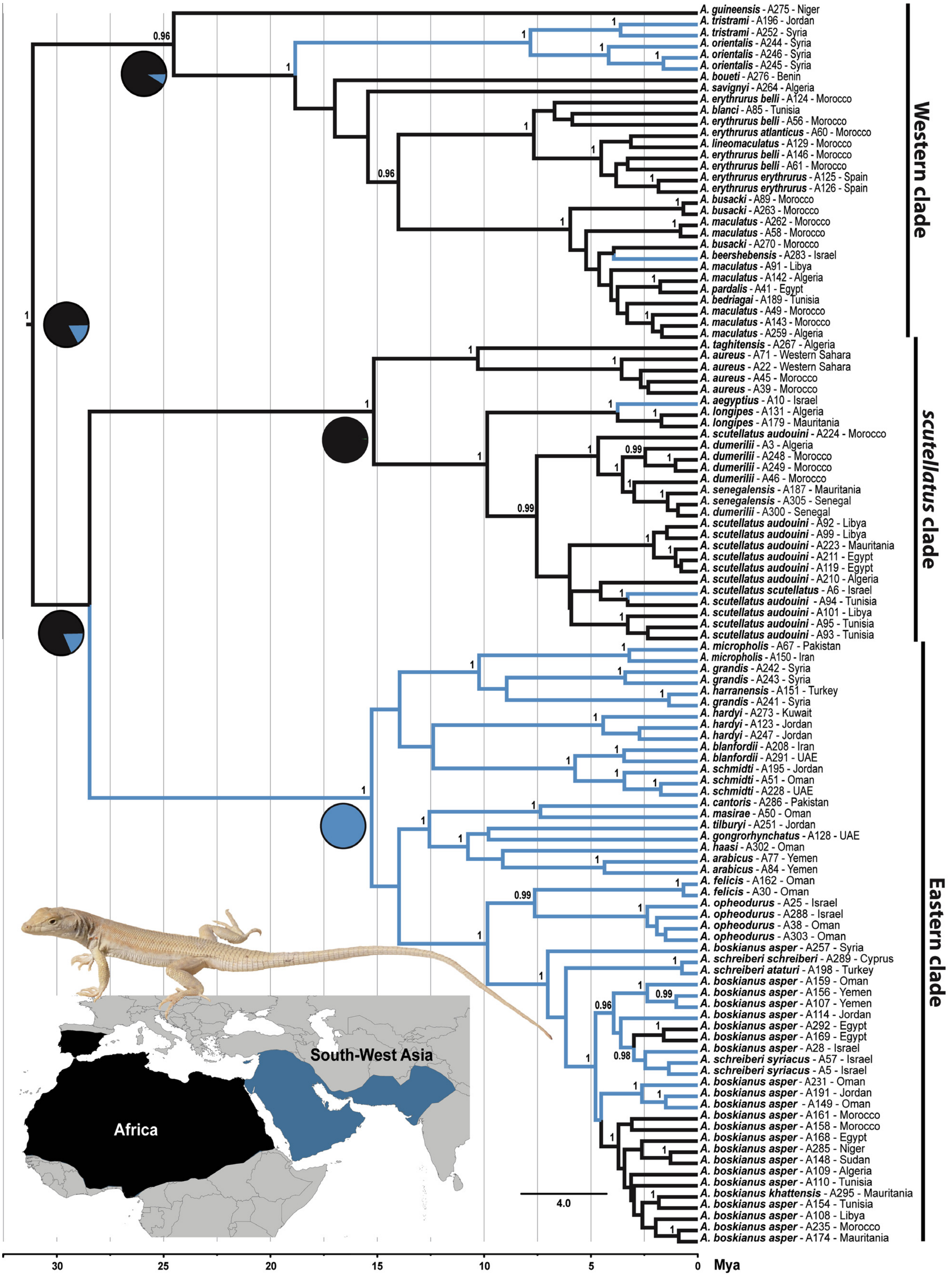

Fig. 5. BEAST consensus tree using the BSSVS method of ancestral area reconstruction with a temporal framework based on evolutionary rates (see Section 2). Branch colour indicates inferred ancestral range (ranges visualized in the lower left map), with posterior probabilities of ancestral range above the nodes (values ⩾ 0.95). A pie chart depicting the probability of each inferred area is presented near the major nodes.

gests a very old divergence, but further sampling is required to determine its status.

The Middle Eastern monophyletic *tristrami* group is phylogenetically closely-related to the north-west African *erythrurus* group, a finding congruent with their morphology (Arnold, 1983; Harris and Arnold, 2000). Despite the geographic gap, the systematic affinity of these two groups suggests a shared ancestral origin between North Africa and the Middle East.

The *erythrurus* group is paraphyletic. The phylogenetic position of the Sub-Saharan species, *A. boueti*, is not well supported in either phylogenetic analysis. It clearly differs from *A. erythrurus,* thus rejecting its derivation from it (Boulenger, 1921). Its high genetic distance from *A. guineensis* (Table S4) and its phylogenetic position may indicate that the two lineages evolved independently within the Sub-Saharan region. *Acanthodactylus savignyi* is sister to the rest of the *erythrurus* group members, a notable finding, as it was expected to be phylogenetically closely-related either to *A. blanci* due to similar morphology and sandy habitat preference; or, alternatively, to *A. erythrurus belli*, as they both co-occur in northern Algeria (Arnold, 1983; Schleich et al., 1996). The nominate species, *A. erythrurus*, is paraphyletic, with both *A. blanci* and *A. lineomaculatus* nested within it (as in Harris et al., 2004; Fonseca et al., 2009). Our results support the phylogenetic affinities of *A. blanci* with *A. erythrurus* rather than with *A. savignyi* (Salvador, 1982). However, the phylogenetic position of *A. blanci* has not been determined either in morphological or molecular revisions, including this study (Boulenger, 1921; Mertens, 1929; Salvador, 1982; Arnold, 1983; Harris et al., 2004; Fonseca et al., 2009), leaving its current specific status unclear. *Acanthodactylus lineomaculatus* was classified as a subspecies of *A. erythrurus* (Salvador, 1982; Arnold, 1983; Schleich et al., 1996), and later elevated to specific status (Bons and Geniez, 1995; Harris and Arnold, 2000). However, the phylogenetic studies of Harris et al. (2004), Fonseca et al. (2009) and this study, show no genetic support for the separation of this species from *A. erythrurus*. We agree with Fonseca et al. (2009) and suggest that *A. lineomaculatus* is an ecotype reflecting local morphological adaptation, and should thus be treated as a junior synonym of *A. erythrurus.*

The *pardalis* group is monophyletic. The sister taxa relationship with its phylogenetically closely-related *erythrurus* group is not supported (agreeing with Fonseca et al., 2009). Although our results support the specific status of *A. beershebensis* and *A. pardalis*, we cannot account for their phylogenetic position. The complex phylogenetic structures and relationships among *A. busacki*, *A. bedriagai* and *A. maculatus* remain unresolved (as in Fonseca et al., 2008). The geographic clustering of these species indicates that environmental conditions have strongly influenced their distribution, which in turn may be responsible for their current systematic complexity (Fonseca et al., 2008). These complex phylogenetic relationships highlight the potential flaws in current taxonomic classifications based on morphological identifications. It is thus necessary to examine and revise the identification of distinctive phenotypic features of each population, especially from contact zones.

4.1.2. The scutellatus clade

Our results show that seven species belong to the psammophilous *scutellatus* clade/group, in contrast to the eight species as was traditionally believed (*A. hardyi* is phylogenetically different, being included instead in the Eastern clade; Salvador, 1982; Arnold, 1983; Figs. 3 and 4 and S1–S2). The *scutellatus* clade began radiating within north-west Africa with the split of two clearly genetically-distinct species, *A. aureus* and *A. taghitensis*; though the phylogenetic position of the latter species is less significant. *Acanthodactylus longipes* and *A. aegyptius* are reciprocally monophyletic sister species and comprise a separate lineage, coinciding with their known taxonomy (Baha El Din, 2007). The remaining species, *A. scutellatus, A. dumerilii* and *A. senegalensis*, exhibit unsupported phylogenetic relationships and the two latter species cluster together. A distinct lineage of *A. scutellatus* from northern Egypt, the Sinai Peninsula and Israel corresponds to the subspecies *A. scutellatus scutellatus* (Bons and Girot, 1964; Crochet et al., 2003). We thus support the validity of the subspecies as discrete. Another monophyletic lineage includes the subspecies *A. scutellatus audouini* from Egypt eastwards, although both bootstrap and pp support values are low. *Acanthodactylus senegalensis* and *A. dumerilii*, sampled from their type localities, are not clearly defined (the latter's type locality is not in Senegal according to the revision by Crochet et al. (2003), but no other locality was given). Since its description, *A. senegalensis* has been assigned by several authors as a subspecies/variant/synonym of *A. scutellatus* or *A. dumerilii* (Boulenger, 1921; Bons and Girot, 1964; Salvador, 1982; Arnold, 1983; Crochet et al., 2003). In addition to the morphological difficulties in establishing taxonomic identification between these two species, our results reveal that they cluster together into two phylogenetic, geographic inner-groups. A further comprehensive and meticulous revision is necessary in order to evaluate the status of the populations assigned to the two species, and to establish the true specific boundaries and their geographical distribution.

4.1.3. The Eastern clade

This clade is comprised of six monophyletic groups (Figs. 4 and S1–S2). The *micropholis* and *grandis* are sister groups (see also Heidari et al., 2014). This phylogenetic relationship conflicts with previous hypotheses regarding the closely-related systematic allocation of the *micropholis* with *cantoris* or the *grandis* with *boskianus* groups (Arnold, 1983; Harris and Arnold, 2000). These results are interesting due to the allopatric distribution of the two groups, and the habitats occupied, as *A. micropholis* occupies sandy habitats (Minton, 1966; Khan, 2006) whereas *A. grandis* prefers semi-desert to desert hamada soils (Disi et al., 2001), although digit pectination indicates that it may occur on a variety of soil types (Arnold, 1983). These two groups may represent an invasion eastwards from the Middle East into Asia, as the separation zone between them is in southern Iran. Within the *grandis* group, the results support the phylogenetically-close affinities between the morphologically-similar *A. grandis* and *A. harranensis* (Baran et al., 2005). The paraphyly and the high genetic diversity of *A. grandis* indicate it is a species complex, as was also suggested by Salvador (1982) and Arnold (1983).

The same pattern of contact zone and dispersal eastwards is also evident in the monophyletic lineage formed by *A. blanfordii* and its sister species *A. schmidti*. Our results suggest that they are not members of the *cantoris* group (Boulenger, 1918; Haas, 1957; Salvador, 1982; Arnold, 1983; Harris and Arnold, 2000), but form a distinct independent group, which we name the *blanfordii* group. Taxonomically, *A. hardyi* is considered a member of the *scutellatus* group (previously a subspecies of *A. scutellatus*; Salvador, 1982; Arnold, 1983; Harris and Arnold, 2000; Crochet et al., 2003). The present known differences between *A. hardyi* and *A. scutellatus* include morphology, a distributional gap (Salvador, 1982; Arnold, 1983, 1986), and preferred substrates (Rifai et al., 2003). We retain the specific status of *A. hardyi*, but phylogenetically allocate it to within the Eastern clade (Fig. 4), though its phylogenetic position there is not well defined.

We support the five species taxonomically recognized within the *cantoris* group: *A. arabicus, A. cantoris, A. gongrorhynchatus, A. haasi,* and *A. tilburyi*. Although *A. masirae* is taxonomically regarded as a member of the *opheodurus* group (Salvador, 1982; Arnold, 1983), it is phylogenetically sister to *A. cantoris* (also in Harris and Arnold, 2000). Our results thus conflict with the known taxonomy, as only a few morphological similarities and shared characters are known between *A. masirae* and *A. cantoris* (Salvador, 1982; Arnold, 1983). Local adaptation of *A. masirae* to different habitats may have accelerated its evolutionary morphological divergence, thus accounting for its morphological disparity from the phylogenetically closely-related *A. cantoris*. This hypothesis may also explain the classification of *A. cantoris* with mostly Arabian species, and the different habitat preferences (Salvador, 1982; Arnold, 1983; Khan, 2006; Sindaco and Jeremčenko, 2008). We thus suggest the systematic relocation of *A. masirae* into the *cantoris* group.

The *opheodurus* and *boskianus* are sister groups, congruent with their morphology (Salvador, 1982; Arnold, 1980, 1983). Our results agree with the assignment of *A. felicis* and *A. opheodurus* within the *opheodurus* group. The *boskianus* group is represented by two paraphyletic species, *A. boskianus* and *A. schreiberi* (see Tamar et al., 2014 for relevant discussion and systematic accounts). We suggest that the two subspecies, *A. boskianus khattensis* (from Mauritania) and *A. b. nigeriensis* (from Niger), are synonyms of the widespread *A. b. asper*, possibly representing phenotypic variations, as they are nested within the latter subspecies with other geographically-adjacent specimens. *Acanthodactylus boskianus* is known to be an extremely morphologically variable species (Salvador, 1982; Arnold, 1980, 1983; Harris and Arnold, 2000), phylogenetically exhibiting geographical groupings (Tamar et al., 2014). The relatively similar morphology of *A. boskianus* and the close phylogenetic relationships between North African and Arabian populations suggest recent migration (Salvador, 1982; Arnold, 1983; Tamar et al., 2014), probably from south-west Asia (Fig. 5). *Acanthodactylus boskianus* inhabits a wide range of dry habitats and displays the largest distribution within the genus. The high degree of genetic diversity within *A. boskianus* (Table S4) may result from a non-uniform geographic sampling of this species in our dataset.

4.2. Biogeography of Acanthodactylus - Origin and diversification

Several authors have suggested that lacertids and the ancestor of the Eremiadini tribe, to which *Acanthodactylus* belongs, dispersed to Africa during the Miocene around 17–19 Mya after the tectonic collision between Africa-Arabia and Eurasia (Arnold, 1989a, 2004; Mayer and Benyr, 1994; Harris et al., 1998; Harris and Arnold, 2000; Arnold et al., 2007; Mayer and Pavlicev, 2007; Pavlicev and Mayer, 2009). Arnold (2004) suggested that the ancestor of the Saharo-Eurasian clade within the Eremiadini, to which *Acanthodactylus* belongs, recolonized Asia through a land bridge between the Horn of Africa and Arabia (~10–5 Mya; Bosworth et al., 2005), with later recolonizations of North Africa. Mayer and Pavlicev (2007) discussed another plausible scenario, in which the Eremiadini diversified in the Near East and members invaded Africa on several occasions. Following this line, the biogeographical assessment by Harris and Arnold (2000) suggested that *Acanthodactylus* originated in south-west Asia and later invaded Africa, probably during the mid-late Miocene (Arnold, 1989a). Others, however, have hypothesized that the Eremiadini originated much earlier, during the Eocene (Wiens et al., 2006; Hipsley et al., 2009; Zheng and Wiens, 2016), and the radiation of the Saharo-Eurasian members occurred approximately 40 Mya (Hipsley et al., 2009). All these studies suggest that the xerophilous members of the Saharo-Eurasian clade within Eremiadini (i.e., *Acanthodactylus, Eremias, Mesalina, Ophisops*) most likely originated in Eurasia, specifically in south-west Asia.

Our phylogenetic and biogeographical reconstructions predate the often suggested Miocene radiation onset and rapid dispersal from a south-west Asian origin, as noted above. Our results support a deeper ancestral diversification of *Acanthodactylus* probably from an African origin (Fig. 5). We show that diversification originated during the Oligocene with the separation of the three clades (33–27 Mya). Radiation within the three clades and groups mostly occurred during the Miocene (Figs. 2–5).

The suggested timeframe in our study is congruent with that of previous studies on the diversification of North-African and Arabian herpetofauna during the Oligocene (e.g., Pook et al., 2009; Šmíd et al., 2013; Metallinou et al., 2012, 2015; Portik and Papenfuss, 2012, 2015). Divergence time estimations in those studies, and ours, suggest that the Oligocene and Miocene radiations may correlate with two major environmental changes that affected the western Palearctic realm at the time. The first event is the separation of the Arabian and African plates, and their later collision with the Eurasian landmass. These tectonic movements resulted in continuous regional geological instability, which subsequently led to the opening of the Red Sea, periodic sea-level fluctuation, the Messinian Salinity Crisis, and the uplift of high mountain ridges such as the Atlas in Morocco, the Zagros in Iran, and the coastal mountains of Arabia (Bohannon et al., 1989; Rögl, 1999; Popov et al., 2004; Bosworth et al., 2005; Edgell, 2006; Jolivet et al., 2006; Mouthereau, 2011). These major tectonic events may explain the split between the three clades, and the ancestral relatives of the Middle Eastern *tristrami* group separating from the original North-African populations of the *erythrurus* and *pardalis* groups within the Western clade. The second major environmental event was the global climate change during the Miocene. Climatic fluctuations and aridification during this period led to the formation, and episodic expansion and contraction, of the Sahara and Arabian deserts, which in turn strongly affected species divergence and distributions within the area (Ruddiman et al., 1989; Flower and Kennett, 1994; Le Houérou, 1992, 1997; Zachos et al., 2001; Griffin, 2002; Kroepelin, 2006; Schuster et al., 2006; Swezey, 2006, 2009). As *Acanthodactylus* is an arid-adapted genus, the aridification process most likely promoted diversification and facilitated dispersal in most lineages.

There are three *Acanthodactylus* groups (*erythrurus, pardalis* and *scutellatus*) inhabiting North Africa, with the *erythrurus* and *pardalis* groups typically inhabiting areas of solid ground in the northern and western coastal areas (Fig. 2), while the psammophilous *scutellatus* group inhabits sandy areas, principally across the Sahara desert (Fig. 3). The expansion/contraction of sands and the rise of the Atlas Mountains during the mid-late Miocene created biogeographical barriers and probably triggered diversification, as has been suggested for other reptile taxa (e.g., Brown et al., 2002; Amer and Kumazawa, 2005; Fritz et al., 2005; Carranza et al., 2008; Gonçalves et al., 2012; Kapli et al., 2015; Metallinou et al., 2012, 2015; Tamar et al., 2016). The Sahara sands constitute a southern barrier for the *erythrurus* and *pardalis* groups, which radiated from the late-Miocene, restricting them to the western and northern coastal areas, characterized by a less arid climate. These groups were influenced both by the shifting Saharan sand area, as well as by sea levels of the Atlantic Ocean and the Mediterranean Sea. The fluctuating climate, sea-level and desert areas (Sarnthein, 1978; Douady et al., 2003; Schuster et al., 2006), are likely to have enhanced diversification and created complex phylogenetic structures within the North-African *Acanthodactylus* groups (e.g., Douady et al., 2003; Fonseca et al., 2008, 2009; Metallinou et al., 2015). The Sahara sands are also likely to have facilitated diversification and dispersal within the *scutellatus* group, similar to other psammophilous North-African reptile taxa (e.g., Carranza et al., 2008; Metallinou et al., 2012). The two evidently separate events in the Sub-Saharan region, the dispersal of *A. guineensis* and the vicariance of *A. boueti*, were probably enabled through the western edges of North Africa, restricted since the Miocene by the Sahara sands.

The members of the Eastern clade (Fig. 4), distributed mostly in Arabia to western India, began radiating during the mid-Miocene.

The dispersal of *Acanthodactylus* eastwards from Arabia further into Asia is estimated to have occurred after the uplift of the Zagros Mountains in Iran during the mid-Miocene, 12.4–10 Mya (Sborshchikov et al., 1981; Agard et al., 2011; Mouthereau, 2011). This accords with the biogeographic patterns observed in other lizard taxa from the region (e.g., Macey et al., 1998; Šmíd and Frynta, 2012). We suggest that the Zagros Mountains acted as a physical barrier, restricting dispersal of *Acanthodactylus* northwards to potential habitats in the Iranian plateau, thus constraining their dispersal eastward along the southern coast (e.g., Heidari et al., 2014). Another possibility is that the Iranian plateau had already been colonized by another lacertid, *Eremias*, with analogous ecological adaptations to *Acanthodactylus*. A more recent dispersal eastwards from Arabia is unlikely considering the profound level of differentiation, indicating a prolonged presence within the region. The biogeographical history of *Acanthodactylus* assemblage in the Arabian Peninsula is harder to interpret, since the area lacks both comprehensive sampling and adequate geological and climatic data. During the Miocene, the peninsula interior, characterized by the existence of a river system and basins, was highly influenced by the changing climate, which led to the formation or migration of desert sands. Local geological events such as periodic volcanism, earthquakes and mountain ridges uplifting also took place during this period (Bosworth et al., 2005; Edgell, 2006). The changing landscapes and habitats within the Arabian Peninsula during the mid-late Miocene are likely to have caused either contact or fragmentation of ancestral *Acanthodactylus* populations, and thus been responsible for the diversification within the Eastern clade.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2016.07.003.

References

Agard, P., Omrani, J., Jolivet, L., Whitechurch, H., Vrielynck, B., Spakman, W., Monié, P., Meyer, B., Wortel, R., 2011. Zagros orogeny: a subduction-dominated process. Geol. Mag. 148, 692–725. http://dx.doi.org/10.1017/S001675681100046X.

Amer, S.A.M., Kumazawa, Y., 2005. Mitochondrial DNA sequences of the Afro-Arabian spiny-tailed lizards (genus *Uromastyx*; family Agamidae): phylogenetic analyses and evolution of gene arrangements. Biol. J. Linn. Soc. 85, 247–260. http://dx.doi.org/10.1111/j.1095-8312.2005.00485.x.

Arnold, E.N., 1980. The scientific results of the Oman flora and fauna survey 1977 (Dhofar). The reptiles and amphibians of Dhofar, southern Arabia. J. Oman Stud. Special Report 2, 273–332.

Arnold, E.N., 1983. Osteology, genitalia and the relationships of *Acanthodactylus* (Reptilia: Lacertidae). Bull. British Mus. (Natural History) Zool. London 44, 291–339.

Arnold, E.N., 1986. A key and annotated check list to the lizards and amphisbaenas of Arabia. Fauna Saudi Arabia 8, 385–435.

Arnold, E.N., 1989a. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. Bull. British Mus. (Natural History) Zool. London 55, 209–257.

Arnold, E.N., 1989b. Systematics and adaptive radiation of equatorial African lizards assigned to the genera *Adolfus*, *Bedriagaia*, *Gastropholis*, *Holaspis* and *Lacerta* (Reptilia: Lacertidae). J. Nat. Hist. 23, 525–555.

Arnold, E.N., 2004. Overview of morphological evolution and radiation in the Lacertidae. In: Pérez-Mellado, V., Riera, N., Perera, A. (Eds.), The Biology of Lacertid Lizards. Evolutionary and Ecological Perspectives. Institut Menorquí d'Estudis, Recerca, 8. Maó, Menorca, pp. 11–36.

Arnold, E.N., Arribas, Ó., Carranza, S., 2007. Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. Zootaxa 1430, 1–86.

Baha El Din, S.M., 2007. A new lizard of the *Acanthodactylus scutellatus* group (Squamata: Lacertidae) from Egypt. Zool. Middle East 40, 21–32.

Baran, I., Kumlutaş, Y., Lanza, B., Sindaco, R., Ilgaz, Ç., Avci, A., Crucitti, P., 2005. *Acanthodactylus harranensis*, a new species of lizard from southeastern Turkey (Reptilia: Sauria: Lacertidae). Boll. Mus. Reg. Sci. Nat. Torino 23, 323–341.

Bellati, A., Carranza, S., Garcia-Porta, J., Fasola, M., Sindaco, R., 2015. Cryptic diversity within the *Anatololacerta* species complex (Squamata: Lacertidae) in the Anatolian Peninsula: evidence from a multi-locus approach. Mol. Phylogenet. Evol. 82, 219–233. http://dx.doi.org/10.1016/j.ympev.2014.10.003.

Bohannon, R.G., Naeser, C.W., Schmidt, D.L., Zimmermann, R.A., 1989. The timing of uplift, volcanism, and rifting peripheral to the Red Sea: a case for passive rifting? J. Geophys. Res.: Sol. Ea. (1978–2012) 94, 1683–1701. http://dx.doi.org/10.1029/JB094iB02p01683.

Bons, J., Geniez, P., 1995. Contribution to the systematics of the lizard *Acanthodactylus erythrurus* (Sauria, Lacertidae) in Morocco. Herpetol. J. 5, 271.

Bons, J., Girot, B., 1964. Révision de l'espèce *Acanthodactylus scutellatus* (Lacertidé-saurien). Bull. Soc. Sci. nat. phys. Maroc 42, 311–336.

Bosworth, W., Huchon, P., McClay, K., 2005. The Red Sea and Gulf of Aden basins. J. Afr. Earth Sci. 43, 334–378. http://dx.doi.org/10.1016/j.jafrearsci.2005.07.020.

Boulenger, G.A., 1887. Catalogue of the lizards in the British Museum (Natural History), . second ed. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleontidae second ed., vol. 3 Trustees of the British Museum (Natural History), London.

Boulenger, G.A., 1918. Sur les lézards du genre *Acanthodactylus* Wieg. Bull. Soc. Zool. France 43, 143–155.

Boulenger, G.A., 1921. Monograph of the Lacertidae, vol. 2. Trustees of the British Museum (Natural History), London.

Brown, R.P., Suárez, N.M., Pestano, J., 2002. The Atlas Mountains as a biogeographical divide in North-West Africa: evidence from mtDNA evolution in the Agamid lizard Agama impalearis. Mol. Phylogenet. Evol. 24, 324–332. http://dx.doi.org/10.1016/S1055-7903(02)00218-X.

Brown, R.P., Terrasa, B., Pérez-Mellado, V., Castro, J.A., Hoskisson, P.A., Picornell, A., Ramon, M.M., 2008. Bayesian estimation of post-Messinian divergence times in Balearic Island lizards. Mol. Phylogenet. Evol. 48, 350–358. http://dx.doi.org/10.1016/j.ympev.2008.04.013.

Carranza, S., Arnold, E.N., 2012. A review of the geckos of the genus *Hemidactylus* (Squamata: Gekkonidae) from Oman based on morphology, mitochondrial and nuclear data, with descriptions of eight new species. Zootaxa 3378, 1–95.

Carranza, S., Arnold, E.N., Geniez, P., Roca, J., Mateo, J.A., 2008. Radiation, multiple dispersal and parallelism in the skinks, *Chalcides* and *Sphenops* (Squamata: Scincidae), with comments on *Scincus* and *Scincopus* and the age of the Sahara Desert. Mol. Phylogenet. Evol. 46, 1071–1094. http://dx.doi.org/10.1016/j.ympev.2007.11.018.

Carretero, M.A., Fonseca, M.M., Garcia-Munoz, E., Brito, J.C., Harris, D.J., 2011. Adding *Acanthodactylus beershebensis* to the mtDNA phylogeny of the *Acanthodactylus pardalis* group. North-West J. Zool. 7, 138–142.

Castresana, J., 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol. Phylogenet. Evol. 17, 540–552.

Cox, S.C., Carranza, S., Brown, R.P., 2010. Divergence times and colonization of the Canary Islands by Gallotia lizards. Mol. Phylogenet. Evol. 56, 747–757. http://dx.doi.org/10.1016/j.ympev.2010.03.020.

Crochet, P.A., Geniez, P., Ineich, I., 2003. A multivariate analysis of the fringe-toed lizards of the *Acanthodactylus scutellatus* group (Squamata: Lacertidae): systematic and biogeographical implications. Zool. J. Linn. Soc. 137, 117–155.

Disi, A., Modry, D., Necas, P., Rifai, L., 2001. Amphibians and Reptiles of the Hashemite Kingdom of Jordan: An Atlas and Field Guide. Chimaira, Frankfurt am Main.

Douady, C.J., Catzeflis, F., Raman, J., Springer, M.S., Stanhope, M.J., 2003. The Sahara as a vicariant agent, and the role of Miocene climatic events, in the diversification of the mammalian order Macroscelidea (elephant shrews). Proc. Natl. Acad. Sci. USA 100, 8325–8330. http://dx.doi.org/10.1073/pnas.0832467100.

Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29, 1969–1973. http://dx.doi.org/10.1093/molbev/mss075.

Edgell, H.S., 2006. Arabian Deserts: Nature, Origin and Evolution. Springer Science & Business Media.

Ezard, T., Fujisawa, T., Barraclough, T.G., 2009. SPLITS: Species Limits by Threshold Statistics. R package version 1.0-11/r29 <http://R-Forge.R-project.org/projects/splits/>.

Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39, 783–791.

Fitzinger, L.J.F.J., 1834. *Acanthodactylus*. In: Wiegman, A.F.A. (Ed.), Herpetologia mexicana, seu Descriptio amphibiorum Novae Hispaniae quae itineribus comitis De Sack, Ferdinandi Deppe et Chr. Guil. Schiede in Museum zoologicum Berolinense pervenerunt. Pars prima saurorum species amplectens, adjecto systematis saurorum prodromo, additisque multis in hunc amphibiorum ordinem observationibus. C.G. Luderitz, Berlin, p. 10.

Flower, B.P., Kennett, J.P., 1994. The middle Miocene climatic transition: east Antarctic ice sheet development, deep ocean circulation and global carbon cycling. Palaeogeogr. Palaeoclimatol. Palaeoecol. 108, 537–555.

Fonseca, M.M., Brito, J.C., Paulo, O.S., Carretero, M.A., Harris, D.J., 2009. Systematic and phylogeographical assessment of the *Acanthodactylus erythrurus* group (Reptilia: Lacertidae) based on phylogenetic analyses of mitochondrial and nuclear DNA. Mol. Phylogenet. Evol. 51, 131–142. http://dx.doi.org/10.1016/j.ympev.2008.11.021.

Fonseca, M.M., Brito, J.C., Rebelo, H., Kalboussi, M., Larbes, S., Carretero, M.A., Harris, D.J., 2008. Genetic variation among spiny-footed lizards in the *Acanthodactylus pardalis* group from North Africa. Afr. Zool. 43, 8–15.

Fritz, U., Fritzsch, G., Lehr, E., Ducotterd, J.M., Müller, A., 2005. The Atlas Mountains, not the Strait of Gibraltar, as a biogeographic barrier for *Mauremys leprosa* (Reptilia: Testudines). Salamandra 41, 97–106.

Fu, J., 2000. Toward the phylogeny of the family Lacertidae-Why 4708 base pairs of mtDNA sequences cannot draw the picture. Biol. J. Linn. Soc. 71, 203–217.

Gonçalves, D.V., Brito, J.C., Crochet, P.A., Geniez, P., Padial, J.M., Harris, D.J., 2012. Phylogeny of North African *Agama* lizards (Reptilia: Agamidae) and the role of the Sahara desert in vertebrate speciation. Mol. Phylogenet. Evol. 64, 582–591. http://dx.doi.org/10.1016/j.ympev.2012.05.007.

Griffin, D.L., 2002. Aridity and humidity: two aspects of the late Miocene climate of North Africa and the Mediterranean. Palaeogeogr. Palaeoclimatol. Palaeoecol. 182, 65–91. http://dx.doi.org/10.1016/S0031-0182(01)00453-9.

Haas, G., 1957. Some amphibians and reptiles from Arabia. Proc. Calif. Acad. Sci. 29, 47–86.

Harris, D.J., Arnold, E.N., 2000. Elucidation of the relationships of spiny footed lizards, *Acanthodactylus* spp. (Reptilia: Lacertidae) using mitochondrial DNA sequence, with comments on their biogeography and evolution. J. Zool. 252, 351–362.

Harris, D.J., Arnold, E.N., Thomas, R.H., 1998. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. Proc. R. Soc. Lond. B. Bio. Sci. 265, 1939–1948.

Harris, D.J., Batista, V., Carretero, M., 2004. Assessment of genetic diversity within *Acanthodactylus erythrurus* (Reptilia: Lacertidae) in Morocco and the Iberian Peninsula using mitochondrial DNA sequence data. Amphibia-Reptilia 25, 227.

Heidari, N., Rastegar-Pouyani, E., Rastegar-Pouyani, N., Faizi, H., 2014. Molecular phylogeny and biogeography of the genus *Acanthodactylus* Fitzinger, 1834 (Reptilia: Lacertidae) in Iran, inferred from mtDNA Sequences. Zootaxa 3860, 379–395.

Hipsley, C.A., Himmelmann, L., Metzler, D., Müller, J., 2009. Integration of Bayesian molecular clock methods and fossil-based soft bounds reveals early Cenozoic origin of African lacertid lizards. BMC Evol. Biol. 9, 151. http://dx.doi.org/10.1186/1471-2148-9-151.

Huelsenbeck, J.P., Rannala, B., 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. Syst. Biol. 53, 904–913. http://dx.doi.org/10.1080/10635150490522629.

Jolivet, L., Augier, R., Robin, C., Suc, J.P., Rouchy, J.M., 2006. Lithospheric-scale geodynamic context of the Messinian salinity crisis. Sediment. Geol. 188, 9–33. http://dx.doi.org/10.1016/j.sedgeo.2006.02.004.

Kaliontzopoulou, A., Pinho, C., Harris, D.J., Carretero, M.A., 2011. When cryptic diversity blurs the picture: a cautionary tale from Iberian and North African *Podarcis* wall lizards. Biol. J. Linn. Soc. 103, 779–800. http://dx.doi.org/10.1111/j.1095-8312.2011.01703.x.

Kapli, P., Botoni, D., Ilgaz, Ç., Kumlutaş, Y., Avcı, A., Rastegar-Pouyani, N., Fathinia, B., Lymberakis, P., Ahmadzadeh, F., Poulakakis, N., 2013. Molecular phylogeny and historical biogeography of the Anatolian lizard *Apathya* (Squamata, Lacertidae). Mol. Phylogenet. Evol. 66, 992–1001. http://dx.doi.org/10.1016/j.ympev.2012.12.002.

Kapli, P., Lymberakis, P., Crochet, P.A., Geniez, P., Brito, J.C., Almutairi, M., Ahmadzadeh, F., Schmitz, A., Wilms, T., Poulakakis, N., 2015. Historical biogeography of the lacertid lizard *Mesalina* in North Africa and the Middle East. J. Biogeogr. 42, 267–279. http://dx.doi.org/10.1111/jbi.12420.

Kapli, P., Poulakakis, N., Lymberakis, P., Mylonas, M., 2011. A re-analysis of the molecular phylogeny of Lacertidae with currently available data. Basic Appl. Herpetol. 25, 97–104.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 30, 772–780. http://dx.doi.org/10.1093/molbev/mst010.

Khan, M.S., 2006. Amphibians and Reptiles of Pakistan. Krieger Publishing Company.

Kroepelin, S., 2006. Revisiting the age of the Sahara Desert. Science 312 (5777), 1138–1139.

Lanfear, R., Calcott, B., Ho, S.Y., Guindon, S., 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol. Biol. Evol. 29, 1695–1701. http://dx.doi.org/10.1093/molbev/mss020.

Le Houérou, H.N., 1992. Outline of the biological history of the Sahara. J. Arid Environ. 22, 3–30.

Le Houérou, H.N., 1997. Climate, flora and fauna changes in the Sahara over the past 500 million years. J. Arid Environ. 37, 619–647. http://dx.doi.org/10.1006/jare.1997.0315.

Lemey, P., Rambaut, A., Drummond, A., Suchard, M., 2009. Bayesian phylogeography finds its roots. PLoS Comput. Biol. 5, e1000520. http://dx.doi.org/10.1371/journal.pcbi.1000520.

Macey, J.R., Schulte, J.A., Ananjeva, N.B., Larson, A., Rastegar-Pouyani, N., Shammakov, S.M., Papenfuss, T.J., 1998. Phylogenetic relationships among Agamid Lizards of the *Laudakia caucasia* species group: testing hypotheses of biogeographic fragmentation and an Area Cladogram for the Iranian Plateau. Mol. Phylogenet. Evol. 10, 118–131.

Mayer, W., Benyr, G., 1994. Albumin-Evolution und Phylogenese in der Familie Lacertidae (Reptilia: Sauria). Ann. Naturhist. Mus. Wien 96, 621–648.

Mayer, W., Pavlicev, M., 2007. The phylogeny of the family Lacertidae (Reptilia) based on nuclear DNA sequences: convergent adaptations to arid habitats within the subfamily Eremiainae. Mol. Phylogenet. Evol. 44, 1155–1163. http://dx.doi.org/10.1016/j.ympev.2007.05.015.

Mellado, J., Olmedo, G., 1990. El género *Acanthodactylus* en Marruecos: problemas de identificación en los grupos de especies *A. pardalis* y *A. scutellatus*. Amphibia-Reptilia 11, 131–146.

Mertens, R., 1929. Beitraege zur Herpetologie Tunesiens. Senckenbergiana 11, 291–310.

Metallinou, M., Arnold, E.N., Crochet, P.A., Geniez, P., Brito, J.C., Lymberakis, P., Baha El Din, S., Sindaco, R., Robinson, M., Carranza, S., 2012. Conquering the Sahara and Arabian deserts: systematics and biogeography of *Stenodactylus* geckos (Reptilia: Gekkonidae). BMC Evol. Biol. 12 (1), 258. http://dx.doi.org/10.1186/1471-2148-12-258.

Metallinou, M., Červenka, J., Crochet, P.A., Kratochvíl, L., Wilms, T., Geniez, P., Shobrak, M.Y., Brito, J.C., Carranza, S., 2015. Species on the rocks: Systematics and biogeography of the rock-dwelling *Ptyodactylus* geckos (Squamata: Phyllodactylidae) in North Africa and Arabia. Mol. Phylogenet. Evol. 85, 208–220. http://dx.doi.org/10.1016/j.ympev.2015.02.010.

Miller, M., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE). IEEE, L.A, pp. 1–8. http://dx.doi.org/10.1109/GCE.2010.5676129.

Minton, S.A., 1966. A contribution to the herpetology of West Pakistan. Bull. Am. Mus. Nat. His. 134, 27–184.

Mouthereau, F., 2011. Timing of uplift in the Zagros belt/Iranian plateau and accommodation of late Cenozoic Arabia-Eurasia convergence. Geol. Mag. 148, 726–738. http://dx.doi.org/10.1017/S0016756811000306.

Nouira, S., Blanc, C., 1999. Description d'une nouvelle espèce d'acanthodactyle de Tunisie: *Acanthodactylus mechriguensis* n. sp. (Sauria, Reptilia). Siciliana 5, 101–108.

Pavlicev, M., Mayer, W., 2009. Fast radiation of the subfamily Lacertinae (Reptilia: Lacertidae): history or methodical artefact? Mol. Phylogenet. Evol. 52, 727–734. http://dx.doi.org/10.1016/j.ympev.2009.04.020.

Pons, J., Barraclough, T.G., Gomez-Zurita, J., Cardoso, A., Duran, D.P., Hazell, S., Kamoun, S., Sumlin, W.D., Vogler, A.P., 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. Syst. Biol. 55, 595–609. http://dx.doi.org/10.1080/10635150600852011.

Pook, C.E., Joger, U., Stümpel, N., Wüster, W., 2009. When continents collide: phylogeny, historical biogeography and systematics of the medically important viper genus *Echis* (Squamata: Serpentes: Viperidae). Mol. Phylogenet. Evol. 53, 792–807. http://dx.doi.org/10.1016/j.ympev.2009.08.002.

Popov, S.V., Rögl, F., Rozanov, A.Y., Steininger, F.F., Shcherba, I.G., Kovac, M., 2004. Lithological-paleogeographic maps of Paratethys 10 maps Late Eocene to Pliocene. Cour. Forsch. Inst. Senckenb 250, 1–46.

Portik, D.M., Papenfuss, T.J., 2012. Monitors cross the Red Sea: the biogeographic history of *Varanus yemenensis*. Mol. Phylogenet. Evol. 62, 561–565. http://dx.doi.org/10.1016/j.ympev.2011.09.024.

Portik, D.M., Papenfuss, T.J., 2015. Historical biogeography resolves the origins of endemic Arabian toad lineages (Anura: Bufonidae): evidence for ancient vicariance and dispersal events with the Horn of Africa and South Asia. BMC Evol. Biol. 15, 152. http://dx.doi.org/10.1186/s12862-015-0417-y.

Poulakakis, N., Lymberakis, P., Valakos, E., Pafilis, P., Zouros, E., Mylonas, M., 2005. Phylogeography of Balkan wall lizard (*Podarcis taurica*) and its relatives inferred from mitochondrial DNA sequences. Mol. Ecol. 14, 2433–2443.

Pyron, R.A., Burbrink, F.T., Wiens, J.J., 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evol. Biol. 13, 93. http://dx.doi.org/10.1186/1471-2148-13-93.

Rambaut, A., Suchard, M.A., Xie, D., Drummond, A.J., 2014. Tracer v1.6. Available from <http://beast.bio.ed.ac.uk/Tracer>.

Rifai, L., Modrý, D., Necas, P., Amr, Z.S., 2003. The occurrence of *Acanthodactylus hardyi* Haas, 1957 in the Hashemite Kingdom of Jordan and notes on its ecology. Zool. Middle East 28, 33–38.

Rögl, F., 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geol. Carpath. 50, 339–349.

Ruddiman, W.F., Raymo, M., Martinson, D.G., Clement, B.M., Backman, J., 1989. Pleistocene evolution: northern hemisphere ice sheets and North Atlantic Ocean. Paleoceanography 4, 353–412.

Salvador, A., 1982. A revision of the lizards of the genus Acanthodactylus (Sauria: Lacertidae). Bonner Zoologische Monographien. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (16).

Sarnthein, M., 1978. Sand deserts during glacial maximum and climatic optimum. Nature 272, 43–46.

Schleich, H.H., Kästle, W., Kabisch, K., 1996. Amphibians and Reptiles of North Africa. Koeltz, Koenigstein.

Sborshchikov, I.M., Savostin, L.A., Zonenshain, L.P., 1981. Present plate tectonics between Turkey and Tibet. Tectonophysics 79, 45–73.

Schuster, M., Duringer, P., Ghienne, J.-F., Vignaud, P., Mackaye, H.T., Likius, A., Brunet, M., 2006. The age of the Sahara desert. Science 311, 821.

Silvestro, D., Michalak, I., 2012. RaxmlGUI: a graphical front-end for RAxML. Org. Divers. Evol. 12, 335–337. http://dx.doi.org/10.1007/s13127-011-0056-0.

Sindaco, R., Jeremčenko, V.K., 2008. The reptiles of the Western Palearctic. 1. Annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaenians and lizards of Europe, North Africa, Middle East and Central Asia. Monografie della Societas Herpetologica Italica, Edizioni Belvedere, Latina.

Šmíd, J., Carranza, S., Kratochvíl, L., Gvoždík, V., Nasher, A.K., Moravec, J., 2013. Out of Arabia: a complex biogeographic history of multiple vicariance and dispersal events in the gecko genus *Hemidactylus* (Reptilia: Gekkonidae). PLoS ONE 8, e64018. http://dx.doi.org/10.1371/journal.pone.0064018.

Šmíd, J., Frynta, D., 2012. Genetic variability of *Mesalina watsonana* (Reptilia: Lacertidae) on the Iranian plateau and its phylogenetic and biogeographic affinities as inferred from mtDNA sequences. Acta Herpetol. 7, 139–153.

Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688–2690. http://dx.doi.org/10.1093/bioinformatics/btl446.

Swezey, C.S., 2006. Revisiting the age of the Sahara Desert. Science 312, 1138–1139. http://dx.doi.org/10.1126/science.312.5777.1138b.

Swezey, C.S., 2009. Cenozoic stratigraphy of the Sahara, northern Africa. J. Afr. Earth Sci. 53, 89–121. http://dx.doi.org/10.1016/j.jafrearsci.2008.08.001.

Talavera, G., Castresana, J., 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Syst. Biol. 56, 564–577. http://dx.doi.org/10.1080/10635150701472164.

Talavera, G., Dinca, V., Vila, R., 2013. Factors affecting species delimitations with the GMYC model: insights from a butterfly survey. Methods Ecol. Evol. 4, 1101–1110. http://dx.doi.org/10.1111/2041-210X.12107.

Tamar, K., Carranza, S., Sindaco, R., Moravec, J., Meiri, S., 2014. Systematics and phylogeography of *Acanthodactylus schreiberi* and its relationships with *Acanthodactylus boskianus* (Reptilia: Squamata: Lacertidae). Zool. J. Linn. Soc. 172, 720–739. http://dx.doi.org/10.1111/zoj.12170.

Tamar, K., Carranza, S., in den Bosch, H., Sindaco, R., Moravec, J., Meiri, S., 2015. Hidden relationships and genetic diversity: molecular phylogeny and phylogeography of the Levantine lizards of the genus *Phoenicolacerta* (Squamata: Lacertidae). Mol. Phylogenet. Evol. 91, 86–97. http://dx.doi.org/10.1016/j.ympev.2015.05.002.

Tamar, K., Scholz, S., Crochet, P.A., Geniez, P., Meiri, S., Schmitz, A., Wilms, A., Carranza, S., 2016. Evolution around the Red Sea: systematics and biogeography of the agamid genus *Pseudotrapelus* (Squamata: Agamidae) from North Africa and Arabia. Mol. Phylogenet. Evol. 97, 55–68. http://dx.doi.org/10.1016/j.ympev.2015.12.021.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., Kumar, S., 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol. Biol. Evol. 28, 2731–2739. http://dx.doi.org/10.1093/molbev/msr121.

Trape, J.F., Trape, S., Chirio, L., 2012. Lézards, Crocodiles Et Tortues d'Afrique Occidentale Et Du Sahara. IRD Éditions, Marseille.

Uetz, P., Hošek, J., 2016. The Reptile Database. Available at <http://www.reptile-database.org>. (April 2016).

Wiens, J.J., Brandley, M.C., Reeder, T.W., 2006. Why does a trait evolve multiple times within a clade? Repeated evolution of snakeline body form in squamate reptiles. Evolution 60, 123–141.

Wilcox, T.P., Zwickl, D.J., Heath, T.A., Hillis, D.M., 2002. Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. Mol. Phylogenet. Evol. 25, 361–371. http://dx.doi.org/10.1016/S1055-7903(02)00244-0.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693. http://dx.doi.org/10.1126/science.1059412.

Zheng, Y., Wiens, J.J., 2016. Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. Mol. Phylogenet. Evol. 94, 537–547. http://dx.doi.org/10.1016/j.ympev.2015.10.009.