Systematics and Biodiversity (2018), **16(4)**: 323–339

Taylor & Francis
Taylor & Francis Group

Research Article

Systematics, biogeography and evolution of *Asaccus gallagheri* (Squamata, Phyllodactylidae) with the description of a new endemic species from Oman

MARC SIMÓ-RIUDALBAS[1], PEDRO TARROSO[1,2], THEODORE PAPENFUSS[3], THURAYA AL-SARIRI[4] & SALVADOR CARRANZA[1]

[1]Institute of Evolutionary Biology (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain
[2]CIBIO/InBIO, Research Centre in Biodiversity and Genetic Resources, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-661 Vairão, Vila do Conde, Portugal
[3]Department of Integrative Biology, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA
[4]Ministry of Environment and Climate Affairs, Thaqafah Street, 100, Muscat, Oman

(Received 20 May 2017; accepted 1 November 2017; published online 15 December 2017)

The Hajar Mountains are the highest mountain range in eastern Arabia. Despite being classified as a mountain desert, it is considered one of the top biodiversity hotspots of Arabia. As a result of its relatively old geological origin, complex topography, environmental heterogeneity and geographic isolation from other mountain ranges, its fauna and flora have diversified significantly producing high levels of endemicity, particularly amongst reptiles. Several genetic studies indicate that this diversity may still be underestimated, especially within some groups containing morphologically similar species like the nocturnal geckos of the genus *Asaccus*. These have radiated extensively on both sides of the Gulf of Oman, in the Hajar Mountains and the Zagros Mountains of south-west Asia, and are a good example of the faunal affinities between these two mountain ranges. In the present work, we analyse *A. gallagheri*, the smallest species of the Arabian radiation, using an unprecedented sampling across its entire distribution range and an integrative approach combining morphological, macroecological and multilocus molecular data with the objective of clarifying its systematics and phylogeography. The results support the presence of two allopatric species within *A. gallagheri* that split approximately 6 Ma. The newly discovered species is endemic to the Eastern Hajars and is described herein mainly on the basis of its smaller size and high genetic divergence from *A. gallagheri*. The molecular analyses also uncovered remarkable levels of genetic diversity within both species. The present study highlights the diversity of the genus *Asaccus* in south-east Arabia and stresses its relevance from a conservation point of view.

http://www.zoobank.org/urn:lsid:zoobank.org:pub:62EB3146-9F79-4857-8CC6-36FE235D84D4

Key words: Arabia, biogeography, endemicity, geckos, Hajar Mountains, hypervolumes, species delimitation, taxonomy

Introduction

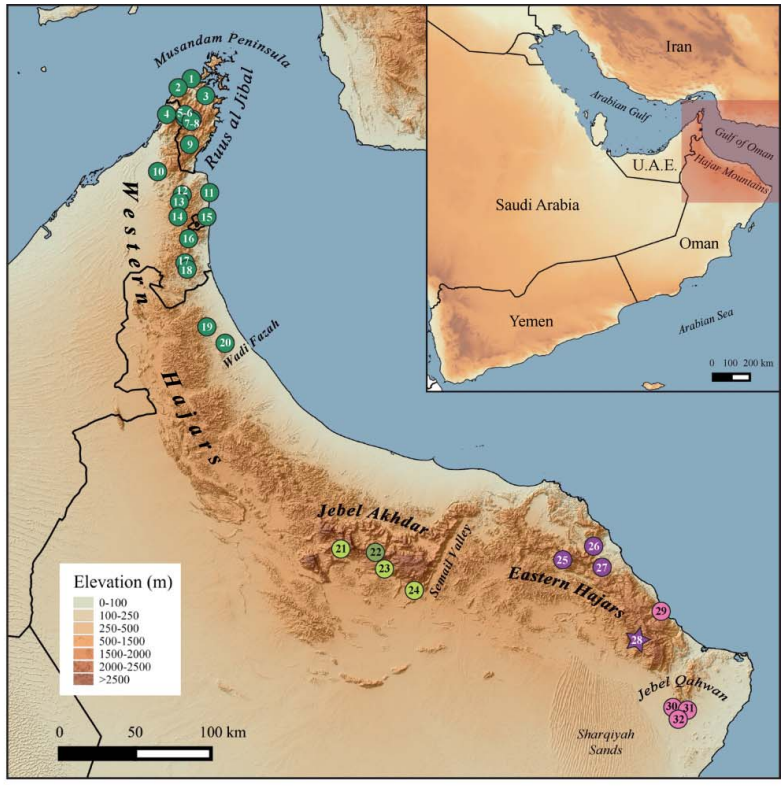
The Hajar Mountains from south-eastern Arabia form a continuous range that runs for about 650 km alongside the coast of the Gulf of Oman; from the Musandam Peninsula and Ruus al Jibal in the north to the Jebel Qahwan in the south-east. Most of the range is within the Sultanate of Oman but a small area, just south of the Musandam Governorate, belongs to the United Arab Emirates, UAE (Fig. 1.1). Cut by deep canyons or wadis, these arid mountains have a complex topography and can be divided into three distinct areas, the Western Hajars, the Jebel Akhdar and the Eastern Hajars (see Fig. 1.1). With a maximum elevation of 3,018 m above sea level (a.s.l.), the Jebel Shams in the Jebel Akhdar is the highest peak of the Hajar Mountains, although high peaks also occur in the Western (2,087 m a.s.l. at Jebel Harim) and Eastern (2,200 m a.s.l. at Jebel Khadar) Hajars. Despite being the only area in eastern Arabia with habitats above 2,000 m in elevation and relatively low annual mean temperatures, average precipitation estimates are below 300 mm over much of its range, evapotranspiration is high and vegetation is very scarce. As a result of that, the Hajar Mountains are often considered a mountain desert (Edgell, 2006; Mandaville, 1977). Similar to other mountain ranges

Correspondence to: Salvador Carranza. Email: salvador.carranza@ibe.upf-csic.es

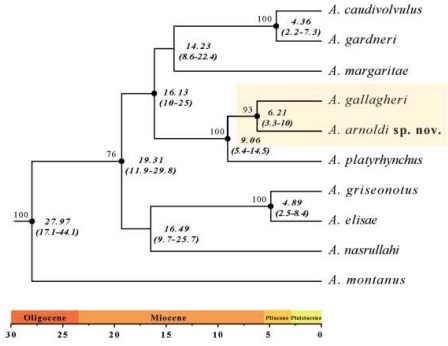
ISSN 1477-2000 print / 1478-0933 online

http://dx.doi.org/10.1080/14772000.2017.1403496

1)


Musandam Peninsula
Ruus al Jibal
Western Hajars
Wadi Fazah
Jebel Akhdar
Semail Valley
Eastern Hajars
Jebel Qahwan
Sharqiyah Sands
Elevation (m)
0-100
100-250
250-500
500-1500
1500-2000
2000-2500
>2500
0 50 100 km
Iran
Arabian Gulf
Gulf of Oman
Hajar Mountains
U.A.E.
Saudi Arabia
Oman
Yemen
Arabian Sea
0 100 200 km

2)


A. caudivolvulus
A. gardneri
A. margaritae
A. gallagheri
A. arnoldi sp. nov.
A. platyrhynchus
A. griseonotus
A. elisae
A. nasrullahi
A. montanus
4.36 (2.2-7.3)
14.23 (8.6-22.4)
16.13 (10-25)
6.21 (3.3-10)
9.06 (5.4-14.5)
19.31 (11.9-29.8)
4.89 (2.5-8.4)
27.97 (17.1-44.1)
16.49 (9.7-25.7)
Oligocene
Miocene
Pliocene Pleistocene
30 25 20 15 10 5 0

3)

A. gallagheri
A. arnoldi sp. nov.
1
2
3
4
5
0.008

in the Arabian Peninsula such as the Western Mountains of Yemen and Saudi Arabia, orogeny in the Hajar Mountains was triggered by the opening of the Gulf of Aden in the Oligocene and continued well into the Miocene, when the latest phase of plate tectonics affected Oman (Bosworth, Huchon, & McClay, 2005; Glennie, 2006). As a result of its relatively old geological origin, complex topography, diversity of habitats with local microclimates and geographic isolation from other mountain areas in Arabia, the Hajar Mountain range is one of the most biodiverse areas of the whole Arabian Peninsula, with high levels of endemicity in reptiles as well as in other animal and plant groups (Brinkmann, Patzelt, Dickhoefer, Schlecht, & Buerkert, 2009; Gardner, 2013; Ghazanfar, 1991; Mandaville, 1977). Since the first biodiversity surveys carried out in the mountains in the 1970s, reptiles have received increasing attention as a result of their abundance and unexpected diversity. With the description of several new species, they became, by far, the vertebrate group with the highest number of endemic species in the Hajar Mountains (Arnold, 1972, 1977, 1986; Arnold & Gallagher, 1977; Arnold & Gardner, 1994; Gardner, 1994, 1999; Gasperetti, 1988). More recently, molecular studies have shown that reptile diversity in the Hajar Mountains was still underestimated, with some gecko groups of the genera *Hemidactylus* (Carranza & Arnold 2012), *Pristurus* (Badiane et al., 2014; Garcia-Porta, Simó-Riudalbas, Robinson, & Carranza, 2017), *Ptyodactylus* (Metallinou et al., 2015; Simó-Riudalbas et al., 2017), *Trachydactylus* (de Pous et al., 2016a) and *Asaccus* (Carranza, Simó-Riudalbas, Jayasinghe, Wilms, & Els, 2016; Papenfuss et al., 2010) harbouring several cryptic species and deep lineages, some of them with restricted distributions of just a few kilometres. From all the reptile genera of the Hajar Mountains, *Asaccus* Dixon & Anderson, 1973 is the one with the highest number of endemics (see below) and a good example of the faunal affinities between the Hajar Mountains in Arabia and the Zagros Mountains in Iran (Carranza et al., 2016; Papenfuss et al., 2010; Torki, Ahmadzadeh, Ilgaz, Avcı, & Kumlutaş, 2011a; Uetz, Goll, & Hallerman, 2017). In a similar way, closely related taxa and populations from various reptile groups are present on both sides of the Gulf of Oman and provide an excellent scenario for reconstructing their evolutionary relationships and to explore the biogeography of the region (Dakhteh, Kami, & Anderson, 2007; de Pous et al., 2016b; Kapli et al., 2008, 2015; Krause, Ahmadzadeh, Moazeni, Wagner, & Wilms, 2013; Metallinou et al., 2012, 2014; Yousofi, Rastegar-Pouyani, & Hojati, 2015).

Commonly known as South-west Asian leaf-toed geckos, the genus *Asaccus* (previously part of *Phyllodactylus* Grey, 1828) is one of the least known genera of the family Phyllodactylidae. All of them are small to medium size, slender, nocturnal, rock climbing geckos with paired terminal scansors in the digits without lamellae and with no femoral or preanal pores, cloacal sacs, postanal bones and left oviduct. By now, 18 species are recognized within the genus, most of them described in the last decade. A total of 12 species are found in south-east Anatolia, east Syria, east Iraq and western Iran (west Zagros Mountains), while the other six species occur in south-east Arabia, along the Hajar Mountains: *Asaccus gallagheri* (Arnold, 1972), *A. montanus* Gardner, 1994, *A. platyrhynchus* Arnold & Gardner, 1994, *A. caudivolvulus* Arnold & Gardner, 1994 and the two recently described *A. gardneri* Carranza et al., 2016 and *A. margaritae* Carranza et al., 2016.

Asaccus gallagheri is a small, delicately built gecko found in stony substrates in wadis and on small cliffs and boulders on open hillsides. It is currently distributed across the Hajar Mountains, from sea level up to 1,900 m a.s.l. in the Jebel Akhdar (pers. obs.). *Asaccus gallagheri* was described by Arnold (1972) based on a single juvenile specimen from Masafi (UAE; locality 14 in Fig. 1.1). Given the lack of material in the original description, the species was later revised including more material collected within 30 km of the type locality (Arnold, 1977). The first phylogenetic relationships carried out by Arnold and Gardner (1994) using 16 morphological characters suggested a sister taxa relationship between *A. gallagheri* and *A. platyrhynchus*, supported mainly by the absence of cloacal tubercles, by the similar dorsal colour pattern and the presence of sexually dimorphic tail colouration. A recent molecular phylogenetic analysis by Papenfuss, Jackman, Bauer, Stuart, Robinson, and Parham (2010) also recovered the clade formed by *A. gallagheri* and *A. platyrhynchus* and revealed a high level of genetic variability between

Fig. 1. Geographic distribution and phylogenetic relationships.
(1.1) Map of the Hajar Mountains showing the localities of the examined material (see Table S1, see supplemental material online). Type locality of *Asaccus arnoldi* sp. nov. indicated by a star. Localities are coloured corresponding to the five mitochondrial lineages identified (see Fig. 1.2). Maps were drawn using QGIS v.2.8 (available at http://www.qgis.org; digital elevation model freely available at http://earthobservatory.nasa.gov/); (1.2) Bayesian inference tree of 10 *Asaccus* species based on the concatenated sequences of two mitochondrial (*12S* and *cytb*) and two nuclear (*c-mos* and *MC1R*) genes. Black dots indicate posterior probability values ≥0.95 and bootstrap values ≥70% are shown next to the nodes (see Fig. S1, see supplemental material online). Age estimates are in italics below the nodes and include the mean and the HPD 95% confidence interval in brackets; (1.3) Bayesian inference tree of 78 *Asaccus* based on the same concatenated genes. Black dots indicate posterior probability values ≥0.95 and bootstrap values ≥70% are shown next to the nodes. Each sequence is labelled with the specimen code followed by the locality code in square brackets (see Fig. 1.1). Colour bars correspond to the five mitochondrial deep lineages. Detailed information on the samples included in both phylogenetic trees is given in Table S1 (see supplemental material online).

specimens of *A. gallagheri* from Nizwa in the Jebel Akhdar and Khasab in the Musandam Peninsula (Fig. 1.1), suggesting that *A. gallagheri* might include more than one species. However, the lack of material from the type locality of *A. gallagheri* in the UAE as well as other localities across the distribution range, as for instance the Eastern Hajar Mountains, precluded any taxonomic conclusions.

The objectives of the present work were: (1) to obtain samples across the whole distribution range of *Asaccus gallagheri* in the Hajar Mountains of south-eastern Arabia; (2) to use phylogenetic tools together with species delimitation algorithms to cluster the samples into lineages and to reconstruct their evolutionary relationships and phylogeography; (3) to contrast the molecular differentiation with measured overlap in morphology and niche; and (4) to use the information from all these different lines of evidence to revise the taxonomy of *Asaccus gallagheri*.

Materials and methods

DNA extraction and sequencing

The molecular study included a total of 86 specimens of *Asaccus* and two specimens of the genus *Haemodracon*, endemic to the Socotra Archipelago. A list of all individuals with their taxonomic identification, sample and voucher codes, geographic distribution and GenBank accession numbers is presented in Table S1 (see online supplemental material, which is available from the article's Taylor & Francis Online page at https://doi.org/10.1080/14772000.2017.1403496). Total genomic DNA was isolated from ethanol preserved tissue samples using the SpeedTools Tissue DNA Extraction kit (Biotools, Madrid, Spain) following the manufacturer's protocol. All specimens were sequenced for both strands for two mitochondrial gene fragments: the ribosomal 12S rDNA (*12S*) and the cytochrome *b* (*cytb*), plus two nuclear gene fragments: the oocyte maturation factor MOS (*c-mos*) and the melanocortin 1 receptor (*MC1R*). Primers and PCR conditions used for the amplification of all fragments are shown in Table S2 (see supplemental material online).

Geneious Pro v. 9.0.5 (Biomatters Ltd) was used for assembling and editing the chromatographs manually. All coding gene fragments started by the first codon position were translated into amino acids to validate the correct reading frame. For the nuclear coding gene fragments, heterozygous positions were identified and coded in both alleles according to IUPAC ambiguity codes. Multiple sequence alignments were performed with the online application of MAFFT v.7 (Katoh & Standley, 2013) with default parameters (Auto strategy, Gap opening penalty: 1.53, Offset value: 0.0). For the *12S* ribosomal fragment the Q-INS-i strategy was applied, in which the secondary structure of the RNA was considered. SeqPHASE (Flot, 2010) was used to convert the input files and the software PHASE v. 2.1.1 was used to reconstruct the gametic haplotypes (Stephens, Smith, & Donnelly, 2001) using default settings except for the phase probability threshold that was set to 0.7 (see Harrigan, Mazza, & Sorenson, 2008). Phased sequences of the nuclear genes were used for the allele network reconstruction (see below). Inter- and intra-specific uncorrected *p*-distances with pairwise deletion were estimated independently for both mitochondrial gene fragments using MEGA v.7 (Kumar, Stecher, & Tamura, 2016).

Phylogenetic analyses and ancestral area reconstruction

A total of three datasets were used in the phylogenetic analyses. Dataset 1 was assembled to infer the phylogenetic relationships and divergence times amongst *Asaccus* species and consisted of 12 terminals including one representative of *A. gallagheri*, one from the new species described herein plus all species of *Asaccus* available in GenBank: five from the Hajar Mountains of Arabia (*A. caudivolvulus*, *A. montanus*, *A. platyrhynchus*, *A. margaritae* and *A. gardneri*) and three from the Zagros Mountains (*A. griseonotus*, *A. elisae* and *A. nasrullahi*). Moreover, one *Haemodracon riebeckii* and one *H. trachyrhinus* were used as outgroups based on published evidence (Gamble, Bauer, Greenbaum, & Jackman, 2008, Gamble, et al., 2011; Gamble, Greenbaum, Jackman, Russell, & Bauer, 2012; Gamble, Greenbaum, Jackman, & Bauer, 2015; Garcia-Porta, Morales, Gómez-Díaz, Sindaco, & Carranza, 2016; Garcia-Porta, Simó-Riudalbas, Robinson, & Carranza, 2017). The dataset was missing nine species from the Zagros Mountains described based only on morphological evidence: *A. andersoni*, *A. barani*, *A. granularis*, *A. iranicus*, *A. kermanshahensis*, *A. kurdistanensis*, *A. saffinae*, *A. tangestanensis* and *A. zagrosicus*. Dataset 2 was assembled with the aim of studying in detail the phylogeographic relationships between the populations previously described as *Asaccus gallagheri*. This dataset consisted of 78 specimens collected from 32 localities distributed across the Hajar Mountains of Oman and the UAE (63 *A. gallagheri* and 15 specimens of the new species described herein) plus one *A. platyrhynchus* used as outgroup in the ML analyses. Dataset 1 and 2 included two concatenated alignments of 1,880 and 1,872 bp (base pair) respectively; 401 and 393 bp of *12S*; 399 bp of *cytb*; 414 bp of *c-mos* and 666 of *MC1R*. Dataset 3 was used for preliminary species delimitation and included 26 unique mitochondrial haplotypes from dataset 2 (only *12S* sequences).

Datasets 1 and 2 were analysed with maximum likelihood (ML) and Bayesian inference (BI) methods, whereas dataset 3 was only analysed with BI. The best-fit partitioning scheme and models of molecular evolution for all datasets were selected with PartitionFinder v.2. (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016) with the following settings: branch lengths linked, only models

available in BEAST evaluated, initial partitions by gene, BIC model selection criterion applied and all partition schemes analysed. The partition scheme and models of sequence evolution selected were *12S* + *cytb*, GTR + I + G; *c-mos*, HKI + I; *MC1R*, HKY + I for dataset 1, *12S*, HKY + G; *cytb*, HKY + G; *c-mos* + *MC1R*, TrN+I+G for dataset 2 and *12S* + *cytb*, GTR + G for dataset 3. ML analyses of datasets 1 and 2 were performed in RAxML v.7.4.2 (Stamatakis, 2006) as implemented in raxmlGUI (Silvestro & Michalak, 2012) with 100 tree searches, using the GTR+G model of sequence evolution and independent model parameters for the three partitions (see above). Reliability of the ML tree was assessed by bootstrap analysis (Felsenstein, 1985) including 1,000 replicates. The software BEAST v.1.8.0 (Drummond, Suchard, Xie, & Rambaut, 2012) was used for BI and dating analyses. Two individual runs of 5×10^7 generations were carried out for datasets 1–3, sampling at intervals of 10,000 generations. The following models and prior specifications were applied, otherwise by default: models of sequence evolution for the different partitions as selected by PartitionFinder (see above); Speciation Yule (dataset 1) and Coalescent Constant Size (datasets 2 and 3) tree prior; uncorrelated lognormal clock for mitochondrial genes and strict clock for nuclear ones; random starting tree; base substitution prior Uniform (0,100); alpha prior Uniform (0,10). Substitution and clock models were unlinked and the xml file was manually modified to set Ambiguities = ''true'' for the nuclear gene partitions in order to account for variability in the heterozygous positions, instead of treating them as missing data. Posterior trace plots and effective sample sizes (ESS) of the runs were monitored in Tracer v1.6 (Rambaut, Suchard, Xie, & Drummond, 2014) to ensure convergence. The results of the individual runs were combined in LogCombiner discarding 10% of the samples and the maximum clade credibility (MCC) ultrametric tree was produced with TreeAnnotator (both provided with the BEAST package). Absolute divergence times were estimated from dataset 1 using BEAST with models and prior specifications as above and applying previously calculated mean rates of molecular evolution for the two mitochondrial markers *12S* (mean: 0.00755, S.D.: 0.00247) and *cytb* (mean: 0.0228, S.D.: 0.00806) (Carranza & Arnold, 2012). Despite the problems associated with using evolutionary rates from other organisms for time tree calibration, the rates inferred by Carranza and Arnold (2012) and applied herein correspond with the rates obtained in other independent studies that used different calibration points and different taxa (Garcia-Porta et al., 2017; Metallinou et al., 2012; Sindaco et al., 2012). Indeed, the rates by Carranza and Arnold (2012) have been applied to several different studies for which reliable internal calibration points based on biogeographic events or fossil evidence do not exist (Carranza et al., 2016; de Pous et al., 2016a; Gómez-Díaz, Sindaco, Pupin, Fasola, & Carranza, 2012; Hawlitschek & Glaw, 2013; Metallinou & Carranza, 2013; Metallinou et al., 2015; Milá, Surget-Groba, Heulin, Gosá, & Fitze, 2013; Simó-Riudalbas et al., 2017; Šmíd et al., 2013; Tamar et al., 2016a; Vasconcelos & Carranza, 2014). Tree nodes were considered strongly supported if they received ML bootstrap values ≥70% and posterior probability (pp) support values ≥0.95 (Huelsenbeck & Rannala, 2004; Wilcox, Zwickl, Heath, & Hillis, 2002).

With the aim of reconstructing the phylogeographic history and inferring the ancestral origin of *Asaccus gallagheri* and the new species described herein, we used the Bayesian Stochastic Search Variable Selection (BSSVS; Lemey, Rambaut, Drummond, & Suchard, 2009) of the discrete phylogeographic model as implemented in BEAST v.1.8.0. To match the best tree topology obtained from the phylogenetic analyses we used dataset 2, which included all specimens collected across the Hajar Mountains (see above). We established the phylogeographic traits according to three discrete topographic discontinuities of the Hajar Mountains: the Western Hajars, the Jebel Akhdar and the Eastern Hajars (Fig. 1.1). Models, prior settings and parameters were the same ones used for the BEAST analysis of dataset 2 (see above).

Species delimitation and haplotype networks

Divergent mitochondrial lineages within populations previously described as *Asaccus gallagheri* were objectively identified using the latest version of the general mixed Yule-coalescent model (GMYC) (Fujisawa & Barraclough, 2013; Pons et al., 2006). The single-threshold approach was tested on the *12S* ultrametric tree (dataset 3) and the analysis was performed using the package 'splits' (Ezard, Fujisawa, & Barraclough, 2009) in R (R Development Core Team, 2016). This approach essentially detects the most likely tree depth at which the pattern of tree branching shifts between a Yule process (reflecting interspecific phylogenetic structure) to a coalescent process (reflecting intra-specific phylogenetic structure). Because inference of lineages relies on point estimates of the topology and branch lengths, the associated phylogenetic error could decrease the accuracy of the delimitation results. Therefore, uncertainty in the phylogenetic tree estimation and model parameters were assessed with a Bayesian implementation of the GMYC model (bGMYC 1.0; Reid & Carstens, 2012), which integrates these potential sources of error via MCMC simulation (Reid & Carstens, 2012). The R package 'bGMYC' was used to calculate marginal posterior probabilities of lineage limits from the posterior distribution of ultrametric trees reconstructed with BEAST. A post-burn-in sample of 250 trees resampled from that posterior was used to calculate the posterior distribution of the GMYC model, running the bGMYC analysis for 100,000 generations with a burn-in of 10,000 generations.

With the aim of exploring patterns of intra-specific genetic diversity and nuclear allele sharing within populations previously classified as *Asaccus gallagheri*, statistical parsimony networks on the phased nuclear genes were constructed independently with the program TCS v.1.21 (Clement, Posada, & Crandall, 2000) using default settings.

Morphological samples, characters examined and univariate analyses

A total of 54 alcohol-preserved adult specimens of *Asaccus* from across its distribution range in the Hajar Mountains of Oman and the UAE were examined and included in the morphological analyses. All voucher specimens were obtained from S. Carranza's field series housed at the Institute of Evolutionary Biology (IBE), Barcelona, Spain; the Natural History Museum, London, UK (NHMUK) and the Oman Natural History Museum, Muscat, Oman (ONHM) (Tables S1 and S4, see supplemental material online). Variables for the morphological analyses were selected based on previous taxonomic studies of *Asaccus* (Afrasiab & Mohamad, 2009; Arnold, 1972; Arnold & Gardner, 1994; Carranza et al., 2016; Dixon & Anderson, 1973; Gardner, 1994; Rastegar-Pouyani, 1996; Rastegar-Pouyani, Nilson, & Faizi, 2006; Torki, 2010; Torki et al., 2011a; Torki, Fathinia, Rostami, Gharzi, & Nazari-Serenjeh, 2011b; Werner, 2006). Specimens were sexed looking at two external characters: presence of hemipenal bulges and colour of original tails (yellow in males). The following measurements were taken twice on the right side of each specimen by the same person (MSR) using a digital calliper with accuracy to the nearest 0.1 mm: snout-vent length (SVL), distance from the tip of the snout to the cloaca; trunk length (TrL), distance between the fore and hind limb insertion points; head length (HL), taken axially from the tip of the snout to the anterior ear border; head height (HH), taken laterally at the anterior ear border; head width (HW), taken at the anterior ear border; snout length (SL), from the snout to the anterior eye border; snout width (SW), taken dorsally at the anterior eye border; eye diameter (ED), maximal longitudinal length of the eye; humerus length (LHu), from the elbow to the insertion of the fore limb on the anterior part of body; ulna length (LUn), from the wrist to the elbow; femur length (LFe), from the knee to the insertion of the hind limb on the posterior side of body and tibia length (LTb), from the ankle to the knee. Tail length was not measured because many individuals had a regenerated tail or had lost it. In addition to these morphometric variables, two pholidotic and one categorical character were collected using a dissecting microscope. Pholidotic characters: number of upper labial scales (ULS) and number of lower labial scales (LLS); categorical character: postmentals (PM) 1: in contact, 0: not in contact. All specimens were

Table 1. Descriptive statistics for all characters examined for males and females of *A. arnoldi* sp. nov. and *A. gallagheri*. Mean ± Standard Deviation (S.D.) and range (Min-Max) are given in millimetres except for the categorical character (PM; percentage of individuals with the first pair of postmentals in contact). Abbreviations of characters as explained in the material and methods.

	A. arnoldi **sp. nov.**		*A. gallagheri*	
Variable	Males ($n = 6$) **Mean±S.D. (Min-Max)**	Females ($n = 7$) **Mean±S.D. (Min-Max)**	Males ($n = 15$) **Mean±S.D. (Min-Max)**	Females ($n = 26$) **Mean±S.D. (Min-Max)**
SVL	29.9±2.5 (27.4-33.6)	30.7±1.7 (28.9-33.3)	33.8±2.2 (30-37.3)	32.8±3 (26.5-37.3)
TrL	11.5±1 (10.5-13.2)	12.1±0.7 (11.4-13.3)	13.5±1.3 (11.3-15.4)	13.5±1.6 (9.8-16.8)
HL	7.8±0.6 (7.1-8.7)	7.9±0.4 (7.4-8.5)	8.9±0.5 (8-9.7)	8.5±0.6 (6.9-9.4)
HW	5.1±0.3 (4.6-5.4)	5±0.2 (4.7-5.3)	5.6±0.4 (4.6-6.2)	5.5±0.5 (4.4-6.1)
HH	2.9±0.3 (2.6-3.2)	2.9±0.2 (2.7-3.1)	3.4±0.2 (3.1-3.8)	3.2±0.3 (2.6-3.6)
SL	3.5±0.3 (3.2-3.9)	3.6±0.2 (3.4-4)	4±0.3 (3.7-4.5)	3.8±0.3 (3.1-4.2)
SW	2.6±0.3 (2.3-2.9)	2.7±0.1 (2.5-2.9)	2.9±0.2 (2.5-3.3)	2.7±0.3 (2.1-3.2)
ED	1.8±0.2 (1.6-2)	1.9±0.2 (1.7-2.1)	2.2±0.2 (1.8-2.5)	2.1±0.2 (1.6-2.4)
LUn	4.5±0.5 (4.1-5.1)	4.6±0.2 (4.3-4.7)	5.1±0.3 (4.5-5.6)	4.8±0.4 (3.7-5.5)
LHu	4.3±0.4 (3.9-5.2)	4.4±0.5 (3.9-5)	4.9±0.5 (4.2-6)	4.7±0.6 (3.6-5.6)
LTb	5.8±0.6 (5.3-6.8)	5.8±0.4 (5.2-6.2)	6.8±0.7 (5.6-7.8)	6.2±0.6 (4.8-7.5)
LFe	6.2±0.5 (5.6-7)	6.5±0.3 (6.1-7)	7.1±0.8 (6-8.5)	6.8±0.8 (5-8.2)
ULS	11±0.8 (10-12)	11±0.8 (10-12)	11±0.8 (10-12)	12±0.8 (10-13)
LLS	9±0.8 (8-10)	8±0.5 (8-9)	9±0.9 (8-11)	9±0.8 (8-11)
PM (%)	17	71	87	69

photographed using a Nikon 300 camera with a 60 mm macro-lens, in order to make all the data easily available to the scientific community. The complete collection of 110 high-resolution photographs has been deposited in MorphoBank (http://morphobank.org/permalink/?P2755).

The final dataset included 41 specimens corresponding to *A. gallagheri* (15 males and 26 females) and 13 (six males and seven females) to the new species. Summary descriptive statistics (mean, maximum, minimum and standard deviation) for males and females independently (Table 1) and together (Table S4, see supplemental material online) were calculated for all the specimens included in the present study. The 12 morphometric, the two meristic and the only categorical variable were analysed independently and used in the description of the new species. All variables were log-transformed to increase the homogeneity of variances. To avoid the effect of strong correlation between size and the other morphometric variables, a linear regression between each variable and the snout-vent length (SVL) as predictor was performed and the residuals were used as a proxy of shape in the PCA in order to estimate the n-dimensional hypervolumes (see below). Regarding body size, differences between both species were tested using a one-way ANOVA on the log-transformed values of SVL. In addition, all pholidotic characters were tested using a one-way ANOVA for each variable for taxonomic purposes (see taxonomic account). Sexual dimorphism was checked for each variable using one-way ANOVAs. As a result of the lower number of available vouchers of the new species described herein, sexual dimorphism was only tested within *Asaccus gallagheri*. All morphological analyses were performed in R.

Environmental and presence data

The full environmental dataset included 19 bioclimatic variables downloaded from WorldClim (http://www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), plus aridity index and potential evapotranspiration obtained from the Consortium for Spatial Information (CGIAR-CSI; http://www.cgiar-csi.org/). The data were downloaded at 30′′ of degree spatial resolution and clipped to the extent of the study area (55.94E, 59.50E, 22.02N, 26.30N). The variables were projected to a world equidistant cylindrical projection centred in the centroid of the sampled presence data (56.88E, 24.57N) with a spatial resolution of 1 km. The Normalized Difference Vegetation Index (NDVI) dataset was obtained from the MODIS MOD13Q1 (Version 5) product, for the period between January 2004 and December 2014, with 16 days frequency and 250 m spatial resolution, resulting in 132 grid images. The data were projected to the study projection and clipped as above. The final dataset was summarized by the maximum value obtained per pixel, allowing a maximum of 34% of missing temporal data for each pixel. A principal component analysis (PCA) was done with all the above variables to summarize the environmental variation of the study area. Prior to the PCA, all variables were standardized to Z-scores due to the different units and magnitudes. Environmental variables were processed in R with 'rgdal' library and PCA performed with function 'princomp'.

Presence data were gathered for *A. gallagheri* ($n = 86$) and the new species described herein ($n = 18$) in the field using a GPS handheld device. Coordinates were stored in the WGS84 coordinate system and re-projected using the study projection. The presence dataset for spatial analyses was processed to remove duplicates within the same pixel at the spatial resolution of the study (30 arc seconds $\approx$ 1 km), resulting in a reduced dataset with 44 records belonging to *A. gallagheri* and 11 to the new species described herein.

Niche and morphological hypervolume overlap

The overlap between both species in the environmental and morphological space was quantified using a three-dimensional hypervolume. The hypervolume allows calculation of the size, overlap (or intersection) and unique parts of each species' niche in a multidimensional space (Blonder, Lamanna, Violle, & Enquist, 2014). This method uses a kernel density estimation using the presences and was shown to produce accurate measurements of the niche hypervolume, even with low sample size (Blonder et al., 2014). Presence data were used to extract the environmental data for each species (see above) and the three most important components from each of the environmental and morphological PCAs were used to estimate the hypervolumes (Table S5, see supplemental material online). The measurement of both hypervolumes was used to study the level of differentiation between *A. gallagheri* and the new species described herein at the ecological and morphological levels. All analyses were performed in R with the 'hypervolume' package. Although the hypervolume method may produce results with any combination of sample size and dimensionality, low sample size increases the sensitivity of the method to the bandwidth value (Blonder et al., 2014). We followed the package guidelines using the maximum of three variables based on the logarithm of the smallest sample size. Hypervolumes were built using a Silverman bandwidth estimator, a quantile threshold of 0% that includes the total probability density, maximizing the niche overlap between species, and a set of 1,000 random points to sample the kernel density.

In order to quantify the overlap in environmental niches and morphospaces between species, we used the Sørenson index (Ahmadzadeh et al., 2016) and the overlap index (OI) as the ratio of the intersection of the hypervolumes to the size of the smallest hypervolume. The OI is related to the Sørenson index (see Appendix 1, see supplemental material online) and is particularly informative in the cases of niches with very different sizes. Both indices range between zero and one, from no overlap to the maximum possible overlap, respectively. To test the significance of the overlap, we followed a randomization procedure similar to Warren, Glor, and Turelli (2008). The hypothesis being tested is if the niche of a pair of species is more different than the niche drawn from both species. For the niche hypervolume we merged the presences of both species and randomly derived a new set of presences with the same number of observations as the originals and measured the Sørenson index and OI. This was performed 999 times in order to generate the null distribution and a *P*-value of the observed overlap was calculated in the R environment. The same procedure was applied to the morphological data.

Species concept

In this manuscript, we have adopted the General Lineage Species Concept (de Queiroz, 1998). This unified species concept considers species as separately evolving metapopulation lineages and treats this property as the single requisite for delimiting species. Other properties, such as phenetic distinguishability, reciprocal monophyly, and pre- and postzygotic reproductive isolation, are not part of the species concept but serve as important lines of evidence relevant to assess the separation of lineages and therefore to species delimitation (de Queiroz, 2007).

Results

Molecular analyses

The results of the phylogenetic analyses of dataset 1 using BI and ML analyses produced similar trees, with most nodes being well supported (Figs 1.2 and S1, see supplemental material online) and with the same topology obtained by Carranza et al. (2016). *Asaccus montanus* branches as a sister taxon to all the other *Asaccus* species included in the analysis. The other five species from the Hajar Mountains (*A. caudivolvulus*, *A. margaritae*, *A. gardneri*, *A. platyrhynchus*, *A. gallagheri* and the new species described herein) form a well-supported clade in the BI analyses and, within it, the latter three species are recovered as a highly supported monophyletic group in both analyses. *Asaccus gallagheri* and the new species described herein are sister species in all the analyses (Figs 1.2 and S1, see supplemental material online). Diversification in the genus *Asaccus* started at least 28 Ma (95% HPD = 17.1–44.1). The clade formed by *A. platyrhynchus*, *A. gallagheri* and the new species described herein started diversifying 9.1 Ma (95% HPD = 5.4–14.5) and, within it, divergence between the two species formerly classified as *A. gallagheri* occurred 6.2 Ma (95% HPD = 3.3–10). The results of the phylogenetic analyses of dataset 2 show the phylogeographic relationships of all the specimens previously classified as *Asaccus gallagheri* (Fig. 1.3). As a result of the high level of genetic variability, we performed a species delimitation approach to objectively identify the number of distinct lineages. The results of the GMYC and bGMYC analyses using dataset 3 congruently support five divergent mitochondrial lineages: three within *A. gallagheri* and two within the new species described herein (Figs 1.3 and Table S1, see supplemental material online).

The examined populations are unequally distributed throughout the Hajar Mountains and adjacent lowlands, from sea level to 1,887 m a.s.l., showing an allopatric pattern for all detected lineages (Fig. 1.1, 1.3 and Table S1, see supplemental material online). Within *Asaccus gallagheri*, lineage 1 is widely distributed in the mountains of northern Oman and eastern UAE (from the Musandam Peninsula to Wadi Fazah), while lineages 2 and 3 are restricted to the Jebel Akhdar, separated 165 km on a straight line from the nearest locality of lineage 1. Despite very good sampling and thorough exploration across the northern Hajar Mountains (Garcia-Porta et al., 2017), not a single specimen was found in this intervening area, in which only one unvouchered record from Jebel Lahqin has ever been reported (see Gardner, 2013). The new species described herein (including lineages 4 and 5) is distributed across the Eastern Hajars. It is physically isolated from lineages 2 and 3 (the Jebel Akhdar populations of *A. gallagheri*) by the Semail Valley (see Fig. 1.1). The results of the discrete phylogeographic analysis carried out with dataset 2 using the BSSVS model suggest that speciation between *Asaccus gallagheri* and the new species described herein likely started in the Eastern Hajars (49% of probability in the deepest node of the phylogenetic tree), where the new species differentiated into two distinct lineages (98% of probability). The origin of *A. gallagheri* is inferred to have been in the Jebel Akhdar (55% of probability), where lineages 2 and 3 split (97% of probability). The widespread lineage 1 diversified in the Western Hajars (99% of probability), an area that was most probably colonised from the Jebel Akhdar (Fig. S2, see supplemental material online).

Genetic distances between intraspecific lineages (lineages 1–3 and 4–5; see Fig. 1) are considerably high, varying between 6%–8% for the *12S* and 8%–13% for the *cytb* (Table 2). Genetic distances between *Asaccus gallagheri* and the new species described herein are very high: 12.7± 1.5% for the *12S* and 20.8±1.7% for the *cytb*; similar to

Table 2. Genetic distances between all *Asaccus* species included in the molecular phylogenetic analyses. Uncorrected *p*-distances (%) for *12S* mitochondrial gene (lower-left) and for *cytb* mitochondrial gene (upper-right). All five mitochondrial lineages identified within *A. gallagheri* and *A. arnoldi* sp. nov. are included. Genetic distances between *A. gallagheri* and *A. arnoldi* sp. nov. in bold.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. *A. caudivolvulus*		12.8	26.3	27.8	27.3	26.8	25.3	27.3	25.6	30.1
2. *A. gardneri*	7		25.1	29.7	26.1	26.6	23.2	25.3	25.3	30.6
3. *A. margaritae*	16	14.5		26.2	22.3	23.1	23.5	26.5	26.1	27.6
4. *A. gallagheri* (1)	18.1	16.4	16.4		13.6	13.6	**21.1**	**20.6**	27.1	31.6
5. *A. gallagheri* (2)	18	16.7	17	7.9		8.1	**19.6**	**18.4**	27.1	29.3
6. *A. gallagheri* (3)	17.4	16.4	15.8	8.2	6		**19.8**	**19.1**	27.1	28.8
7. *A. arnoldi* sp. nov. (4)	17.4	15.7	15.3	**13.3**	**12.8**	**11.6**		12.5	21.9	29.3
8. *A. arnoldi* sp. nov. (5)	17.9	16	15.2	**12.4**	**11.8**	**11.4**	6.5		23.2	30.6
9. *A. platyrhynchus*	18.2	17.4	13.7	13.5	15.8	14.7	12.4	13.1		30.8
10. *A. montanus*	23.2	21.9	22	20.6	20.2	20.8	17.5	17.1	19.7	

the genetic distances calculated between other *Asaccus* species (Table 2 and Fig. S3, see supplemental material online). The level of intraspecific genetic variability for *A. gallagheri* is 1.7 ± 0.3 for the *12S* and 2.7 ± 0.4 for the *cytb*, and for the new species described herein 3.8 ± 0.6 for the *12S* and 7.1 ± 0.8 for the *cytb*.

The results of the haplotype network analyses show that *A. gallagheri* and the new species described herein do not share a single haplotype (all haplotypes of each species are private) in both nuclear genes analysed (Fig. S3, see supplemental material online). Within each species, allele sharing between all mitochondrial lineages is very low. Regarding lineages 1, 2 and 3 (*Asaccus gallagheri*), they share two haplotypes in the *c-mos* from a total of 17 haplotypes and do not share any of the 19 haplotypes of the *MC1R* gene. Similarly, the two lineages belonging to the new species described herein (lineages 4 and 5) share two of the eight haplotypes in the *c-mos* gene and none of the eight haplotypes in the *MC1R* gene. The different haplotypes of *A. gallagheri* and the new species described herein do not present any geographic structure within them, being distributed evenly over their specific sampling sites (see Fig. 1.1, Fig. S3 and Table S1, see supplemental material online).

Morphological differentiation

Descriptive statistics for all 15 morphological traits are shown in Tables 1 and S4 (see supplemental material online). Sexual dimorphism between species was not detectable, so both sexes were pooled together in all posterior analyses (results not shown). Size difference between species (SVL) was highly significant. The new species described herein is significantly smaller than *A. gallagheri* ($F = 12.464$; d.f. $= 1$; $P = 0.001$). Shape differentiation was assessed with a three-dimensional hypervolume including the two species (see Fig. 2.1). Nearly 80% of the total variation in the morphological dataset was explained by the first three PCs used to calculate the hypervolumes (Table S5.1, see supplemental material online). The hypervolume of *A. gallagheri* is 2.6 times broader than the hypervolume of the new species described herein. The species' morphospaces overlap to a large extent that is ~90% of the total morphospace of the new species and 34% of the morphospace of *A. gallagheri* (Fig. S4.1, see supplemental material online). This large overlap is also suggested by the Sørenson index, although it is significantly lower than expected under the hypothesis of morphospace overlap ($K = 0.48$; $P < 0.05$). The OI is high ($OI = 0.88$) suggesting that the morphospace of *A. gallagheri* mostly includes the new species described herein (Fig. S5.1, see supplemental material online) and, therefore, that we cannot differentiate each other with the current morphometric data. The significant Sørenson score is just describing the differences of the morphological hypervolume from *A. gallagheri* to the smaller subset that represents its sister species described herein.

Niche divergence

The niche overlap between both species was quantified using three-dimensional hypervolumes (see Fig. 2.2). Nearly 90% of the total variation in the environmental dataset was explained by the first three PCs used to calculate the hypervolumes (Table S5.2, see supplemental material online). The entire hypervolume of *A. gallagheri* is 3.7 times broader than the hypervolume of the newly described species. The species' niches overlap to a small extent with an intersection that is ~48% of the total niche of the new species described herein and 13% of the niche of *A. gallagheri* (Fig. S4.2, see supplemental material online). The Sørenson score and OI are low ($K = 0.19$, $OI = 0.46$) and significantly lower than expected under the null hypothesis of niche equivalence (Fig. S5.2, see supplemental material online), suggesting that both species have different niches despite a considerable

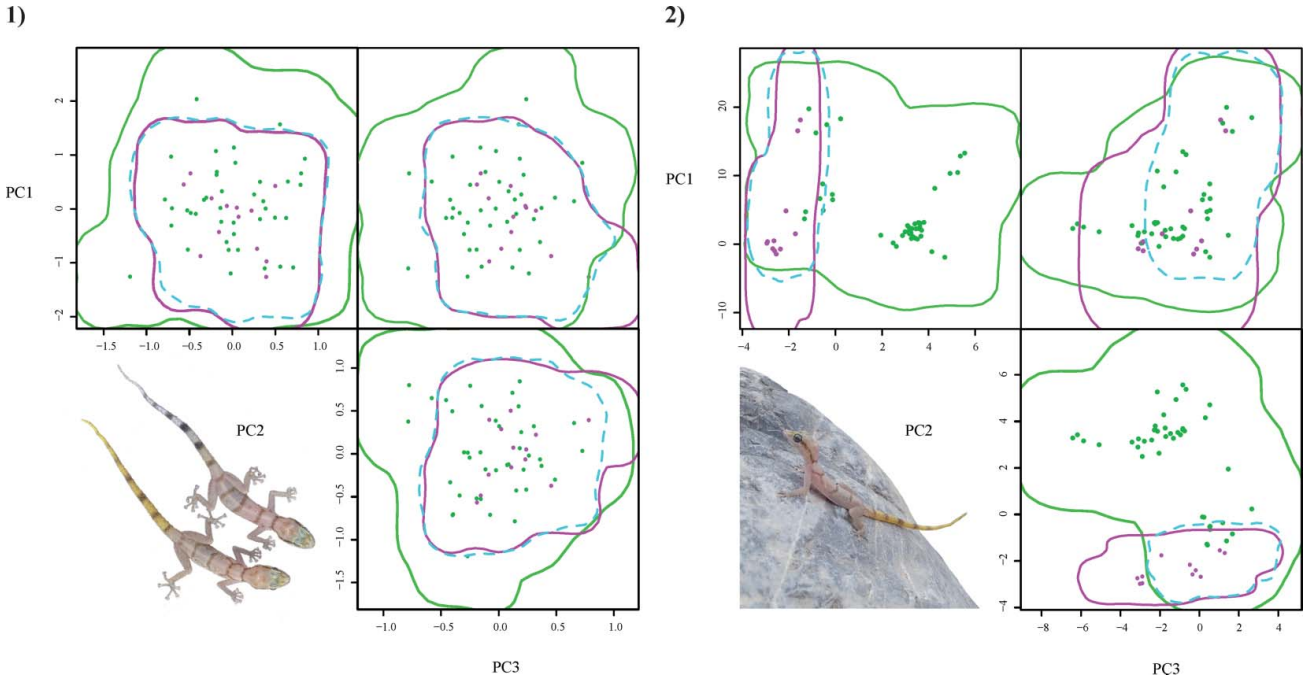


Fig. 2. Estimated three dimensional morphological (2.1) and environmental (2.2) hypervolumes for *Asaccus gallagheri* (green) and *A. arnoldi* sp. nov. (purple). The intersection (dashed blue) between the hypervolumes is also shown.
The three dimensional hypervolumes were calculated with the first three components of the PCA (Table S5.1 and S5.2, see supplemental material online). Coloured dots correspond to PCA-derived observations. Inset pictures show different specimens of *A. arnoldi* sp. nov. from Oman.

intersection between them. The new species described herein occupies a smaller niche that, although partly contained within the other species, is not fully overlapping and has a unique component that differentiates it from *A. gallagheri*. The hypervolume overlap shows that the second component is where most differentiation between both species resides (Fig. 2.2). In the comparison with the respective PCA loadings (Table S5.2, see supplemental material online), variables with most influence are temperature annual range (BIO7), mean diurnal range (BIO2), precipitation seasonality (BIO15), temperature seasonality (BIO4) and precipitation of the wettest month (BIO13). The unique component of the new species' niche is, thus, mostly related to a smaller range of precipitation and temperature.

Taxonomic account

Despite the high level of crypsis between the populations from the Eastern Hajars and the rest of the distribution range of *A. gallagheri* across all size corrected morphometric characters analysed here (Fig. 2.1), the results of the four gene fragments analysed clearly show that these two evolutionary units have been evolving independently for a long time (Figs 1.2, 1.3 and S3, see supplemental material online). Moreover, this differentiation is also supported by the macroecological analyses (Fig. 2.2) and a few morphological traits including size (see diagnosis below, Tables 1 and S4, see supplemental material online). Therefore, we describe the unnamed populations from the Eastern Hajars as a new species endemic to Oman. Data for the comparison with other *Asaccus* species were obtained from our own morphological dataset (Table 1 and Fig. S4, see supplemental material online) and also from morphological information available from the original descriptions of all 18 species of *Asaccus* (Afrasiab & Mohamad, 2009; Arnold, 1972; Arnold & Gardner, 1994; Carranza et al., 2016; Dixon & Anderson, 1973; Gardner, 1994; Rastegar-Pouyani, 1996; Rastegar-Pouyani et al., 2006; Torki, 2010; Torki et al., 2011a, 2011b; Werner, 2006).

Family Phyllodactylidae

Asaccus Dixon and Anderson, 1973

Asaccus arnoldi sp. nov.

(Figs 1–3, Figs S1–S3, see supplemental material online; Tables 1–2, Tables S1 and S3–S4, see supplemental material online)

http://www.zoobank.org/urn:lsid:zoobank.org:act:BF77A117-EA38-4D9C-AF44-9E700348F092

Asaccus gallagheri. Arnold & Gardner, 1994: 427 (part.); van der Kooij, 2000: 108 (part.); Sindaco & Jeremcenko, 2008: 99 (part.); Gardner, 2013: 95 (part.).

Holotype. BMNH2008.961, adult male, from Wadi Bani Khalid (Oman), 22.6161N 59.0937E WGS84, elevation 647 m a.s.l. (locality 28 in Fig. 1.1; Table S1), collected by S. Carranza, F. Amat, E. Gómez-Díaz on 3 May 2011, tissue code S7555.

Paratypes. BMNH2008.962 and ONHM4234, two adult females and IBES7576, adult male, same data as holotype, tissue codes S7554, S7252 and S7556, respectively.

Other material examined. Nine specimens used for genetic and morphological analyses and two specimens used only for genetic analyses (no voucher available, juvenile or damaged specimen); all listed in Table S1 and S4 (see supplemental material online).

Etymology. The species epithet '*arnoldi*' is a genitive Latin noun to honour the British herpetologist, Dr E. Nicholas Arnold, for his life-long dedication and contribution to Arabian herpetology, including the description of the little-known gecko *Asaccus gallagheri* 45 years ago.

Fig. 3. View of the type locality and general appearance in life of *Asaccus arnoldi* sp. nov.
(3.1) Holotype of *A. arnoldi* sp. nov. (male; voucher code BMNH.2008.961); (3.2) Rocky sides of Wadi Bani Khalid in 2016 (locality 28 in Fig. 1.1; Table S1, see supplemental material online); (3.3) Female (above) and male (below) *A. arnoldi* sp. nov. with the characteristic dimorphic tail colouration. All photographs taken by Salvador Carranza.

Diagnosis. A new species of *Asaccus* from the Eastern Hajar Mountains of Oman characterized by the combination of the following morphological characters: (1) small size with maximum SVL 33.6 mm; (2) first pair of postmentals in contact in less than half of the studied specimens; (3) scales across supraorbital region fine; (4) dorsal tubercles absent on back, occiput, upper arm and elsewhere; (5) small subtibial scales; (6) paired terminal scansors on digits not extending markedly beyond claws; (7) cloacal tubercle minute or absent; (8) tail tip not laterally compressed or vertically expanded; (9) absence of enlarged tubercles on tail; (10) subcaudal series of expanded scales do not reach the vent area anteriorly; (11) dorsum with a pattern of narrow dark transverse bars; (12) tail colour sexually dimorphic in non-regenerated tails, being white barred black in females and yellow in males (see Fig. 3.3); (13) dorsal dark bars on the tail of females extend ventrally; (14) tail not coiled and waved in life.

Comparison with other *Asaccus* species. *Asaccus arnoldi* sp. nov. differs from its sister taxon *A. gallagheri* mainly in its smaller size (SVL max. 33.6 mm, compared with max 37.3 mm) and in having less proportion of individuals with the first pair of postmentals in contact (46% vs. 76%). It further differs in having fewer upper and lower labial scales (ANOVA comparison of ULS and LLS significant, $P < 0.001$), by a genetic distance of 12.7% and 20.8% in the mitochondrial *12S* and *cytb* genes, respectively (Tables 2 and S3), and by the absence of allele sharing in the *c-mos* and *MC1R* nuclear gene regions analysed here (Fig. S3). It can be clearly differentiated from all the other species of *Asaccus* described to date (*A. andersoni*, *A. elisae*, *A. caudivolvulus*, *A. gardneri*, *A. granularis*, *A. griseonotus*, *A. iranicus*, *A. kermanshahensis*, *A. kurdistanensis*, *A. margaritae*, *A. montanus*, *A. nasrullahi*, *A. platyrhynchus*, *A. saffinae*, *A. tangestanensis*, *A. zagrosicus*) by its smaller size (SVL max. 33.6 mm vs. 39.4–71) and by the absence of enlarged dorsal tubercles on back, occiput, upper arm and elsewhere.

Description of the holotype. BMNH2008.961 (Fig. 3.1). Specimen with the tip of the tongue missing (used for DNA extraction) and the tail partially broken. Data on all 15 morphological traits are provided in Table S4 (see supplemental material online). Adult male, SVL 31.43 mm, depressed head and body, well-marked neck, limbs and tail slender. Head length 26% of SVL and head width 66% of head length. Tail not regenerated, 1.3 times the SVL. Rostral scale twice as wide as high, entire but with a slight medial depression. Internasals in contact behind

rostral, each one bordering nostril together with two postnasal, first labial and rostral scales. Two distinct depressions, one in the anterior loreal region and the other medially, just anterior to the eyes. Upper scales in the posterior loreal region enlarged (over twice the interorbitals) and occiput and supraorbital areas covered by homogeneous juxtaposed scales, rather smaller than those on the snout. Eye large, with a diameter of about 24% of the head length and half of the snout length. Palpebral fold anteriorly edged with large scales decreasing in size posteriorly, where a row of small ciliate scales projects from below and two rows of small granules separate the palpebral fold from the supraorbital region. Ear opening almost twice as long as wide with no denticulation on the border. Eleven upper labials on both sides and 8 lower labials on the right side and 9 on the left side. Mental scale large and triangular, extending backwards to the level of the sutures between the second and third lower labials. Two pairs of elongated postmental scales. The first pair is larger, touching the first lower labials anteriorly and running along the posterior edge of the mental scale without contacting each other medially, split by one small rounded scale. The second pair is bordered by inner postmentals and slightly separated from the second lower labials by two granular scales. Gular scales small and granular. Dorsum covered with uniform, rounded non-imbricated granules. Ventral scales slightly larger than dorsals and generally similar in shape, not flat and overlapping, distinctly larger in the interfemoral region. Fore and hind limbs covered with small granular scales. Digits with a series of enlarged scales beneath that become distally smaller and divided to form transverse series of two or three scales. Two terminal pads truncated and surrounding an exposed claw. Tail with rounded section, not vertically expanded and divided externally into segments covered above by small juxtaposed scales (equal size to dorsal body-scales) and with some irregular extended tubercles situated on the lateral margin of the segment. Ventral scales of tail enlarged and overlapping on the tail-base, becoming distally smaller and interspersed by smaller scales until the tip of the tail.

Colouration faded after fixation, pale whitish-yellow, and translucent underneath so that viscera are discernible. A dark stripe from the posterior border of the orbit until the neck, passing through the upper margin of the ear, and a small dark mark on the upper loreal region. Dorsum with five dark crossbands (one on neck, three between pairs of limbs and one on sacrum). Tail with seven dark transverse bands not extending onto ventral surface and decreasing in intensity distally, only the first three ones clearly visible. Colour in life much richer than in the preserved specimen (Fig. 3.1), pale pink with more evident pattern of dark brownish marks. Yellow shading encircling the eyes and surrounding all the above-described stripes present on the head area. Iris golden with dark venations and tail substantially yellow.

Variation. Data on all 15 morphological traits for the three paratypes (see above) are provided in Table S4 (see supplemental material online). Specimens BMNH2008.962 and IBES7576 with missing tail and specimen ONHM4234 with broken tail. In all three specimens, the tip of the tongue was cut and used for DNA extraction. All the specimens are very similar to each other, with more marked transverse bands on the body compared with the holotype and darker stripes on the head joining each other on the neck with the first crossbands.

Distribution and ecology. As a result of the intensive sampling across the Hajar Mountain range carried out between 2005 and 2016, *Asaccus arnoldi* sp. nov. has been found from latitude 23.219N in the Wadi Sareen Nature Reserve, close to Qurayyat (50 km south-east of Muscat, Oman), to latitude 22.107N in the Ash Sharqiyah South, around the Jebel Qahwan massif (see Fig. 1.1; Table S1, see supplemental material online). Thus, it can be considered an endemic species to the Eastern Hajars, isolated from its sister taxon *A. gallagheri* by the Semail Valley (the minimum distance between them is 100 km by air). *Asaccus arnoldi* sp. nov. has been found from sea level up to 1,683 m a.s.l. (localities 29 and 25, respectively), moving swiftly amongst the rocky terrain in mountains and coastal wadis, small cliffs on open hillsides and hiding in caves and fissures (Fig. 3.2). Strictly nocturnal, all specimens were captured during the night and avoided the beam of the flashlight, hiding cautiously in crevices and holes. This species is not very common and, even in places where it occurs, sometimes one researcher needs several hours to find one or two specimens.

Conservation status. Not evaluated.

Proposed common name. English: Arnolds' Leaf-toed Gecko;
Arabic: وزغـــة أرنولـــــد ورقيـــة الاصـــــبع

Discussion

With several species of reptile not found anywhere else in the world, the Hajar Mountains represent one of the top biodiversity hotspots in Arabia and an important refuge for montane species, some of them with clear affinities with the fauna of south-western Iran and neighbouring territories (Arnold, 1986; Balletto, Cherchi, & Gasperetti, 1985; Dakhteh et al., 2007; de Pous et al., 2016a; Garcia-Porta et al., 2017; Gasperetti, 1988; Gasperetti, Stimson, Miller, Ross, & Gasperetti, 1993; Kapli et al., 2008, 2015; Krause et al., 2013; Mandaville, 1977; Metallinou et al., 2012, 2014; Simó-Riudalbas et al., 2017; Tamar et al., 2016b; Yousofi et al., 2015). As shown in previous molecular studies of the genus *Asaccus* (Carranza et al., 2016;

Papenfuss et al., 2010), the Arabian species are not monophyletic, with the Jebel Akhdar endemic *Asaccus montanus* branching as sister taxon to all other species included in the phylogenetic analyses. Pending the inclusion of the remaining species of *Asaccus*, these results suggest a provisional Arabian origin for the genus, which has undergone a substantial radiation across the Zagros and the Hajar Mountains (Fig. 1.2). This research also provided the first evidence for the existence of high genetic differentiation within populations of *Asaccus* from the northernmost section of the Hajar Mountains, revealing the existence of two new species of the *A. caudivolvulus* species complex living across very short distances (Carranza et al., 2016). In the present study, we have uncovered a new speciation event which occurred more than 6 Ma on the opposite extreme of the Hajar Mountains, involving populations previously described as *A. gallagheri*.

Asaccus arnoldi sp. nov. is the smallest species of the genus, measuring less than 33.6 mm from snout to vent. Similar to its sister taxon, *A. gallagheri*, it is characterized by the absence of enlarged tubercles throughout its body and the presence of sexual dimorphism in tail colouration, with yellow tails in males and banded black and white tails in females. In fact, both *Asaccus* species from the Hajar Mountains are morphologically similar, presenting very conserved proportions in terms of body shape. Despite the apparent morphological stasis, the genetic distances inferred from the mitochondrial genes are of similar magnitude to other interspecific distances within the genus *Asaccus* (Table 2 and Table S3, see supplemental material online). Moreover, the lack of shared haplotypes in the two nuclear markers analysed further supports the conclusion that the two species have been genetically isolated for a long time without gene flow (Fig. S3, see supplemental material online). The first-step species delimitation approach included in this work also reveals great levels of intraspecific genetic variability, identifying up to five deep lineages living in allopatry: three within *A. gallagheri* and two within *A. arnoldi* sp. nov. (Fig. 1.1, 1.3 and Table S1, see supplemental material online). However, we prefer to apply a conservative approach until more material is available and have decided not to describe them as independent taxa. The main reasons are the presence of allele sharing in at least one of the two nuclear genes and lack of any morphological diagnostic characters between the divergent mitochondrial lineages. The ancestral area reconstruction suggests that the first speciation event occurred in the Eastern Hajars, where lineages 4 and 5 of *A. arnoldi* sp. nov. are currently distributed. Afterwards, range expansion progressed northwards, from the Jebel Akhdar to the Musandam Peninsula, giving rise to the three lineages detected within *A. gallagheri* (Fig. S2, see supplemental material online). A similar phylogeographic pattern has already been reported for other two endemic geckos from the Hajar Mountains: *Trachydactylus hajarensis* (de Pous et al., 2016a) and *Pristurus rupestris rupestris* (Garcia-Porta et al., 2017).

Regarding habitat occupation, *A. arnoldi* sp. nov. has a smaller environmental niche with a unique component that differentiates it from *A. gallagheri* and that is likely to be related to the supported variation of temperature and precipitation. These results highlight the climatic distinctiveness of the only known area inhabited by *A. arnoldi* sp. nov. With a total area of 10,436 km^2, the Eastern Hajars constitute almost half of the total area of the Hajar Mountains. Extending from Jebel Qahwan to the northwest, the Eastern Hajars are isolated from the Jebel Akhdar by the Semail Valley and limits with the Sharqiyah Sands to the south-east (Fig. 1.1). The discovery of these distinct populations reinforces the importance of this relatively poorly studied area of the Hajar Mountains as a centre of diversification for this and other reptile groups such as *Hemidactylus* (Carranza & Arnold, 2012), *Trachydactylus* (de Pous et al., 2016a) and *Pristurus* (Garcia-Porta et al., 2017). Despite these recent findings, the knowledge of its fauna and flora is still deficient, especially if one compares it with the much better-studied areas of Oman, such as the Jebel Akhdar (Harrison, 1976, 1977). In contrast to the Western Hajars that do not present a single protected area, the Eastern Hajars contain five protected areas in the mountains and surrounding areas (Al Sareen, Ras al Shajer, Al Saleel, Jebel Qahwan and the Turtle reserve) with a total area of 1382.26 km^2. Interestingly, the two divergent lineages detected within *A. arnoldi* sp. nov. have already been found in two protected areas. The specimen collected in the Al Sareen Nature Reserve (locality 25, Fig. 1.1, Table S1, see supplemental material online) belongs to lineage 4, while two other localities found within the Jebel Qahwan Protected Area belong to lineage 5 (localities 30 and 31; Fig. 1.1, Table S1, see supplemental material online). Al Sareen, a Protected Area of ~785 km^2 created primarily for the conservation of the Arabian Tahr, is also home to a new isolated species within the *P. r. rupestris* species complex (candidate species 16; Garcia-Porta et al., 2017). These results exemplify how some emblematic species such as the Arabian Tahr can act as 'umbrella species' and contribute to the protection of other, less visible, but equally relevant species. The relatively high level of genetic variability between lineages 4 and 5 of *A. arnoldi* sp. nov. and the six candidate species endemic to the Eastern Hajars found within the diversification of the *P. r. rupestris* species complex (Garcia-Porta et al., 2017), suggest that the Eastern Hajars are still poorly explored despite their interest from a biodiversity point of view.

Our findings present the advantage of combining molecular, morphological and macroecological data to investigate the existence of morphologically very similar species, an integrative approach that has already been done to uncover hidden diversity in Arabia,

resulting in several taxonomic changes and new species descriptions (see for example, Badiane et al., 2014; Busais & Joger, 2011a, 2011b; Carranza et al., 2016; Carranza & Arnold, 2012; de Pous et al., 2016b; Garcia-Porta et al., 2017; Metallinou & Carranza, 2013; Papenfuss et al., 2010; Simó-Riudalbas et al., 2017; Šmíd et al., 2013, 2015, 2016; Tamar, Šmíd, Göçmen, Meiri, & Carranza, 2016c; Vasconcelos & Carranza, 2014). The present study also highlights the diversity of the genus *Asaccus* in south-east Arabia, with up to seven endemic species occurring in the Hajar Mountains and stresses its relevance from a conservation point of view. Additional taxonomic work combining carefully planned fieldwork from geographically intervening areas together with molecular, morphological and ecological analyses should be applied to clarify species boundaries for the lineages identified within *A. gallagheri* and *A. arnoldi* sp. nov.

Acknowledgements

We wish to thank Ali Alghafri, Sultan Khalifa, Hamed Al Furkani, Johnnes Els, Margarita Metallinou, Thomas Wilms, Jiri Smíd, Raquel Vasconcelos, Roberto Sindaco, Philip de Pous and Fèlix Amat for assisting in sample collection in the field. Special thanks are due to Saleh Al Saadi, Ahmed Said Al Shukaili, Mohammed Al Shariani, Ali Al Kiyumi, Mohammed Abdullah Al Maharmi and the other members of the Nature Conservation Department of the Ministry of Environment and Climate, Sultanate of Oman for their help and support. We also wish to thank the following people for their help with the shipment of tissue samples: J. Vindum from the California Academy of Sciences (CAS), USA; C. Spencer from the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, USA. Thanks also to Hessa Saif Al Shamsi for the Arabic translation. Specimens were collected and manipulated with the authorization and under control and permission of the governments of Oman (Ministry of Environment and Climate Affairs, MECA) and the United Arab Emirates (Environment and Protected Areas Authority, Government of Sharjah). Specimens were captured and processed following the guidelines and protocols stated in the collecting permits and agreements obtained from the competent authorities (see references below). Members of the government supervised collecting activities. All efforts were made to minimize animal suffering. All the necessary collecting and export permits for this study in Oman were issued by the Nature Conservation Department of the Ministry of Environment and Climate Affairs, Oman (Refs: 08/2005; 16/2008; 38/2010; 12/2011; 13/2013; 21/2013) and the research in the United Arab Emirates was done under the supervision and permission of the Environment and Protected Areas Authority, Government of Sharjah. This work was supported by the Ministerio de Economía y Competitividad, Spain (co-funded by FEDER) under grant numbers CGL2012-36970 and CGL2015-70390-P; Ministry of Environment and Climate Affairs under Grant number 22412027; Secretaria d'Universitats i Recerca del Departament d'Economia i Coneixement de la Generalitat de Catalunya under grant number 2014-SGR-1532; MSR is funded by a FPI grant from the Ministerio de Economía y Competitividad, Spain (BES-2013-064248); PT is funded with a grant from Fundação para a Ciência e Tecnologia with reference SFRH/BPD/93473/2013.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Ministerio de Economía y Competitividad, Spain (co-funded by FEDER) under [grant numbers CGL2012-36970], [grant numbers CGL2015-70390-P]; Ministry of Environment and Climate Affairs under [grant number 22412027]; Secretaria d'Universitats i Recerca del Departament d'Economia i Coneixement de la Generalitat de Catalunya under [grant number 2014-SGR-1532]; MSR is funded by a FPI grant from the Ministerio de Economía y Competitividad, Spain [grant number BES-2013-064248]; PT is funded with a grant from Fundação para a Ciência e Tecnologia with reference [grant number SFRH/BPD/93473/2013].

Supplemental data

Supplemental data for this article can be accessed here: https://doi.org/10.1080/14772000.2017.1403496.

References

Afrasiab, S. R., & Mohamad, S. I. (2009). A study on cave-dwelling geckos in Iraq, with the description of a new species from Saffine mountain: (Reptilia: Gekkonidae). *Zoology in the Middle East*, *47*, 49–56.

Ahmadzadeh, F., Flecks, M., Carretero, M. A., Böhme, W., Ihlow, F., Kapli, P., … Rödder, D. (2016). Separate histories in both sides of the Mediterranean: Phylogeny and niche evolution of ocellated lizards. *Journal of Biogeography, 43*, 1242–1253.

Arnold, E. N. (1972). Lizards with northern affinities from the mountains of Oman. *Zoologische Meded Leiden, 47*, 111–128.

Arnold, E. N. (1977). The scientific results of the Oman flora and fauna survey 1975. Little-known geckoes (Reptilia: Gekkonidae) from Arabia with descriptions of two new species from the Sultanate of Oman. *Journal of Oman Studies Special Report, 1*, 81–110.

Arnold, E. N. (1986). A key and annotated checklist to the lizards and amphisbaenians of Arabia. *Fauna of Saudi Arabia*, *8*, 385–435.

Arnold, E. N., & Gallagher, M. D. (1977). The scientific results of the Oman flora and fauna survey 1975. Reptiles and amphibians from the mountains of northern Oman with special reference to the Jebel Akhdar region. *Journal of Oman Studies Special Report, 1*, 59–80.

Arnold, E. N., & Gardner, A. S. (1994). A review of the middle eastern leaf-toed geckoes (Gekkonidae: *Asaccus*) with descriptions of two new species from Oman. *Fauna of Saudi Arabia, 14*, 424–441.

Badiane, A., Garcia-Porta, J., Červenka, J., Kratochvíl, L., Sindaco, R., Robinson, M. D., … Carranza, S. (2014). Phylogenetic relationships of Semaphore geckos (Squamata: Sphaerodactylidae: *Pristurus*) with an assessment of the taxonomy of *Pristurus rupestris. Zootaxa, 3835*, 33–58.

Balletto, E., Cherchi, M. A., & Gasperetti, J. (1985). Amphibians of the Arabian Peninsula. *Fauna of Saudi Arabia, 7*, 318–392.

Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n−dimensional hypervolume. *Global Ecology and Biogeography, 23*, 595–609.

Bosworth, W., Huchon, P., & McClay, K. (2005). The Red Sea and Gulf of Aden Basins. *Journal of African Earth Sciences, 43*, 334–378.

Brinkmann, K., Patzelt, A., Dickhoefer, U., Schlecht, E., & Buerkert, A. (2009). Vegetation patterns and diversity along an altitudinal and a grazing gradient in the Jabal al Akhdar mountain range of northern Oman. *Journal of Arid Environments*, *73*, 1035–1045.

Busais, S., & Joger, U. (2011a). Molecular phylogeny of the gecko genus *Hemidactylus* Oken, 1817 on the mainland of Yemen: (Reptilia: Gekkonidae). *Zoology in the Middle East, 53*, 25–34.

Busais, S. M., & Joger, U. (2011b). Three new species and one new subspecies of *Hemidactylus* Oken, 1817 from Yemen (Squamata, Gekkonidae). *Vertebrate Zoology, 61*, 267–280.

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

Carranza, S., Simó-Riudalbas, M., Jayasinghe, S., Wilms, T., & Els, J. (2016). Microendemicity in the northern Hajar Mountains of Oman and the United Arab Emirates with the description of two new species of geckos of the genus *Asaccus* (Squamata: Phyllodactylidae). *PeerJ, 4*, e2371.

Clement, M., Posada, D., & Crandall, K. A. (2000). TCS: A computer program to estimate gene genealogies. *Molecular Ecology, 9*, 1657.

Dakhteh, S. M. H., Kami, H. G., & Anderson, S. C. (2007). *Stenodactylus khobarensis* (Haas, 1957): An addition to the Iranian herpetofauna (Reptilia: Squamata: Gekkonidae). *Russian Journal of Herpetology, 14*, 229–231.

de Pous, P., Machado, L., Metallinou, M., Červenka, J., Kratochvíl, L., Paschou, N., … Carranza, S. (2016a). Taxonomy and biogeography of *Bunopus spatalurus* (Reptilia; Gekkonidae) from the Arabian Peninsula. *Journal of Zoological Systematics and Evolutionary Research*, *54*, 67–81.

de Pous, P., Simó-Riudalbas, M., Els, J., Jayasinghe, S., Amat, F., & Carranza, S. (2016b). Phylogeny and biogeography of Arabian populations of the Persian Horned Viper *Pseudocerastes persicus* (Duméril, Bibron & Duméril, 1854). *Zoology in the Middle East, 62*, 231–238.

de Queiroz, K. (1998). The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. In D. J. Howard & S. H. Berlocher (Eds.), *Endless forms: Species and speciation* (pp. 57–75). Oxford: Oxford University Press.

de Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology, 56*, 879–886.

Dixon, J. R., & Anderson, S. C. (1973). A new genus and species of gecko (Sauria: Gekkonidae) from Iran and Iraq. *Bulletin of the Southern California Academy of Sciences, 72*, 155–160.

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution, 29*, 1969–1973.

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*, 1.0-19/r51. Retrieved from http://R-Forge.R-project.org/projects/splits/ (accessed 7 November 2017).

Felsenstein, J. (1985). Confidence-limits on phylogenies: An approach using the bootstrap. *Evolution, 39*, 783.

Flot, J. F. (2010). Seqphase: A web tool for interconverting phase input/output files and fasta sequence alignments. *Molecular Ecology Resources, 10*, 162–166.

Fujisawa, T., & Barraclough, T. G. (2013). Delimiting species using single-locus data and the Generalized Mixed Yule Coalescent approach: A revised method and evaluation on simulated data sets. *Systematic Biology*, *62*, 707–24.

Gamble, T., Bauer, A. M., Colli, G. R., Greenbaum, E., Jackman, T. R., Vitt, L. J., & Simons, A. M. (2011). Coming to America: Multiple origins of New World geckos. *Journal of Evolutionary Biology*, *24*, 231–244.

Gamble, T., Bauer, A. M., Greenbaum, E., & Jackman, T. R. (2008). Evidence for Gondwanan vicariance in an ancient clade of gecko lizards. *Journal of Biogeography, 35*, 88–104.

Gamble, T., Greenbaum, E., Jackman, T. R., & Bauer, A. M. (2015). Into the light: Diurnality has evolved multiple times in geckos. *Biological Journal of the Linnean Society*, *115*, 896–910.

Gamble, T., Greenbaum, E., Jackman, T. R., Russell, A. P., & Bauer, A. M. (2012). Repeated origin and loss of adhesive toepads in geckos. *Public Library of Science ONE, 7*, e39429.

Garcia-Porta, J., Morales, H. E., Gómez-Díaz, E., Sindaco, R., & Carranza, S. (2016). Patterns of diversification in islands: A comparative study across three gecko genera in the Socotra Archipelago. *Molecular Phylogenetics and Evolution, 98*, 288–299.

Garcia-Porta, J., Simó−Riudalbas, M., Robinson, M., & Carranza, S. (2017). Diversification in arid mountains: Biogeography and cryptic diversity of *Pristurus rupestris rupestris* in Arabia. *Journal of Biogeography, 44*, 1694–1704.

Gardner, A. (1999). The Reptiles and Amphibians of Oman: Herpetological history and current status. In *The Natural History of Oman: A Festschrift for Michael Gallagher* (pp. 65–88). Leiden: Backhuys Publishers.

Gardner, A. S. (1994). A new species of *Asaccus* (Gekkonidae) from the mountains of northern Oman. *Journal of Herpetology*, *28*, 141–145.

Gardner, A. S. (2013). *The Amphibians and Reptiles of Oman and the UAE*. Frankfurt am Main: Chimaira.

Gasperetti, J. (1988). Snakes of Arabia. *Fauna of Saudi Arabia, 9*, 169–450.

Gasperetti, J., Stimson, A. F., Miller, J. D., Ross, J. P., & Gasperetti, P. R. (1993). Turtles of Arabia. *Fauna of Saudi Arabia*, *13*, 70–367.

Ghazanfar, S. A. (1991). Vegetation structure and phytogeography of Jabal Shams, an arid mountain in Oman. *Journal of Biogeography, 18*, 299–309.

Glennie, K. (2006). *Oman's Geological Heritage*. London: Stacey International Publishers.

Gómez-Díaz, E., Sindaco, R., Pupin, F., Fasola, M., & Carranza, S. (2012). Origin and in situ diversification in *Hemidactylus* geckos of the Socotra Archipelago. *Molecular Ecology, 21*, 4074–4092.

Harrigan, R. J., Mazza, M. E., & Sorenson, M. D. (2008). Computation vs. cloning: Evaluation of two methods for haplotype determination. *Molecular Ecology Resources, 8*, 1239–1248.

Harrison, D. (1976). The Oman Flora and Fauna Survey 1975. *Journal of Oman Studies, 1*, 181–186.

Harrison, D. (1977). The scientific results of the Oman Flora and Fauna Survey 1975. *Journal of Oman Studies Special Report*, *1*, 10–11.

Hawlitschek, O., & Glaw, F. (2013). The complex colonization history of nocturnal geckos (*Paroedura*) in the Comoros Archipelago. *Zoologica Scripta, 42*, 135–150.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology, 25*, 1965–1978.

Huelsenbeck, J. P., & Rannala, B. (2004). Frequentist properties of bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic Biology, 53*, 904–913.

Kapli, P., Lymberakis, P., Crochet, P., Geniez, P., Brito, J. C., Almutairi, M., … Poulakakis, N. (2015). Historical biogeography of the lacertid lizard *Mesalina* in North Africa and the Middle East. *Journal of Biogeography, 42*, 267–279.

Kapli, P., Lymberakis, P., Poulakakis, N., Mantziou, G., Parmakelis, A., & Mylonas, M. (2008). Molecular phylogeny of three *Mesalina* (Reptilia: Lacertidae) species (*M. guttulata*, *M. brevirostris* and *M. bahaeldini*) from North Africa and the Middle East: Another case of paraphyly? *Molecular Phylogenetics and Evolution, 49*, 102–110.

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution, 30*, 772–780.

Krause, V., Ahmadzadeh, F., Moazeni, M., Wagner, P., & Wilms, T. M. (2013). A new species of the genus *Tropiocolotes* Peters, 1880 from western Iran (Squamata: Sauria: Gekkonidae). *Zootaxa, 3716*, 22–38.

Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, *33*, 1870–1874.

Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., & Calcott, B. (2016). PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, *34*, 772–773.

Lemey, P., Rambaut, A., Drummond, A. J., & Suchard, M. A. (2009). Bayesian phylogeography finds its roots. *Public Library of Science Computational Biology, 5*, e1000520.

Mandaville, J. (1977). The scientific results of the Oman flora and fauna survey 1975. Plants. *Journal Oman Studies Special Report, 1*, 229–267.

Metallinou, M., Arnold, E. N., Crochet, P.-A., Geniez, P., Brito, J. C., Lymberakis, P., … Carranza, S. (2012). Conquering the Sahara and Arabian deserts: Systematics and biogeography of *Stenodactylus* geckos (Reptilia: Gekkonidae). *BioMed Central Evolutionary Biology*, *12*, 1–17.

Metallinou, M., & Carranza, S. (2013). New species of *Stenodactylus* (Squamata: Gekkonidae) from the Sharqiyah Sands in northeastern Oman. *Zootaxa, 3745*, 449–468.

Metallinou, M., Červenka, J., Crochet, P.-A., Kratochvíl, L., Wilms, T., Geniez, P., … Carranza, S. (2015). Species on the rocks: Systematics and biogeography of the rock-dwelling *Ptyodactylus* geckos (Squamata: Phyllodactylidae) in North Africa and Arabia. *Molecular Phylogenetics and Evolution, 85*, 208–220.

Metallinou, M., Vasconcelos, R., Šmíd, J., Sindaco, R., & Carranza, S. (2014). Filling in the gap: Two new records and an updated distribution map for the Gulf Sand gecko Pseudoceramodactylus khobarensis Haas, 1957. *Biodiversity Data Journal. 2*, e4011. doi:10.3897/BDJ.2.e4011

Milá, B., Surget-Groba, Y., Heulin, B., Gosá, A., & Fitze, P. S. (2013). Multilocus phylogeography of the common lizard *Zootoca vivipara* at the Ibero-Pyrenean suture zone reveals lowland barriers and high-elevation introgression. *BioMed Central Evolutionary Biology, 13*, 1.

Papenfuss, T. J., Jackman, T. R., Bauer, A. M., Stuart, B. L., Robinson, M. D., & Parham, J. F. (2010). Phylogenetic relationships amongst species of Southwest Asian Leaf-toed geckos (*Asaccus*). *Proceedings of the California Academy of Sciences, 61*, 587–596.

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., … Vogler, A. P. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology*, *55*, 595–609.

R Development Core Team. (2016). *R: A language and environment for statistical computing*. Vienna: The R Foundation for Statistical Computing. ISBN: 3-900051-07-0. http://www.R-project.org/ (accessed 5 December 2017).

Rambaut, A., Suchard, M. A., Xie, D., & Drummond, A. J. (2014). *Tracer* v1.6. Retrieved from http://beast.bio.ed.ac.uk/Tracer (accessed 7 November 2017).

Rastegar-Pouyani, N. (1996). A new species of *Asaccus* (Sauria: Gekkonidae) from the Zagros mountains, Kermanshahan province, western Iran. *Russian Journal of Herpetology, 3*, 11–17.

Rastegar-Pouyani, N., Nilson, G., & Faizi, H. (2006). A new species of *Asaccus* (Sauria: Gekkonidae) from Kurdistan province, western Iran. *Hamadryad, 30*, 141–150.

Reid, N. M., & Carstens, B. C. (2012). Phylogenetic estimation error can decrease the accuracy of species delimitation: A Bayesian implementation of the general mixed Yule-coalescent model. *BioMed Central Evolutionary Biology, 12*, 196.

Silvestro, D., & Michalak, I. (2012). raxmlGUI: A graphical front-end for RAxML. *Organisms Diversity & Evolution*, *12*, 335–337.

Simó-Riudalbas, M., Metallinou, M., de Pous, P., Els, J., Jayasinghe, S., Péntek-Zakar, … Carranza, S. (2017). Cryptic diversity in *Ptyodactylus* (Reptilia: Gekkonidae) from the northern Hajar Mountains of Oman and the United Arab Emirates uncovered by an integrative taxonomic approach. *Public Library of Science ONE, 12*, e0180397.

Sindaco, R., Metallinou, M., Pupin, F., Fasola, M., & Carranza, S. (2012). Forgotten in the ocean: Systematics, biogeography and

evolution of the *Trachylepis* skinks of the Socotra Archipelago. *Zoologica Scripta, 41*, 346–362.

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). *Public Library of Science ONE, 8*, e64018.

Šmíd, J., Moravec, J., Kratochvíl, L., Nasher, A. K., Mazuch, T., Gvoždík, V., & Carranza, S. (2015). Multilocus phylogeny and taxonomic revision of the *Hemidactylus robustus* species group (Reptilia, Gekkonidae) with descriptions of three new species from Yemen and Ethiopia. *Systematics and Biodiversity*, *13*, 346–368.

Šmíd, J., Shobrak, M., Wilms, T., Joger, U., & Carranza, S. (2016). Endemic diversification in the mountains: Genetic, morphological, and geographical differentiation of the *Hemidactylus* geckos in southwestern Arabia. *Organisms Diversity & Evolution*, *17*, 267–2865.

Stamatakis, A. (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics, 22*, 2688–2690.

Stephens, M., Smith, N. J., & Donnelly, P. (2001). A new statistical method for haplotype reconstruction from population data. *The American Journal of Human Genetics, 68*, 978–989.

Tamar, K., Carranza, S., Sindaco, R., Moravec, J., Trape, J.-F., & Meiri, S. (2016a). Out of Africa: Phylogeny and biogeography of the widespread genus *Acanthodactylus* (Reptilia: Lacertidae). *Molecular Phylogenetics and Evolution*, *103*, 6–18.

Tamar, K., Scholz, S., Crochet, P.-A., Geniez, P., Meiri, S., Schmitz, A., … Carranza, S. (2016b). Evolution around the red sea: Systematics and biogeography of the agamid genus *Pseudotrapelus* (Squamata: Agamidae) from North Africa and Arabia. *Molecular Phylogenetics and Evolution, 97*, 55–68.

Tamar, K., Šmíd, J., Göçmen, B., Meiri, S., & Carranza, S. (2016c). An integrative systematic revision and biogeography of *Rhynchocalamus* snakes (Reptilia, Colubridae) with a description of a new species from Israel. *PeerJ, 4*, e2769.

Torki, F. (2010). Beschreibung eines neuen *Asaccus* (Reptilia: Phyllodactylidae) aus der Provinz Lorestan, Iran. *Sauria*, *32*, 3–16.

Torki, F., Ahmadzadeh, F., Ilgaz, Ç., Avcı, A., & Kumlutaş, Y. (2011a). Description of four new *Asaccus* Dixon and Anderson, 1973 (Reptilia: Phyllodactylidae) from Iran and Turkey. *Amphibia-Reptilia, 32*, 185–202.

Torki, F., Fathinia, B., Rostami, H. A., Gharzi, A., & Nazari-Serenjeh, F. (2011b). Beschreibung eines neuen *Asaccus* (Sauria: Phyllodactylidae) aus dem Iran. *Sauria, 33*, 51–62.

Uetz, P., Goll, J., & Hallerman, J. (2017). *The reptile database*. Retrieved from http://www.reptile–database.org (accessed 24 March 2016).

Vasconcelos, R., & Carranza, S. (2014). Systematics and biogeography of *Hemidactylus homoeolepis* Blanford, 1881 (Squamata: Gekkonidae), with the description of a new species from Arabia. *Zootaxa, 3835*, 501–527.

Warren, D. L., Glor, R. E., & Turelli, M. (2008). Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution*, *62*, 2868–2883.

Werner, Y. (2006). Retraction of *Ptyodactylus* Goldfuss from the fauna of Iran and its replacement by a new species of *Asaccus* Dixon and Anderson (Reptilia: Sauria: Gekkonidae). *Hamadryad, 30*, 135–140.

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. *Molecular Phylogenetics and Evolution*, *25*, 361–371.

Yousofi, S., Rastegar-Pouyani, E., & Hojati, V. (2015). Phylogenetic relationships amongst populations of *Pristurus rupestris* Blanford, 1874 (Sauria: Sphaerodactylidae) in southern Iran. *Turkish Journal of Zoology, 39*, 1–6.

Associate Editor: Mark Wilkinson