



Ancient diversification, biogeography, and the role of climatic niche evolution in the Old World cat snakes (Colubridae, *Telescopus*)

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ABSTRACT

The process of species diversification is often associated with niche shifts in the newly arising lineages so that interspecific competition is minimized. However, an opposing force known as niche conservatism causes that related species tend to resemble each other in their niche requirements. Due to the inherent multidimensionality of niche space, some niche components may be subject to divergent evolution while others remain conserved in the process of speciation. One such possible component is the species' climatic niche. Here, we test the role of climatic niche evolution on the diversification of the Old World cat snakes of the genus *Telescopus*. These slender, nocturnal snakes are distributed in arid and semiarid areas throughout Africa, southwest Asia and adjoining parts of Europe. Because phylogenetic relationships among the *Telescopus* species are virtually unknown, we generated sequence data for eight genetic markers from ten of the 14 described species and reconstructed a time-calibrated phylogeny of the genus. Phylogenetic analyses indicate that the genus is of considerably old origin that dates back to the Eocene/Oligocene boundary. Biogeographical analyses place the ancestor of the genus in Africa, where it diversified into the species observed today and from where it colonized Arabia and the Levant twice independently. The colonization of Arabia occurred in the Miocene, that of the Levant either in the Late Oligocene or Early Miocene. We then identified temperature and precipitation niche space and breadth of the species included in the phylogeny and examined whether there is phylogenetic signal in these climatic niche characteristics. Despite the vast range of the genus and its complex biogeographic history, most *Telescopus* species have similar environmental requirements with preference for arid to semiarid conditions. One may thus expect that the genus' climatic niche will be conserved. However, our results suggest that most of the climatic niche axes examined show no phylogenetic signal, being indicative of no evolutionary constraints on the climatic niche position and niche breadth in *Telescopus*. The only two variables with positive phylogenetic signal (temperature niche position and precipitation niche breadth) evolved under the Brownian motion model, also indicating no directional selection on these traits. As a result, climatic niche evolution does not seem to be the major driver for the diversification in *Telescopus*.

1. Introduction

The process of species diversification is accompanied by two contradictory forces that influence the level of ecological niche differentiation between newly arising lineages. One is niche conservatism, the tendency of species and clades to retain their niches over time and

resulting in related species being more similar to each other in their niche requirements than they are to more distant species (Wiens and Graham, 2005; Wiens et al., 2010). Niche conservatism is widespread in nature (Peterson et al., 1999; Peterson, 2011) and may be related to various patterns of niche and diversity dynamics, such as niche stasis (Alexander, 2013), phylogenetic signal in climatic niches (Hof et al.,

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2010), and spatial biodiversity gradients (Buckley et al., 2010). In contrast, speciation is often associated with niche divergence that allows species to expand or shift their niches and thus diversify. This may have a plethora of evolutionary causes, such as release of competitive pressures through island colonization (Diamond, 1970), acquisition of key innovations (Arakaki et al., 2011), and many others. The interplay between niche conservatism and niche divergence thus plays a key role in structuring the diversity of life on Earth. A pivotal role in this process plays the character of species spatial distributions. Species that originated in allopatry, which has been implicated as the predominant mode of speciation, often show signs of niche conservatism, while those that speciated sympatrically or parapatrically tend to diverge in their niche requirements (Kozak and Wiens, 2006 and references therein).

Arid biomes occupy a substantial portion of Earth's land surface, but compared to other biomes the diversity of life they support is relatively poor (Orme et al., 2005; Davies et al., 2008; Fritz and Rahbek, 2012). Yet, there are groups that thrive in arid conditions and reptiles are one such example. Of all vertebrates, squamate reptiles dominate deserts (Powney et al., 2010; Roll et al., 2017). Being ectothermic, they are greatly affected by the environmental conditions they live in. Because of the extreme conditions prevailing in deserts (high temperatures, low annual precipitation), desert-dwelling reptiles may already live at their physiological limits (Vale and Brito, 2015) and climate may, therefore, present one of the dominant selection forces (Angilletta, 2009).

Telescopus Wagler, 1830 is an Old World colubrid genus distributed in most of Africa and through the Arabian Peninsula to southwestern Asia and south-eastern Europe. They are slender, crepuscular or nocturnal snakes, occurring in savanna, desert and semidesert habitats (Disi et al., 2001; Baha El Din, 2006; Egan, 2007; Bates et al., 2014). The preference for arid conditions is most apparent in species that thrive in the deserts of southern Africa (*T. beetzi*), northern Africa (*T. obtusus*, *T. tripolitanus*), Arabia (*T. dhara*), the Levant (*T. hoogstraali*), and Iran (*T. rhinopoma*), while only some occur in more mesic environments (*T. variegatus*). However, it should be mentioned that some of the desert-dwelling species also seek mesic microhabitat pockets within their distribution (e.g., *T. obtusus* along the Nile in Egypt). In Africa, the distribution of the genus follows the arid dispersal corridors such as the Sahel, the North African corridor, and the corridor from the Horn of Africa to southwestern Africa (Kissling et al., 2016). This may suggest that *Telescopus* has strict climatic niche requirements possibly constrained by phylogenetic conservatism caused by, for example, stabilizing selection (Wiens and Graham, 2005). Also, one may expect that species that prefer extreme climatic conditions will tend to have similar range of conditions they can occupy (niche breadths), while niche breadths will differ in species with different climatic optima (Wiens et al., 2013).

Currently, there are 14 recognized species in *Telescopus* (Uetz et al., 2018). Together with the African genera *Crotaphopeltis*, *Dasyplepis*, *Dipsadoboa*, and *Toxicodryas* and the Asian genus *Boiga* the genus forms a distinct clade of the Colubridae, the boigas (Pyron et al., 2013; Zheng and Wiens, 2016). Until very recently, nothing was known about the phylogenetic relationships among *Telescopus* species as there was only one species investigated with phylogenetic methods - the European and eastern Mediterranean *T. fallax*. Some contributions in this regard were made by Figueroa et al. (2016) and Tonini et al. (2016), who each had four *Telescopus* species included in their snake-wide, respectively squamate-wide, phylogenies. According to these studies, *T. fallax* is the sister taxon to the remaining species, but otherwise the two studies were not congruent. Figueroa et al. (2016) found *T. beetzi* sister to the clade of *T. semiannulatus* and *T. dhara*, while Tonini et al. (2016) reconstructed *T. dhara* as sister to *T. semiannulatus* and *T. tripolitanus*. Although the results are not mutually exclusive and may be attributed to the different sets of taxa used in the two studies, they only accentuate our poor knowledge of the evolutionary history of the genus.

There are some taxonomic issues within *Telescopus* that can only be resolved with a robust phylogeny as a backbone. For instance, the

morphological uniqueness of *T. pulcher* resulted in its description as a distinct genus *Migiurtinophis* Scortecci, 1935. Because the species was until last year known only from the type material (Mazuch et al., 2018), the validity of the genus name could not be confirmed with the use of genetic methods. The specific/subspecific status of several taxa also remains uncertain. The Levantine and Iranian *T. hoogstraali*, *T. nigriceps*, and *T. tessellatus* are treated as subspecies of *T. fallax* by some authorities, while others consider them full species (Wallach et al., 2014 and references therein). Likewise, the northeast African *T. obtusus* and *T. somalicus* are sometimes regarded as species (Wallach et al., 2014), and in other instances as subspecies of *T. dhara* (Crochet et al., 2008).

In this study, we use an unprecedented genetic dataset to make a first attempt to infer the phylogenetic relationships and temporal and spatial origins of *Telescopus*. Furthermore, we obtain climatic data from individual point localities for all species included in the phylogeny and identify their relative positions and niche breadths in the climatic niche space. We test for phylogenetic signal and the model of evolution of the climatic niche characteristics to infer the role of climate in the evolutionary history of these arid-dwelling snakes.

2. Material and methods

2.1. Taxon sampling

We assembled a dataset comprising ten of the 14 described *Telescopus* species. Of these, we newly sequenced 41 samples of eight species, *T. dhara* (10 samples), *T. fallax* (14 samples), *T. hoogstraali* (6 samples), *T. nigriceps* (3 samples), *T. obtusus* (3 samples), *T. pulcher* (1 sample), *T. tripolitanus* (2 samples), and *T. variegatus* (2 samples). Five of these species (*T. hoogstraali*, *T. nigriceps*, *T. obtusus*, *T. pulcher*, *T. variegatus*) have never been included in a phylogenetic study. We also included six sequences of four *Telescopus* species (*T. beetzi*, *T. dhara*, *T. fallax*, and *T. semiannulatus*) that were available in GenBank. In total, the dataset comprised 47 *Telescopus* samples (Table 1). We added sequences of the closely related genera *Boiga* (16 species included), *Crotaphopeltis* (2 species), *Dasyplepis* (9 species), *Dipsadoboa* (5 species), and *Toxicodryas* (2 species) that have been repeatedly confirmed to form a clade with *Telescopus* (Pyron et al., 2013; Figueroa et al., 2016; Tonini et al., 2016). To root the tree, we used sequences of all species of the 'Western Palearctic clade' of Colubrinae (*sensu* Šmíd et al., 2015a; sequences of 54 species of the following genera were available on GenBank: *Bamanophis*, *Dolichophis*, *Eirenis*, *Hemerophis*, *Hemorrhois*, *Hierophis*, *Lytrochilus*, *Macropododon*, *Moparveldophis*, *Muhtarophis*, *Orientocoluber*, *Platycephalus*, *Rhynchocalamus*, *Spalerosophis*, *Wallaceophis*, *Wallopis*). All ingroup and outgroup taxa used in the analyses are listed in Table S1, along with respective GenBank accession numbers.

2.2. DNA extraction and sequencing

Genomic DNA was extracted from tissue samples preserved in ethanol using Geneaid Extraction Kit. We PCR-amplified five mitochondrial (mtDNA: 12S rRNA [12S], 16S rRNA [16S], cytochrome *b* [Cytb], NADH dehydrogenase subunits 2 [ND2] and 4 [ND4]) and three nuclear (nDNA: oocyte maturation factor MOS [Cmos], recombination activating protein 1 [Rag1], neurotrophin-3 [NT3]) markers using primers and PCR conditions provided in Table S2. Sanger sequencing of both the forward and reverse strands was carried out at Macrogen (Amsterdam, The Netherlands). Quality of sequences was checked and contigs were assembled in Geneious v.8 (Kearse et al., 2012). The ND4-flanking tRNAs amplified with the gene were removed. Heterozygous positions in the nDNA genes were identified by Heterozygote Plugin in Geneious and confirmed by eye based on the presence of two approximately equal peaks at a single nucleotide site, and were coded using IUPAC ambiguity codes.

As for the GenBank sequences, we initially downloaded all available data for *Telescopus* and the related genera (see above). For each gene, a

Table 1

Telescopus samples used in this study. Sample and voucher numbers are given as well as locality of origin for each sample. For respective GenBank accession numbers see [Table S1](#). Sample codes are those shown in the figures. Voucher codes refer to the following collections: BEV - CEFÉ – EPHE collection of the Biogeography and Ecology of the Vertebrates team in Montpellier, France; CUP - Charles University, Prague, Czech Republic; IBE - Institute of Evolutionary Biology, Barcelona, Spain; IRD - Institut de Recherche pour le Développement, Dakar, Senegal; LSUMN, LSUMZ - Louisiana State University Museum of Natural Science, Baton Rouge, USA; MVZ - Museum of Vertebrate Zoology, Berkeley, USA; MZCR - Museum of Comparative Zoology, Cambridge, USA; NMP - National Museum in Prague, Czech Republic; SMNH - Steinhardt Museum of Natural History, Tel Aviv University, Israel; TMHC - Tomas Mazuch herpetological collection (private), Dřiteč, Czech Republic; ZDEU - Zoology Department of the Ege University, Izmir, Turkey; ZMHRU Zoology Museum of Harran University, Şanlıurfa, Turkey.

Species	Sample	Voucher	Country	Locality	Lat	Long	Source
<i>T. beetzii</i>	MVZ226830	MVZ226830	Namibia	–	–	–	Figuerola et al. (2016)
<i>T. dhara</i>	CN3797	IBE CN3797	Oman	10 km N of Al Kamil	22.309	59.221	This study
<i>T. dhara</i>	CN3900	–	Oman	Al Khitaym	23.192	57.199	This study
<i>T. dhara</i>	CN3755	IBE CN3755	Oman	30 km SSW of Al Ashkharah	21.634	59.429	This study
<i>T. dhara</i>	CN8354	–	Oman	Wadi Ayoun	17.235	53.895	This study
<i>T. dhara</i>	CN10774	–	Oman	Wadi Ayoun	17.253	53.894	This study
<i>T. dhara</i>	34	–	Saudi Arabia	–	27.521	41.509	Alshammari and El-Abd unpubl.
<i>T. dhara</i>	JEM198	CUP JEM198	Yemen	Damqawt	16.572	52.834	This study
<i>T. dhara</i>	SMNH16922	SMNH16922	Israel	Hare Gilboa'	32.442	35.434	This study
<i>T. dhara</i>	SMNH16454	SMNH16454	Israel	Moshav Tomer	32.018	35.434	This study
<i>T. dhara</i>	SMNH16946	SMNH16946	Israel	Horvot Shivta	30.93	34.58	This study
<i>T. dhara</i>	SMNH17819	SMNH17819	Israel	Mo'a	30.547	35.169	This study
<i>T. fallax fallax</i>	SPM002394	–	Turkey	Bodrum	37.035	27.43	This study
<i>T. fallax cyprianus</i>	SPM003127	–	Cyprus	Vrysoules	35.077	33.878	This study
<i>T. fallax cyprianus</i>	2003_34	ZDEU2003/34	Cyprus	Dörtyol	35.176	33.765	This study
<i>T. fallax cyprianus</i>	127_3	ZMHRU2007/127_3	Cyprus	Karpaz	35.629	34.486	This study
<i>T. fallax cyprianus</i>	127_4	ZMHRU2007/127_4	Cyprus	Karpaz	35.629	34.486	This study
<i>T. fallax cyprianus</i>	127_5	ZMHRU2007/127_5	Cyprus	Karpaz	35.629	34.486	This study
<i>T. fallax syriacus</i>	SMNH17990	SMNH17990	Israel	Hare Gilboa'	32.453	35.428	This study
<i>T. fallax syriacus</i>	SMNH17887	SMNH17887	Israel	Merav	32.452	35.423	This study
<i>T. fallax syriacus</i>	SMNH17755	SMNH17755	Israel	Hare Gilboa'	32.436	35.438	This study
<i>T. fallax syriacus</i>	LEB49	–	Lebanon	El Barouk	33.712	35.69	This study
<i>T. fallax syriacus</i>	HLMD_S90	–	Jordan	Tasan	–	–	Nagy et al. (2003)
<i>T. fallax syriacus</i>	2007_142	ZMHRU2007_142	Turkey	Şanlıurfa	37.287	38.64	This study
<i>T. fallax syriacus</i>	2017_186	ZMHRU2017_186	Turkey	Şanlıurfa	37.42	39.715	This study
<i>T. fallax syriacus</i>	2017_191	ZMHRU2017_191	Turkey	Şanlıurfa	37.887	39.25	This study
<i>T. fallax syriacus</i>	2012_103	ZMHRU2012_103	Turkey	Şanlıurfa	37.212	37.969	This study
<i>T. fallax</i>	LSUMZ37967	LSUMZ37967	–	–	–	–	Lawson et al. (2005)
<i>T. hoogstraali</i>	SMNH15896	SMNH15896	Israel	Zomet HaNegev	31.07	34.84	This study
<i>T. hoogstraali</i>	SMNH15819	SMNH15819	Israel	Yeroham	31	34.92	This study
<i>T. hoogstraali</i>	SMNH16620	SMNH16620	Israel	Zomet Zipporim	30.829	34.743	This study
<i>T. hoogstraali</i>	SMNH15968	SMNH15968	Israel	Road no. 40 - Zin bridge	30.71	34.785	This study
<i>T. hoogstraali</i>	SMNH17082	SMNH17082	Israel	Mizpe Ramon	30.602	34.726	This study
<i>T. hoogstraali</i>	SMNH16873	SMNH16873	Israel	Nahal Nizzana	30.551	34.651	This study
<i>T. nigriceps</i>	2007_141	ZMHRU2007_141	Turkey	Kilis	36.746	37.253	This study
<i>T. nigriceps</i>	2007_143	ZMHRU2007_143	Turkey	Kilis	36.947	39.461	This study
<i>T. nigriceps</i>	2007_184	ZMHRU2007_184	Turkey	Şanlıurfa	36.846	37.111	This study
<i>T. obtusus</i>	TMHC841	TMHC841	Somaliland	9 km SE of Boorama	9.86	43.244	This study
<i>T. obtusus</i>	TMHC575	TMHC575	Ethiopia	11 km E of Metehara	8.915	40.029	This study
<i>T. obtusus</i>	TMHC842	TMHC842	Eritrea	Dissei Island	15.443	39.757	This study
<i>T. pulcher</i>	TMHC843	NMP75609	Somaliland	15 km SE of Sheikh	9.825	45.29	This study
<i>T. semiannulatus</i>	MCZR184862	MCZR184862	Namibia	–	–	–	Pyron unpubl.
<i>T. semiannulatus</i>	LSUMNS6065	LSUMNS6065	South Africa	–	–	–	Figuerola et al. (2016)
<i>T. tripolitanus</i>	BEV.9377	BEV.9377	Mauritania	–	20.554	–12.596	This study
<i>T. tripolitanus</i>	BEV.12821	BEV.12821	Morocco	–	28.48	–9.85	This study
<i>T. variegatus</i>	9195	IRD 9195.S	Senegal	Darfa Kunda	13.033	–14.633	This study
<i>T. variegatus</i>	2513N	IRD 2513.N	Chad	Laobida	9.217	15.117	This study

cursorry tree was constructed with the RAXML plugin in Geneious to identify sequences that were obviously erroneous, misidentified, contained misplaced insertions indicating poor quality of the original sequence, or produced exceptionally long branches on the gene trees suggesting any of the above. Those were then removed from the dataset. It should be noted that a worryingly large set of GenBank sequences could not be used for the above reasons; their list and reasoning for exclusion are given in [Table S3](#). For each species, we used sequences derived from the same individual whenever possible and only in a few cases we created chimeric sequences by combining markers from different individuals ([Table S1](#)). We did not use data for *Telescopus* produced by [Kyriazi et al. \(2013\)](#) because they only had one

mtDNA gene sequenced and we generated sequences of more loci for all the species included in their analyses.

2.3. Alignments

We used two different approaches to align the markers. The non-coding 12S and 16S we aligned with MAFFT v.7 ([Katoh and Standley, 2013](#)) using the Q-INS-I strategy that considers the secondary structure of RNA. The remaining six protein-coding genes were aligned using TranslatorX ([Abascal et al., 2010](#)) that first translates the DNA sequences into amino acids, aligns these amino acids and then back-translates the alignment to nucleotides. Gblocks ([Castresana, 2000](#))

were applied to the 12S and 16S alignments to trim poorly aligned regions with indels and long ragged ends. No stop codons were present in the protein coding genes when translated using appropriate genetic codes.

2.4. Phylogenetic analyses and divergence time estimates

We reconstructed the phylogeny of *Telescopus* and related species by three means. Dataset 1 consisted of 135 samples, of which 47 were *Telescopus*, 34 species of the boigas, and 54 of the Western Palearctic clade. Phylogenetic analysis of the concatenated dataset 1 of 5888 bp (3830 bp mtDNA, 2058 bp nDNA) was conducted by maximum likelihood (ML) using RAxML v.7.3 (Stamatakis, 2006). The ML heuristic search included 100 random addition replicates and 1000 bootstrap pseudoreplications. The dataset was partitioned by gene and the GTRCAT model was applied to each partition. We also generated gene trees for individual loci with the same settings to assess whether the markers studied provide congruent phylogenetic signal.

Dataset 2 was similar to dataset 1 in that it contained all samples of the boigas and Western Palearctic clades, but *Telescopus* was reduced to one sample per species. Exceptions to this were *T. dhara*, *T. obtusus*, and *T. fallax* that showed considerable genetic differentiation and of which two samples (the former two species) and five samples (the latter) were retained (see Results below). These samples are indicated in Table S1. Dataset 2 that consisted of a total of 104 samples was used as an input for a Bayesian analysis run in BEAST 2.4.8 (Bouckaert et al., 2014). The concatenated dataset was partitioned by gene, and site and clock models were unlinked across partitions. Ambiguous nucleotide positions indicating heterozygotes present in the nDNA markers were included in the analysis. For each partition, we estimated the best nucleotide substitution model by the reversible-jump based method (the RB model; Bouckaert et al., 2013) with four gamma-distributed categories. The RB model jumps between models in a hierarchy of models without the need to choose a specific model *a priori*. To assess the clock-likeness of each partition, we tested for nucleotide substitution rate heterogeneity among lineages using a likelihood ratio test (LRT; Huelsenbeck and Crandall, 1997) implemented in MEGA v.7 (Tamura et al., 2013). Clock-likeness was statistically rejected for all markers, we therefore employed the relaxed lognormal clock model for all partitions. We applied the Yule process tree prior with the birth rate prior set to uniform (lower: 0, upper: 1000). Exponential distributions were selected for the clock parameter (ucldMean) priors, with the mean and initial value being 0.1. Gamma distributions with the alpha and beta values of 2 were chosen for the among-lineage rate heterogeneity parameters (ucldStdev).

The genus *Telescopus* is known from the fossil record with remains reported from several localities in Europe and Turkey and ranging in age from the Middle Miocene to the Pleistocene (ca. 0.5–16.5 million years ago [Mya]; Böhme and Ilg, 2003; Szyndlar, 2012; Čerňanský et al., 2017). Phylogenetic affiliations of the fossils remain only vaguely known, which renders them difficult to use for node-dating calibration or the recently developed fossilized birth-death model (Heath et al., 2014). Therefore, to estimate absolute ages of diversification events we used two calibration points within the Western Palearctic clade that have been previously used for calibrating colubrid phylogenies (Nagy et al., 2003, 2004; Tamar et al., 2016c). (1) The split between the western (*H. algirus*, *H. hippocrepis*) and eastern (*H. ravergeri*, *H. nummifer*) clades of *Hemorrhois* that is believed to have occurred when Afro-Arabia came in contact with Eurasia ca. 16–18 Mya; (2) the divergence of the *Hierophis* subgroup that currently includes all *Eirenis* species, the genus *Orientocoluber*, *Hierophis viridiflavus*, *H. gemonensis*, and *Dolichophis cypriensis* and which is dated to ca. 18 Mya based on paleontological evidence. We applied normal distributions to both node priors with the mean = 18.0 and standard deviation (sd) = 2.0 for the former calibration point and sd = 1.0 for the latter. We ran three independent runs, each for 10⁸ generations with parameters logged every 10⁴

generations. Stationarity, convergence of runs and effective sample size (ESS) were inspected in Tracer v.1.5 (Rambaut and Drummond, 2007). In each run, 10% of trees sampled in the posterior were discarded as burnin, which resulted in a total of 27,000 trees obtained from Log-Combiner from which the maximum clade credibility tree was identified using TreeAnnotator (both part of BEAST).

The third phylogenetic method performed was a coalescent-based species-tree estimation using StarBEAST2 (Ogilvie et al., 2017) implemented in the BEAST2 software. For this analysis, we generated dataset 3 that consisted of only *Telescopus* samples without outgroup taxa, as adding an outgroup is generally discouraged in Bayesian analyses (Drummond and Bouckaert, 2017). We reconstructed haplotypes of the nDNA loci using PHASE 2.1 (Stephens et al., 2001) with the probability threshold set to 0.7. SeqPHASE (Flot, 2010) was used for preparing the input files. Dataset 3 contained 90 samples (45 individuals; Table S1). Most species-tree methods, including StarBEAST2, require knowledge of the correct assignment of individuals to species. We assigned samples to species based on current taxonomy. An exception to this were samples of *T. fallax*, *T. hoogstraali*, and *T. nigriceps* that based on the results of analyses of datasets 1 and 2 form a clade with shallow divergences and the former species is paraphyletic with respect to the latter two (see Results below). Samples of these three species were thus all assigned to one tree tip representing the *fallax* species complex. StarBEAST2 does not support the RB substitution model, so we estimated the best model for each partition using PartitionFinder 1.1 (Lanfear et al., 2012) with the following settings: branch lengths linked, only models available in BEAST evaluated, model selection based on BIC. The resulting models were as follows: GTR + Γ for 12S; HKY + I + Γ for 16S, ND2, ND4, Rag1; TrN + I + Γ for Cytb; HKY + I for Cmos; K80 + I + Γ for NT3. GTR was used for Cytb and HKY for NT3 as the closest alternatives to the TrN and K80 models available in BEAST, respectively. The parameter for invariant sites (+I) was not included, as it is accounted for by the among-site rate variation parameter (+ Γ ; Mayrose et al., 2005). The 1/x distribution was chosen for the speciation rate prior. We assumed gamma-distributed priors (alpha = 2, beta = 2) for the base substitution parameters and uniformly-distributed mean species population size priors with the lower and upper bounds being 0 and 1000, respectively. Other StarBEAST2 settings were as described above for the BEAST analysis. All phylogenetic analyses were run through the CIPRES Science Gateway (Miller et al., 2010).

2.5. Biogeographic reconstructions

To estimate biogeographic origins of *Telescopus*, we performed likelihood-based analyses in BioGeoBEARS (Matzke, 2013) implemented in R (R Core Team 2014). As an input tree we used the tree inferred with dataset 2 from which we removed the Western Palearctic clade but retained the boigas to account for the origin of closely related taxa. We defined four discrete biogeographic areas based on the current distribution of the clade: (i) Africa, (ii) southern Arabia, (iii) eastern Mediterranean including northern Arabia, the Levant, Turkey and adjoining parts of Europe, and (iv) Asia (a state not present in *Telescopus*). We also tested an alternative scenario, in which we partitioned Africa into five smaller biogeographic regions based on the results of Linder et al. (2012), but it did not provide conclusive results, so we do not give more details on that here. Tree tips were assigned to these areas based on available range information for each species (Fig. 1). We applied all analytical approaches available in BioGeoBEARS, namely dispersal-extinction-cladogenesis (DEC; Ree and Smith, 2008), dispersal-vicariance analysis (DIVA; Ronquist, 1997), and BayArea (Landis et al., 2013). In all models we implemented the +J parameter, which allows new lineages to be directly established by colonization without the intermediate existence of a widespread ancestor. The fit of the models was assessed by the Akaike Information Criterion corrected for sample size (AICc; Akaike, 1973).

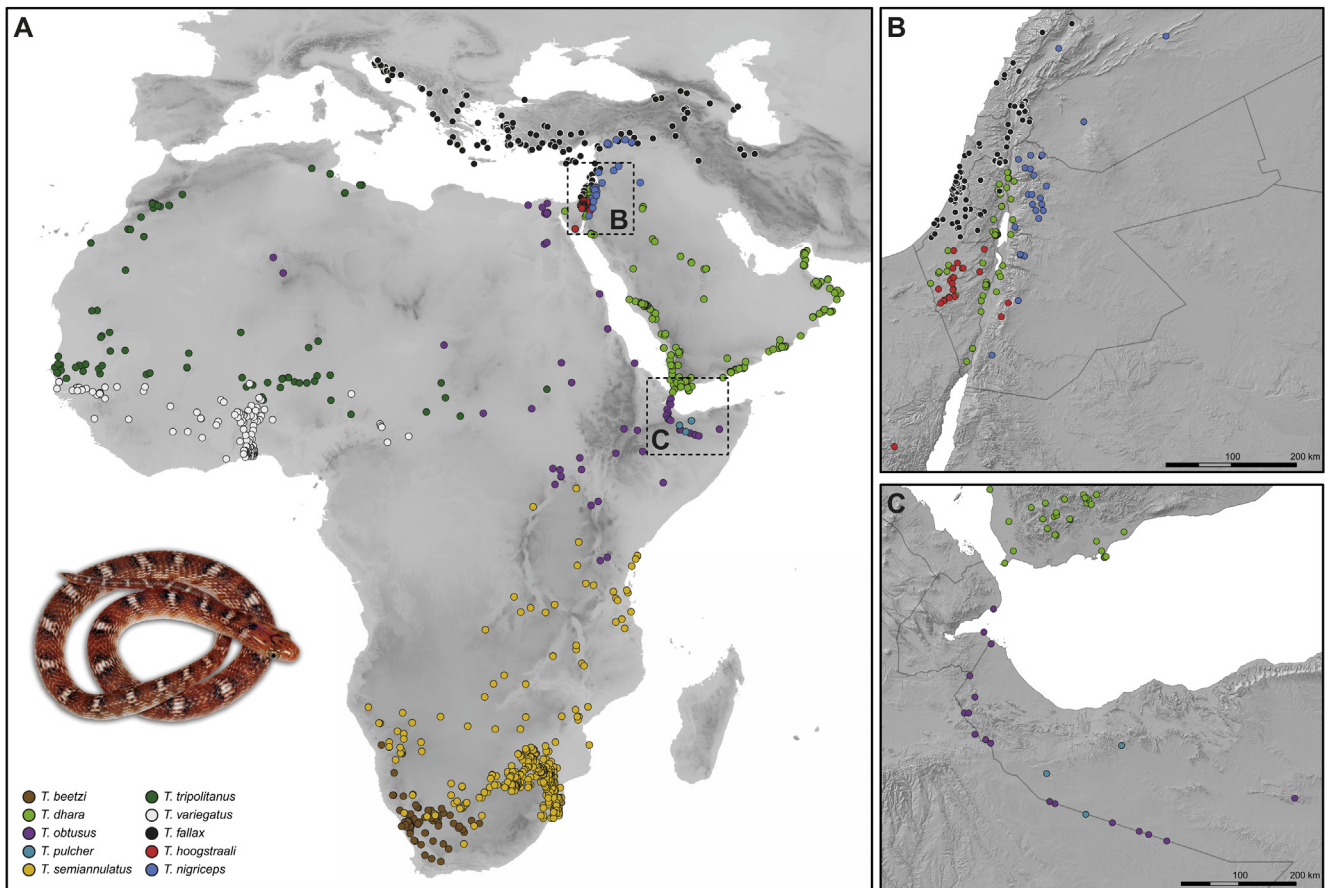


Fig. 1. Point localities showing the distributions of the *Telescopus* species used in this study. The distribution of the African subspecies of *T. dhara*, *T. d. somalicus*, is not shown as its taxonomic status is unclear. For locality data sources see Supplementary references. Specimen depicted is *T. pulcher* from Somaliland.

2.6. Identifying temperature and precipitation niche positions and niche breadths

Georeferenced occurrence data were obtained from sources listed in [Supplementary references](#) and are plotted in [Fig. 1](#). Locality data were carefully vetted to ensure that no records were outside known species ranges. The dataset was filtered to unique entries. For the ten species included in our analyses, we assembled a dataset of a total of 1348 unique localities, with a range of 3 (*T. pulcher*) to 381 (*T. semiannulatus*).

For each point locality, we extracted climate data from the CHELSA Bioclim layers ([Karger et al., 2017](#)) at 30 arc sec (~1 km) resolution using ArcGIS 10.4 ([ESRI, 2011](#)). The CHELSA Bioclim layers include global monthly mean temperature and precipitation patterns for the time period 1979–2013. We identified the temperature niche for each species by subsampling the temperature-related variables (Bio1, 2, 4–11; see <http://chelsa-climate.org/bioclim/> for explanations) from the dataset. To reduce the dimensionality of the variables, we then performed a principal component analysis (PCA) on the standardized temperature-related variables. Based on the broken-stick model ([Frontier, 1976](#)), we determined that the first two principal components were significant and factor scores of those were used for subsequent analyses. The same procedure was repeated with the precipitation-related variables (Bio12–19), for which the first two principal components were significant as well. We inferred the species' temperature and precipitation niche positions by calculating the mean value of the PC scores across sampled localities of each species. To identify the species niche breadth, we calculated the standard deviation of the PC scores for each species. It is important to note that analyses of datasets 1 and 2 both confirmed *T. fallax* to be paraphyletic with respect to *T. hoogstraali*

and *T. nigriceps* (see Results). Given this and the shallow phylogenetic structure observed in this clade, localities of these three species were pooled together and niche position and niche breadth were inferred for this clade as a whole (the *fallax* complex).

2.7. Analyses of niche position and niche breadth evolution

To test for evidence of a phylogenetic signal in the temperature and precipitation niche positions and niche breadths we calculated **Blomberg's *K*** ([Blomberg et al., 2003](#)) and **Pagel's λ** ([Pagel, 1999](#)) for the mean and sd values of the PC scores using the 'phytools' package in R ([Revell, 2012](#)). Blomberg's *K* values lower than 1 indicate that related species resemble each other less than expected under the Brownian motion (BM) model (i.e. no signal), while values larger than 1 indicate stronger trait similarity between related species. Pagel's λ generally ranges between 0 (no phylogenetic signal) and 1 (BM mode of evolution), however values larger than 1 can be adopted under some circumstances (see [Münkemüller et al., 2012](#) for a review). We used the Bayesian tree of dataset 2 as an input because it was time-calibrated and had all major nodes supported (see below). We pruned the tree to one tip for each species and one for the *fallax* complex. We visualized the relationship between *Telescopus* phylogeny and temperature and precipitation niche positions using the 'phenogram' and 'contMap' functions in phytools. To explore modes of niche evolution, we used the 'geiger' package in R ([Harmon et al., 2007](#)) to compare the BM, Ornstein–Uhlenbeck (OU), and early burst (EB) evolutionary models. The BM model is a purely neutral model of evolution, under which the trait value changes randomly, in both direction and distance, over any time interval ([Butler and King, 2004](#)). Under the OU model, traits evolve with an underlying phylogenetic pattern and are pulled towards an

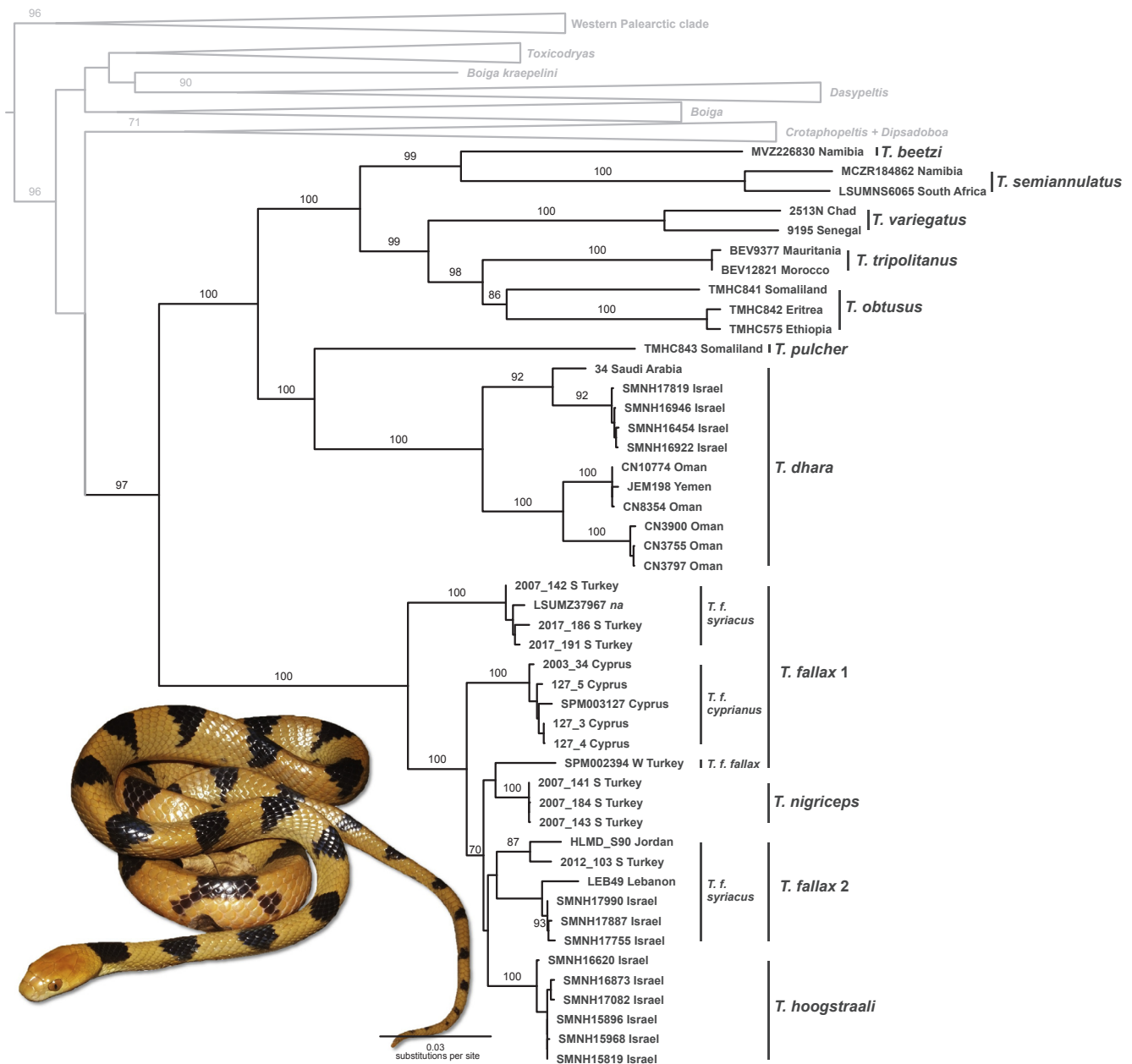


Fig. 2. Phylogenetic tree of dataset 1 resulting from the ML analysis. Only the genus *Telescopus* is shown in full, other related genera and the Western Palearctic clade are collapsed for brevity. Bootstrap values > 70 are shown above branches. Sample codes match those in Tables 1 and S1. For a complete tree see Fig. S1. Specimen depicted is *T. semiannulatus* from South Africa.

optimum value (Kozak and Wiens, 2010). The EB model assumes that highest rate of trait divergence occurred early in the clade's history and that rate evolution slows through time (Harmon et al., 2010).

3. Results

3.1. Phylogenetic analyses

The concatenated analyses of datasets 1 (Fig. 2 and S1) and 2 (Fig. 3 and S2) resulted in identical topologies with high bootstrap support and posterior probabilities (pp), respectively, for all *Telescopus* lineages except for some minor differences close to the tree tips. Monophyly of the genus was strongly supported in all analyses (bootstrap support 97, pp = 1; support values in this order hereafter). The three northernmost species (*T. fallax*, *T. hoogstraali*, *T. nigriceps*) formed a clade termed the *fallax* complex (100, 1), which was sister to the remaining Afro-Arabian

species (100, 1). In the latter clade, *T. pulcher* was sister to the Arabian *T. dhara* (100, 1), and these two species were sister to the remaining species (100, 1), all strictly African. This African clade comprised of two subclades, one of the southern *T. beetzi* and *T. semiannulatus* (99, 1), the other of the northern *T. variegatus*, which was sister (99, 1) to the clade of *T. tripolitanus* and *T. obtusus* (98, 1). In the *fallax* complex, four samples of *T. fallax* from southern Turkey were sister to all remaining samples (100, 1). Further, samples of *T. fallax cyprianus* from Cyprus formed a monophyletic group which was sister to the rest (70, 1). Relationships within this latter group were not supported in the analysis of dataset 1. According to the tree of dataset 2, *T. hoogstraali* split off next (-, 1) and the rest of the samples formed two groups, one of *T. nigriceps* and *T. fallax* from western Turkey, although weakly supported (36, 0.7), and the other of *T. fallax* from Israel and Lebanon and from southern Turkey and Jordan (34, 1). Of interest are deep divergences found in *T. dhara* and *T. obtusus*. In the former, samples from southern

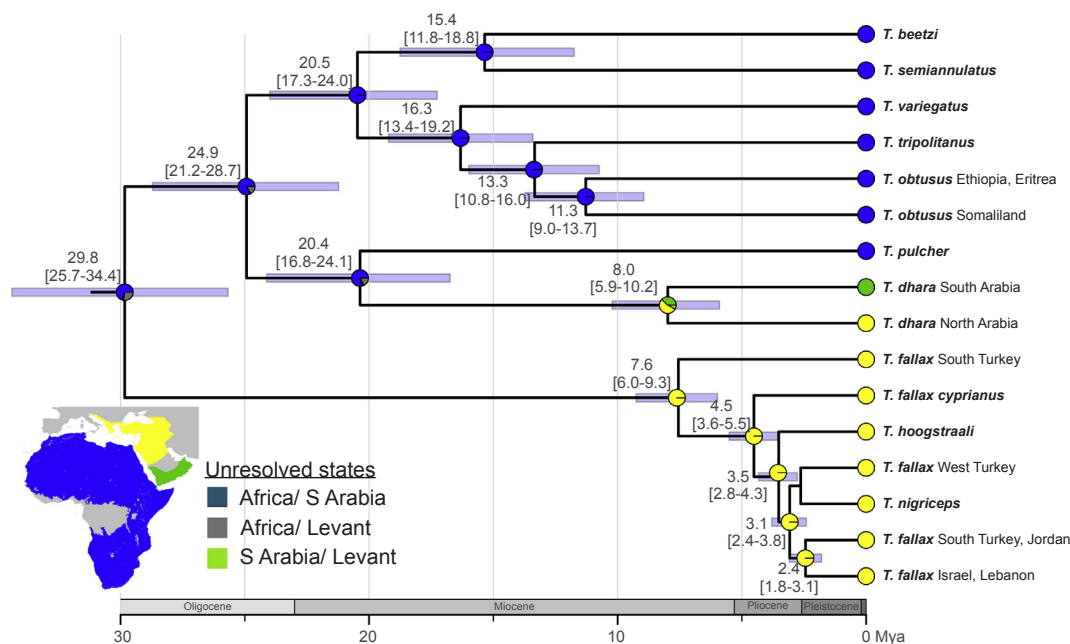


Fig. 3. Time-calibrated tree resulting from the Bayesian analysis of dataset 2, showing also results of the biogeographic reconstruction. Mean age estimates are given by nodes together with their 95% HPD intervals (also indicated by blue bars). The biogeographical origin of each lineage is marked at the tree tip with a color corresponding to the map in the lower left corner. Pie charts at the nodes show the probability of each ancestral area. All species of the related genera were included in the biogeographic analysis but are not depicted in the figure; for a complete biogeographic tree see Fig. S3. Age estimates and ancestral reconstructions are shown only for supported nodes ($pp > 0.95$). For the complete tree with original posterior probability values see Fig. S2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Arabian Peninsula (Oman, Yemen; ML bootstrap 100) were well separated from the northern populations from Israel and Saudi Arabia (ML bootstrap 92); in the latter, an even more pronounced divergence was observed between a sample from western Somaliland and two samples from central Ethiopia and coastal Eritrea (ML bootstrap 100).

Topology of the species-tree inferred with StarBEAST2 based on dataset 3 corresponded to that described above in all nodes but one. In the species-tree, the clade of *T. dhara* and *T. pulcher* ($pp = 1$) was reconstructed as sister to the *fallax* complex, albeit with inconclusive support ($pp = 0.91$; Fig. 4). Otherwise, the relationships between the African species of *Telescopus* were identical to the trees of datasets 1 and 2.

3.2. Divergence time estimations and biogeographic reconstructions

According to the divergence time estimations, the stem origin of *Telescopus* dates to the Eocene/Oligocene boundary (about 34 Mya; Fig. S2). The genus started diversifying approximately 30 Mya (95% highest posterior density [HPD]: 25.7–34.4; Fig. 3), which produced the monophyletic *fallax* complex and the Afro-Arabian clade. The present lineages that form the crown *fallax* complex diversified in the Late Miocene, at ca. 7.6 Mya (HPD: 6.0–9.3) with subsequent diversification events following in rapid succession during the Pliocene: separation of *T. f. cyprianus* 4.5 Mya (HPD: 3.6–5.5); separation of *T. hoogstraali* 3.5 Mya (HPD: 2.8–4.3), split between *T. nigriceps* + *T. fallax* from western Turkey and *T. fallax* from the Levant 3.1 Mya (HPD: 2.4–3.8). Diversification within the Afro-Arabian clade was more gradual. The separation of *T. pulcher* + *T. dhara* was estimated to the Late Oligocene, approximately 25 Mya (HPD: 21.2–28.7) and the split between these two to the Early Miocene, about 20 Mya (HPD: 16.8–24.1). The separation of the northern and southern populations of the Arabian *T. dhara* was estimated to 8 Mya (HPD: 5.9–10.2). In the African clade, the basal split took place 20.5 Mya (HPD: 17.3–24.0). All subsequent speciation events in this clade occurred in the Middle Miocene. *Telescopus variegatus* diverged from *T. tripolitanus* + *T. obtusus* about 16 Mya (HPD:

13.4–19.2), the two then split about 13 Mya (HPD: 10.8–16.0). The two clades of *T. obtusus* diverged 11 Mya (HPD: 9.0–13.7). The separation of *T. beetzi* and *T. semiannulatus* was estimated at approximately 15 Mya (HPD: 11.8–18.8).

The results of the biogeographic analyses showed that the DEC + J was the model that best explains the biogeographic history of *Telescopus* based on the weights of the AICc values (Table S4). The biogeographic origin of *Telescopus* was most likely African (probability 70%; 27% for an unresolved African or Levantine origin). Likewise, all but one nodes in the Afro-Arabian clade were estimated as of an African origin (Fig. 3; see Fig. S3 for a tree that includes the related genera). The node with non-African origin was the ancestor of *T. dhara*, whose origin was either in northern (probability 54%) or southern (probability 38%) Arabia. The origin of the *fallax* complex, as well as of all its inner nodes, was unequivocally reconstructed as the Levant (probability 100%).

3.3. Temperature and precipitation niche positions and niche breadths

Of the temperature-related variables, Bio11, Bio6 and Bio1 contributed most to the first principal component (PC1) of the PCA and Bio5, Bio10 and Bio9 to PC2. PC1 explained 58.3% and PC2 24.1% of the PCA variance. Based on the character of variables contributing to these axes, PC1 represents a continuum of “low to high mean temperatures in the cold season” and PC2 a continuum of “high to low mean temperatures in the warm season”. Of the precipitation-related variables, PC1 was most influenced by Bio12, Bio16 and Bio13 and explained 47.8% of the PCA variance. Bio15, Bio17 and Bio14 contributed most to PC2, which explained 29.4% of variance. PC1 of the precipitation niche space represents a “high to low mean precipitation in the wet season” axis, PC2 is a “aseasonal to seasonal” continuum (Figs. 5 and 6). In the temperature-based PCA, species of the *fallax* complex formed a cluster together with *T. beetzi*, while the other species were dispersed in the niche space. In the precipitation-based PCA, *T. variegatus* was clearly differentiated from the other species along both PC axes, while the others formed an undifferentiated cloud (Fig. 5).

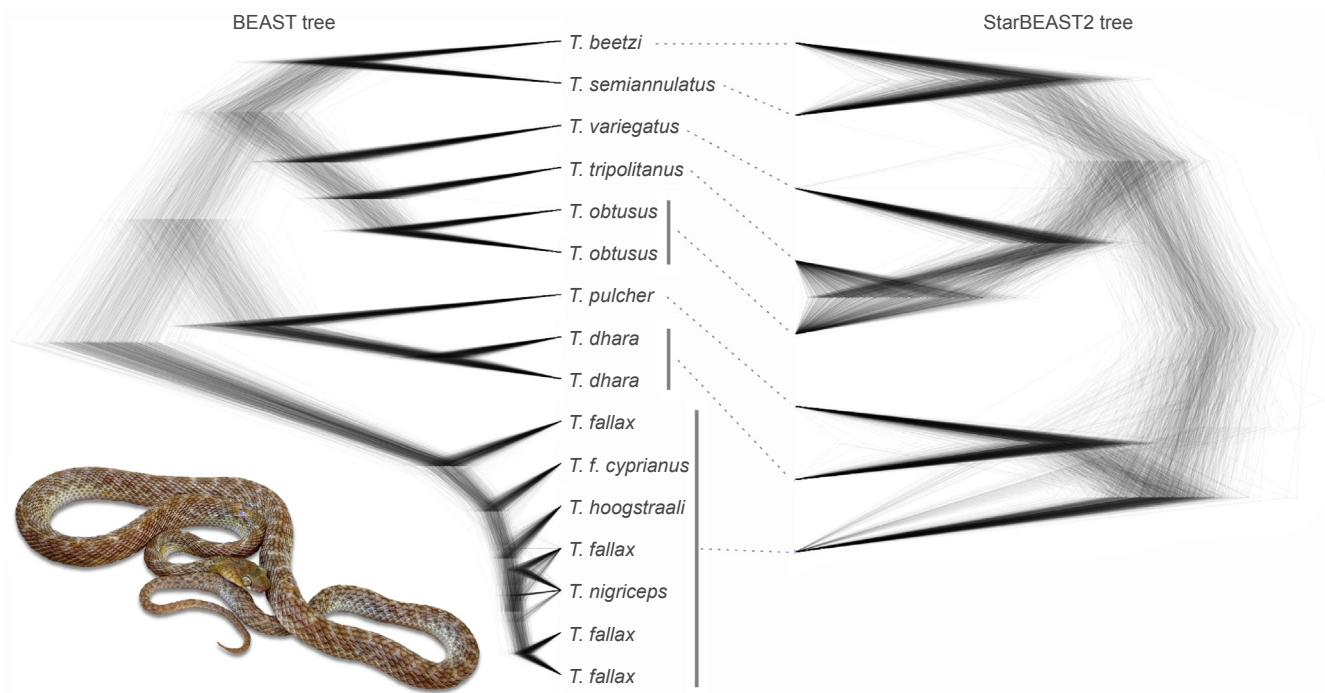


Fig. 4. Cloudograms of random sets of 1000 posterior trees resulting from the analysis of the concatenated dataset 2 (left) and the species-tree analysis of dataset 3 (right). Higher color densities represent higher levels of certainty that a given clade exists. Specimen depicted is *T. dhara* from Oman.

Regarding niche breadths, *T. pulcher* had of all species the narrowest niche breadth in both temperature and precipitation niche spaces, perhaps owing to the low number of localities the species is known from. On the contrary, *T. dhara* was the species with the widest temperature niche breadth along both PC axes. Precipitation niche breadth was widest for *T. obtusus* along PC1 and *T. fallax* along PC2 (Table 2).

the temperature niche position in PC1 and precipitation niche breadth in PC2 close to that expected under a BM model of evolution ($K > 1$, $\lambda \sim 1$). For all other variables, no phylogenetic signal was detected ($K < 1$, $\lambda \sim 0$; Table 3) indicating that these climatic niches are not dependent on the phylogeny. Considering models of divergence rates, the BM model provided the best fit for all climatic variables tested given the AICc statistic (Table 3).

3.4. Phylogenetic signal and modes of climatic niche evolution

Blomberg's K and Pagel's λ values showed phylogenetic signal for

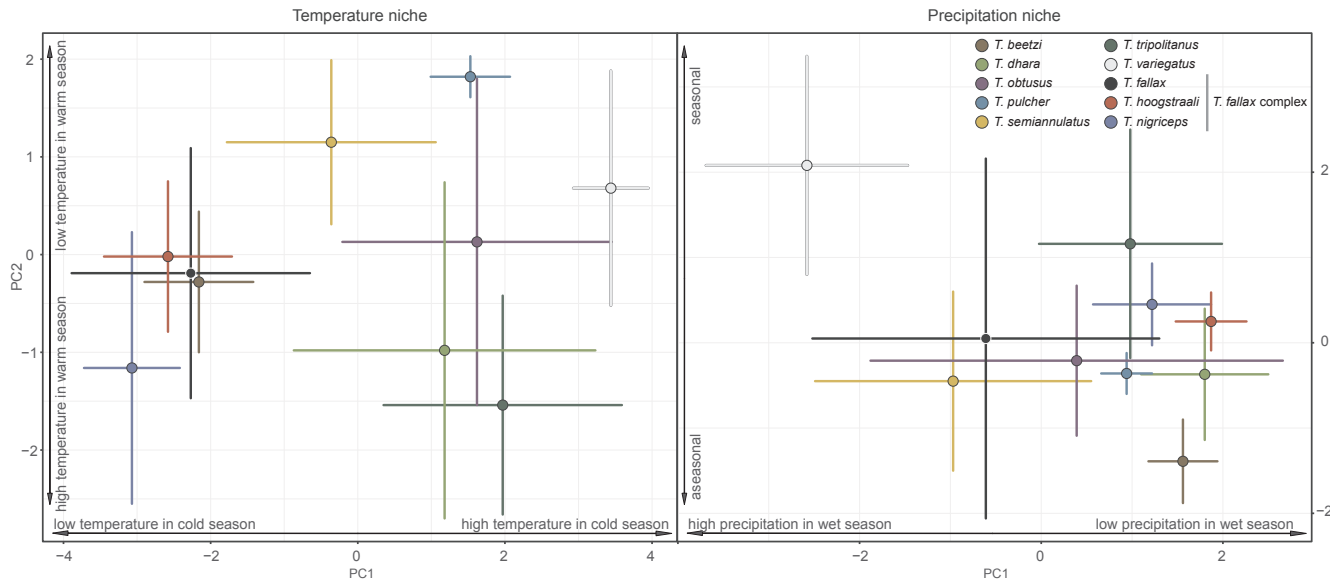


Fig. 5. The positions of the *Telescopus* species in the temperature and precipitation niche spaces as identified by the PCA of the respective Bioclim variables. Mean values of the PC scores were used as the niche space position of each species and are indicated by circles; sd values were used as proxies for niche breadths and are plotted as whiskers around the mean. Interpretation of the PC axes is indicated within each box. The three species of the *fallax* complex (*T. fallax*, *T. hoogstraali*, *T. nigriceps*) are plotted separately, although they were treated as one taxon in the niche position and niche breadth analyses.

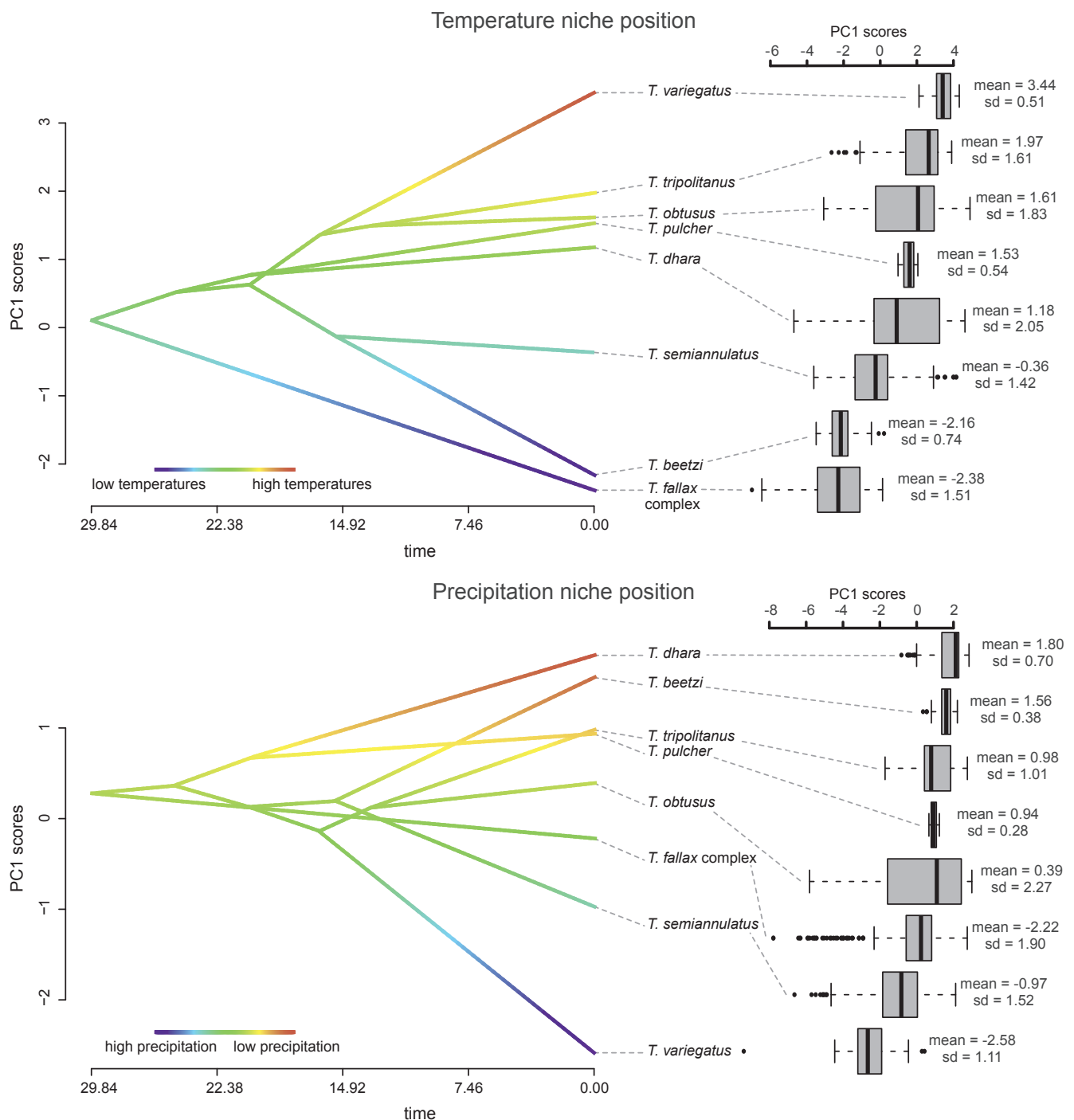


Fig. 6. Phenograms showing the first PCA components of the temperature (upper) and precipitation (lower) niche spaces in relation to the phylogeny of *Telescopus*. The horizontal axis reflects time in Mya. The boxplots on the right show the distribution of the PC1 scores and the mean and sd values for each species. The color schemes of the phenograms were reconstructed using the 'contMap' function in R and superimposed over the phenograms manually.

4. Discussion

In this study, we provide a comprehensive phylogenetic and biogeographic reconstruction and assessment of the climatic niche evolution of the colubrid genus *Telescopus*. Five of the ten species included here have never been sequenced before, namely *T. hoogstraali*, *T. nigriceps*, *T. obtusus*, *T. pulcher*, and *T. variegatus*, and some had only a single individual sequenced for mtDNA (*T. dhara*, *T. tripolitanus*). Producing a multilocus dataset of eight markers (both mtDNA and nDNA) for multiple individuals of most species provided a solid basis for robust inference of the evolutionary history of the genus as well as

the assessment of intraspecific variation.

4.1. Phylogenetic relationships within *Telescopus*

The topologies recovered in the different phylogenetic analyses that were based on different datasets were mostly congruent. The trees of dataset 1 and 2 show that the *fallax* complex represents a clade sister to the remaining taxa. Although evidence from previous studies is scarce because most of them only had one species included (*T. fallax*), recent phylogenetic analyses support this basal dichotomy between *T. fallax* and the Afro-Arabian species (Figuerola et al., 2016; Tonini et al., 2016).

Table 2

Niche positions and niche breadths of the *Telescopus* species along the first two principal components of the temperature and precipitation niche spaces. Niche positions were calculated as the mean values of the PC scores across sampled localities of each species, niche breadths as the standard deviations of these values. Values for species of the *fallax* complex are shown both separately for each species and together for the complex as a whole. For a graphical visualization see Fig. 5.

Species	Temperature niche				Precipitation niche			
	PC1		PC2		PC1		PC2	
	Niche position	Niche breadth	Niche position	Niche breadth	Niche position	Niche breadth	Niche position	Niche breadth
<i>T. beetzii</i>	−2.16	0.74	−0.28	0.72	1.56	0.38	−1.39	0.49
<i>T. dhara</i>	1.18	2.05	−0.98	1.72	1.80	0.70	−0.37	0.77
<i>T. fallax</i>	−2.27	1.62	−0.19	1.28	−0.61	1.91	0.05	2.11
<i>T. hoogstraali</i>	−2.58	0.87	−0.02	0.77	1.87	0.39	0.25	0.34
<i>T. nigriceps</i>	−3.07	0.66	−1.16	1.39	1.22	0.65	0.45	0.48
<i>T. obtusus</i>	1.62	1.83	0.13	1.67	0.39	2.27	−0.21	0.88
<i>T. pulcher</i>	1.53	0.54	1.82	0.21	0.94	0.28	−0.36	0.24
<i>T. semiannulatus</i>	−0.36	1.42	1.15	0.84	−0.97	1.52	−0.45	1.05
<i>T. tripolitanus</i>	1.97	1.62	−1.54	1.12	0.98	1.01	1.16	1.34
<i>T. variegatus</i>	3.44	0.51	0.68	1.20	−2.58	1.11	2.08	1.28
<i>T. fallax</i> complex	−2.38	1.51	−0.29	1.30	−0.22	1.90	0.11	1.93

Table 3

Estimates of Blomberg's *K* and Pagel's λ tests of phylogenetic signal and statistics for models of trait evolution. The temperature and precipitation niches were determined based on a PCA of temperature and precipitation-related Bioclim variables, respectively. For both, the first two components were analyzed. The mean and standard deviation were examined for each component as proxies of the niche-space position and niche breadth, respectively. The evolutionary models tested were: BM = Brownian motion, OU = Ornstein-Uhlenbeck, EB = Early burst. Models selected based on the AICc are in bold.

				Blomberg's <i>K</i>	Pagel's λ	Log likelihood			AICc		
						BM	OU	EB	BM	OU	EB
Temperature niche	PC1	Mean	1.15		1.79	−16.32	−16.32	−16.28	39.03	44.63	44.56
		Sd	0.76		7.4e−5	−7.91	−6.74	−7.91	22.21	25.49	27.81
	PC2	Mean	0.74		7.4e−5	−12.89	−11.63	−12.89	32.17	35.25	37.77
		Sd	0.84		7.4e−5	−6.05	−5.31	−6.05	18.51	22.62	24.11
Precipitation niche	PC1	Mean	0.76		7.4e−5	−14.97	−13.83	−14.97	36.35	39.66	41.95
		Sd	0.82		7.4e−5	−8.91	−8.07	−8.91	24.22	28.14	29.82
	PC2	Mean	0.85		7.4e−5	−12.11	−11.40	−12.11	30.62	34.81	36.22
		Sd	1.10		1.23	−5.56	−5.56	−5.46	17.53	23.13	22.93

The topological discrepancy between the trees based on concatenation (Figs. 2, 3) and the species-tree approach (Fig. 4), the latter recovering the *fallax* complex sister to *T. dhara* + *T. pulcher* (albeit with low support), may point towards the need of even more genomic markers to be sampled to fully understand the basal relationships in *Telescopus*.

Our broader sampling reveals that samples of *T. hoogstraali* and *T. nigriceps* are nested within those of *T. fallax*, rendering this species paraphyletic. Precise phylogenetic positions of the two species in the complex could not be resolved due to low nodal support, but in all analyses they clustered with populations of *T. fallax* from Turkey and the Levant. Interestingly, the clade in the *fallax* complex that branched off first also comprises samples from southern Turkey, demonstrating that the Levant is a major center of diversification for the *fallax* complex. All Cypriot samples assigned to the subspecies *T. f. cyprianus* form a genetically differentiated monophyletic group. A close relationship between *T. fallax*, *T. hoogstraali* and *T. nigriceps* has been suggested based on their morphological similarity (Göçmen et al., 2007; Amr and Disi, 2011). The latter two were sometimes even treated as subspecies of *T. fallax* (Zinner, 1977; Leviton et al., 1992; El-Oran et al., 1994), however more recent literature considers them species (Sindaco et al., 2013; Wallach et al., 2014). The sampling in our study does not permit drawing conclusions about the question of subspecies in *T. fallax sensu stricto* and it was also beyond the scope of this study. It is nonetheless worthwhile mentioning that the subspecific taxonomy is unsatisfactory and needs revision. Populations from southern Turkey and adjoining regions are currently assigned to the subspecies *T. f. syriacus* (Fig. 2), but the diversity of clades in the region is not reflected in the diversity of recognized taxa. Moreover, different lineages of the *fallax* complex

show virtually no genetic variation in two nDNA loci studies (Figs. S5, S7) and traces of introgression between the three species can be seen in the Rag1 gene (Fig. S6), indicating a complex phylogeographic history. Also, the two Iranian species that could not be included in the analyses, *T. rhinopoma* and *T. tessellatus*, are traditionally placed in the *fallax* complex on the basis of morphological evidence (Böhme, 1977). Therefore, sampling throughout the *fallax* complex range, inclusion of the missing species and detailed genetic screening will be necessary to be able to resolve this issue.

All the African and one Arabian species of *Telescopus* form a well-supported clade that is sister to the *fallax* complex. The clade is subdivided into two groups: one of *T. beetzii*, *T. semiannulatus*, *T. variegatus*, *T. tripolitanus*, and *T. obtusus*, all of which are of African distribution; and the other that comprises the Arabian *T. dhara* and the little-known *T. pulcher* from Somaliland. Monophyly of all species in this clade is well supported in all analyses. Given that *T. pulcher* is nested among other *Telescopus* species, there is no justification for recognizing it as a distinct genus, *Migiurtinophis*, despite its morphological uniqueness (Mazuch et al., 2018). The name *Migiurtinophis* is thus a junior synonym of *Telescopus*. The sister relationship of *T. beetzii* and *T. semiannulatus* contrasts with previous results of Figueroa et al. (2016), who recovered *T. semiannulatus* closer to *T. dhara*. The difference may be due to the larger sampling of *Telescopus* taxa used by us. All our results show that *T. dhara* and *T. obtusus* are not closely related species, and settle the dispute about whether *T. obtusus* is a subspecies of *T. dhara* or not (Crochet et al., 2008).

There is a considerable degree of genetic variation observed in *T. dhara* that clearly separates populations from southern Arabia from

those from northern Arabia, and an even greater variation in *T. obtusus* between geographically close samples. The genetic diversity observed in *T. dhara* underlines the notion that our understanding of the reptile diversity in the Arabian Peninsula is still vastly underestimated (Ficetola et al., 2013), as has been documented on many relevant studies (e.g. Šmíd et al., 2013, 2017; Metallinou et al., 2015; de Pous et al., 2016; Tamar et al., 2016a,b). The same is likely to be true for the arid Horn of Africa where *T. obtusus* forms two deeply separated lineages and where the unsampled *T. dhara somalicus* occurs. This regions has been shown to support unexpected diversity of locally endemic species of squamate reptiles (Lanza and Nistri, 2005; Wallach et al., 2010; Wagner et al., 2013a, 2013b; Šmíd et al., 2015b; Mazuch et al., 2016; Bates and Broadley, 2018) as well as other vertebrates (Freilich et al., 2014; Petzold et al., 2014; Šumbera et al., 2018). Interestingly, none of the other examples of deep diversification within the Horn of Africa dates as deep as the Middle Miocene as documented here for *T. obtusus*.

There are two more species of *Telescopus* that occur in Africa and that could not be included in the phylogenetic analyses because they are both known only from a few specimens. One is *T. gezirae* from eastern Sudan, the other is *T. finkeldeyi* from the arid savannas of Namibia and southwestern Angola. *Telescopus gezirae* shares numerous morphological apomorphies with *T. tripolitanus* (Broadley, 1994; Crochet et al., 2008), while *T. finkeldeyi* is supposed to belong to the biogeographically close south African taxa (Haacke, 2013). Detailed phylogeny of the south African species is underway (Haacke, pers. com.).

4.2. Historical biogeography

Our age estimates show that the genus *Telescopus* is of a considerably old origin that dates back to the Eocene/Oligocene boundary. The stem age of the genus as estimated here (approximately 34 Mya, Fig. S2) is in concert with other studies that were based on squamate-wide taxon sampling (31.8 Mya in Pyron and Burbrink, 2014; 27.9 Mya in Zheng and Wiens, 2016), which lends support to the age estimates inferred by us. The ancestor of *Telescopus* occurred in Africa, where the subsequent diversification also started.

Diversification in the Afro-Arabian clade occurred through a gradual series of events. It started in the Late Oligocene (about 25 Mya) when *T. dhara* + *T. pulcher* separated from the other African species. This was followed by two simultaneous events about 20.5 Mya, when *T. dhara* separated from *T. pulcher* and, at about the same time, the south African *T. beetzii* + *T. semianulatus* diverged from the ancestor of the north African *T. variegatus*, *T. tripolitanus* and *T. obtusus*. Diversification between southern and northern elements of the arid-adapted African biota is often assumed to be associated with the Middle Miocene climatic and habitat shifts towards more arid conditions and expansion of savannas (Douady et al., 2003; Leaché et al. 2014). The age estimated for the split between the southern and northern *Telescopus* clades predates these shifts considerably and places it into a climatically relatively stable period of the Early Miocene, well before the massive decline of the pan-African forests (Zachos et al. 2001; Kissling et al., 2012). However, the break-up of the pan-African forests was not a one-time event. It was a gradual process that started already in the Eocene as a result of the northern movement of the African continent and the closure of the Tethys Sea (Matthee et al., 2004). It is therefore possible that new ecological opportunities had opened up even before the massive contraction of the African forests and allowed the arid-adapted snakes to colonize new areas. Better understanding of the dispersal routes of *Telescopus* within Africa will require a denser sampling across the continent as well as sampling of taxa not sampled for this study (*T. dhara somalicus*, *T. finkeldeyi*, and *T. gezirae*).

The common ancestor of *T. dhara* and its sister species *T. pulcher* was of African origin. There are two biogeographic explanations for the presence of *T. dhara* in Arabia. The first plausible scenario is vicariance. Arabia was historically connected with the African landmass until the

Red Sea started emerging and subsequently expanding in the Oligocene (around 24–30 Mya; Courtillot, 1980; Bosworth et al., 2005), which marginally overlaps with the extreme upper bound of the HPD interval of the *T. dhara* – *T. pulcher* split (24 Mya). Alternatively, the ancestor of *T. dhara* might have colonized Arabia from Africa across the Red Sea sometime between 20.5 and 8 Mya either by transmarine dispersal or using land bridges. Temporary land bridge re-connections existed between Africa and Arabia after the two separated and enabled exchanges of fauna through the northern route across the Sinai Peninsula about 10–14 Mya or the southern route across the Bab el Mandeb Strait, approximately 5.3–10 Mya (Bosworth et al., 2005). Both vicariance and Afro-Arabian dispersal scenarios have been supported for various reptile groups, with vicariance having been documented for example in the saw-scaled vipers of the genus *Echis* (Pook et al., 2009) and the gecko genera *Hemidactylus* (Šmíd et al., 2013) and *Stenodactylus* (Metallinou et al., 2012). Transmarine or land bridge dispersals across the Red Sea were shown to have occurred in monitor lizards (*Varanus*; Portik and Papenfuss, 2012), spiny-tailed lizards (*Uromastix*; Tamar et al., 2018), cobras (*Naja*; Trape et al., 2009), *Pseudotrapelus* agamids (Tamar et al., 2016b), lacertids (genera *Acanthodactylus* and *Mesalina*; Kapli et al. 2015; Tamar et al. 2016a), among others. The crown diversification within *T. dhara* then occurred *in situ* in the Arabian Peninsula around 8 Mya.

In contrast to the old stem age of the *fallax* complex (29.8 Mya), the crown diversification of its extant lineages occurred with a long delay in the Late Miocene (7.6 Mya; Fig. 3). Considering the African origin of the genus, the stem age of the *fallax* complex, and current distributions of its species in the Levant, Turkey, western Iran, and southeastern Europe we conclude that the ancestor of the *fallax* complex dispersed from Africa to Eurasia across the closing Tethys Sea. The fossil record shows that *Telescopus* has been present in central Europe at least since the Middle Miocene (Szyndlar, 2012; Čerňanský et al., 2017). Although the fossils cannot be placed in a phylogenetic framework with certainty, they show affinities to *T. fallax* (Venczel, 1998; Szyndlar, 2005). This evidence of *Telescopus* being present in Europe narrows down the time frame for the transmarine dispersal to an era between approximately 29.8 and 16 Mya. It is well possible that the dispersal was enabled by the existence of a land connection between Afro-Arabia and Eurasia, termed the *Gomphotherium* land bridge (Rögl, 1998). The land bridge temporarily closed the Tethyan Seaways between the Mesopotamian Basin and East Mediterranean Basin during the Early to Middle Miocene (~17–19 Mya) and allowed bidirectional faunal exchanges (Harzhauser et al., 2007). The initial radiation of the *fallax* complex in the Levant during the Late Miocene was soon followed by a series of speciation events in the area. This time period was characteristic for extensive tectonic activity in the eastern Mediterranean (Over et al., 2004; Boulton and Robertson, 2007; Inwood et al., 2009), which might have been the trigger for the radiation. Indeed, a similar diversification pattern has been confirmed for various Levantine reptile taxa (Moravec et al., 2011; Kornilios et al., 2012; Ahmadvadeh et al., 2013; Tamar et al., 2015).

Of a particular biogeographic interest is the subspecies *T. f. cyprianus*, which is endemic to the island of Cyprus. Our results show that it branched off from the *fallax* complex in the Early Pliocene, about 4.5 Mya, which corresponds to the age estimate by Poulakakis et al. (2013). The HPD interval of the node age overlaps partially with the Messinian salinity crisis (MSC; 5.33–5.96 Mya), a geological event during which the Strait of Gibraltar sealed the Mediterranean Sea off from the Atlantic Ocean, which resulted in a drastic decrease of the sea level in the Mediterranean (Gautier et al., 1994; Krijgsman et al., 1999). Whether Cyprus was or was not connected to the Eurasian mainland during the MSC is still a matter of disputes (Steininger and Rögl, 1984; Popov et al., 2004; Jolivet et al., 2006). If the connection existed, dispersal from the mainland would be facilitated for many terrestrial organisms. But even if no land bridges existed at that time, lowered sea level would decrease the transmarine distance, which would in turn

result in higher rate of overseas dispersals to Cyprus. Available evidence suggests that no land bridge existed between Cyprus and Turkey since the Pliocene, even at times of minimum sea levels during the glacial cycles (Hadjisterkotis et al., 2000). Both MSC-associated and more recent transmarine dispersals have been suggested for some Cypriot reptiles (see Poulakakis et al., 2013 for a review). According to our results, the colonization of Cyprus by *Telescopus* could have happened during the MSC, but also slightly later once the island became more isolated. In parallel to the colonization of Cyprus, a land bridge dispersal was suggested for *Telescopus* as the most probable way of colonization of the island of Crete during the MSC (Kyriazi et al., 2013).

4.3. Climatic niche evolution in *Telescopus*

Our results show that of all the climatic variables tested, phylogenetic signal was found only for the niche position along temperature PC1 axis and niche breadth along precipitation PC2 axis. Blomberg's *K* and Pagel's λ values for these two variables suggest that evolution of these traits followed the BM model, which is also supported by the selection of models of trait evolution (Table 3). Although several *Telescopus* species share temperature niche positions (Fig. 6; PC1 score ~ 1.5), which might indicate that they are pulled towards a single climatic optimum on this niche axis (as would be evidenced by the OU model), our results suggest that evolution of this trait was more drift-like and not constrained by selection pressures (BM model of evolution). Interestingly, no phylogenetic signal was detected for any other climatic variable tested. In other words, there is no association between *Telescopus* phylogeny and most of the climatic niche characteristics of its species. In the two cases where phylogenetic signal was present (temperature PC1, precipitation PC2), the diversification process was random without selective constraints. The positions of species across the climatic gradient thus seem to have arisen from neutral biogeographic processes and be the result, not the cause, of adaptation to locally specific climatic conditions (Boucher et al., 2014).

The absence of phylogenetic signal for most niche breadth variables indicates no association between *Telescopus* phylogeny and the amount of niche space each species occupies; meaning that specialists are not clustered together and generalists are not clustered together. Breadth of precipitation PC2 is the variable that shows phylogenetic signal. Its evolution followed the BM evolutionary model, which again means that it was affected by genetic drift or selection in random directions, not pulled towards an optimum (Pearman et al., 2008). Although most *Telescopus* species are desert specialists, their level of climate specialization ranges from very narrow (*T. beetzii*, *T. pulcher*; Table 2, Fig. 5) to extremely wide (*T. fallax* complex, *T. variegatus*) without any obvious relation to the species niche positions. This supports Wiens et al.'s (2013) findings that species in more extreme environments (deserts in this case) are broadly distributed with wide niches and not specialized to narrow climatic bands. Generally, species with broad niches tend to have larger range sizes (Slatyer et al., 2013). It is therefore possible that the differences observed in precipitation niche breadths across *Telescopus* species correlate with their range sizes, as can be tentatively concluded from the two species with extreme ranges: *T. pulcher* has the smallest range and the narrowest temperature and precipitation niches in three of the four PC axes analyzed; on the contrary, *T. obtusus* with a vast distribution spans across a wide variety of temperature and precipitation conditions (Table 2, Fig. 5). This niche breadth–range size relationship was, however, not tested here because range sizes would be difficult to estimate for species with complex range shapes (*T. obtusus*, *T. tripolitanus*; Graham and Hijmans, 2006).

Phylogenetic signal is a commonly used measure of climatic niche evolution (Hof et al., 2010; Kamilar and Muldoon, 2010; Schnitzler et al., 2012). However, a possible caveat of our study is that we assume that species' niches can be described by a single continuous trait capturing the adaptation to those environmental conditions. We realize that this may over-simplify the dimensional complexity of the climatic

niche, but we believe that reducing dimensionality by PCA helped to better capture this complexity. We moreover build on a solid base of studies that have used similar rationale for identifying species niche positions and niche breadths (e.g. Quintero and Wiens, 2013; Lin and Wiens, 2017).

By inspecting the pattern of *Telescopus* species distributions (Fig. 1), it is apparent that most are allopatric or parapatric (which also applies to species not included in our analyses). Those, whose distributions overlap in the geographical space (e.g., *T. beetzii* and *T. semiannulatus*) differ in their climatic niche space (Fig. 5). If diversification in *Telescopus* was not mediated by climatic factors, other selection pressures may have played a more significant role. What factors were responsible for the diversification of these snakes awaits further exploration.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ympev.2019.01.015>.

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