Small and overlooked: Phylogeny of the genus *Trigonodactylus* (Squamata: Gekkonidae), with the first record of *Trigonodactylus arabicus* from Jordan

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**A B S T R A C T**

Geckos of the genus *Trigonodactylus* are widely distributed in the sand deserts of the Arabian Peninsula. Three species of this genus are currently recognized, with a fourth one, *Stenodactylus pulcher*, which placement within *Trigonodactylus* has been tentatively suggested, but not yet confirmed. We present a phylogenetic analysis of the genus *Trigonodactylus* with new specimens collected in central Saudi Arabia and southern Jordan. New genetic data has been generated from three mitochondrial markers to investigate the phylogenetic relationships of all species of the genus and to assess the putative generic assignment of *S. pulcher*. Our results confirm that *S. pulcher* indeed belongs within *Trigonodactylus*, branching as a sister lineage to all other species of the genus. The new samples cluster within *Trigonodactylus arabicus*, thus confirming the genetic homogeneity of the species across its large and seemingly inhospitable range. The new specimen collected in southern Jordan represents the first record for the country and a considerable range extension to the northwest from all previously reported localities. Our findings and discovery of a new species for Jordan highlight the need of more field surveys to be carried out in the underexplored parts of Jordan and northern Saudi Arabia, as these places still hold a potential for new discoveries and are crucial for understating the biogeography of the Arabian herpetofauna.

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1. Introduction

*Trigonodactylus* are small, nocturnal and psammophilous geckos. The genus was originally described for the species *Trigonodactylus arabicus* from Abqaiq, Saudi Arabia (Haas, 1957). Later on, Kluge (1967) synonymized *Trigonodactylus* with *Stenodactylus* based on the morphological similarity of the two genera. For about 50 years, this taxonomic conclusion was generally followed (e.g. Fujita and Papenfuss, 2011; Metallinou et al., 2012; Metallinou and Carranza, 2013) until recently, when Nazarov et al. (2018) resurrected *Trigonodactylus* for a clade comprising four species (*Stenodactylus arabicus*, *S. sharqiyahensis*, *S. persicus*, and tentatively *S. pulcher*). The latter was, however, missing in the phylogenetic analysis of Nazarov et al. (2018) and is still listed under its former generic name *Stenodactylus* in the Reptile Database (Uetz et al., 2021), despite that morphological and genetic evidence indicate...
a close relationship to *T. arabicus* and *T. sharqiyanensis* (see Arnold, 1980; Metallinou et al., 2012).

Members of the genera *Stenodactylus* and *Trigonodactylus* belong to one of the most characteristic and abundant herpetofaunal elements of North African and Arabian deserts, showing a clear Saharo-Arabian distribution pattern (Arnold, 1980; Sindaco and Jeremčenko, 2008; Metallinou et al., 2012). The four species of *Trigonodactylus* are, however, restricted only to the Arabian Peninsula, with *T. persicus* reaching Mesopotamia (Metallinou and Carranza, 2013; Nazarov et al., 2018). *Trigonodactylus arabicus* is widely distributed in the deserts of the Arabian Peninsula (Fig. 1). Besides central and eastern Saudi Arabia, from where it was described, it has been reported from Kuwait, Bahrain, Qatar, the United Arab Emirates, Oman, and Yemen (Delima and Al-Nasser, 2007; Gallagher, 1971; Arnold, 1980; Sindaco and Jeremčenko, 2008; Metallinou et al., 2012; Gardner, 2013; Carranza et al., 2018; Burriel-Carranza et al., 2019). It was recently reported from Khuzestan province in southwestern Iran (Fathinia et al., 2014), however this record very likely represents *T. persicus* (Nazarov, pers. comm.; Fathinia, pers. comm.).

Herein, we produce new genetic data for *Trigonodactylus* species to infer a complete phylogeny of the genus with the aim to finally confirming the generic assignment of *T. pulcher*. Alongside that, we provide a considerable range extension for *T. arabicus* that we report for the first time from the Hashemite Kingdom of Jordan and demonstrate the genetic homogeneity of this species across the largest sand-dune deserts of Arabia, suggesting the presence of high levels of gene-flow across this extreme and inhospitable habitat.

2. Material and methods

2.1. New material

Field work was carried out in Saudi Arabia and Jordan in June and September 2019, respectively. One *Trigonodactylus* specimen was collected in Jordan ca. 2 km E of Mudawwara (Fig. 2; sample JIR446, collected on 17.9.2019 at 29.32N 36.01E, 717 m a.s.l., and deposited in the National Museum Prague [voucher code NMP6V 76022], Czech Republic) and two specimens were collected in Saudi Arabia ca. 100 km NE of Riyadh (sample CN15785, collected at 25.21N 47.70E, 649 m a.s.l., and deposited at the Institute of Evolutionary Biology [IBECN15785], Barcelona, Spain; sample CN15789, collected at 25.147N, 47.56E, 665 m a.s.l., deposited at Taif University, Taif, Saudi Arabia). The specimens were stored in 96% ethanol.

2.2. DNA extractions, PCR and sequence alignment

Genomic DNA was extracted using the Tissue Genomic DNA Mini Kit (Geneaid, Taiwan). To be able to combine our results with previously published sequence data, we PCR-amplified and sequenced in both directions three mitochondrial markers: 12S rRNA (12S), 16S rRNA (16S), and cytochrome oxidase I (COI). Primers, their sequences, amplicon sizes and PCR conditions, and original references for all markers are provided in Table S1. Apart from sequencing the newly obtained samples, we also generated 17 new COI sequences for samples used in the study by Metallinou and Carranza (2013) and downloaded available sequences of all *Trigonodactylus* species from GenBank (Metallinou et al., 2012; Metallinou and Carranza, 2013; Nazarov et al., 2018). Five *Stenodactylus* species were used as outgroups. All samples and GenBank accessions used in this study are listed in Table S2. Geneious v.11 (Kearse et al., 2012) was used to edit and assemble the chromatograms. Sequences of COI were translated into amino acids and no stop codons were revealed, suggesting that no pseudogene was amplified. Each gene was aligned independently using the online version of MAFFT v.7 (Katoh et al., 2019). We applied the Q-INS-i strategy for the 12S and 16S genes because it considers the secondary structure of the RNA, while COI was aligned using default settings.
constant population tree prior with a 1/X population size prior (Drummond & Bouckaert, 2017). Gamma priors (alpha = 0.05, beta = 10) were used for all substitution rate parameters. The BI analysis ran three times for 3 × 10^6 generations with parameters and trees sampled every 3 × 10^4 generations. Convergence of runs, their stationarity and effective sample sizes of all estimated parameters were inspected in Tracer v.1.7.1 (Rambaut et al., 2018). In each run, 10% of posterior trees were discarded as burnin and the remaining trees were combined using LogCombiner. The Maximum clade credibility tree was then identified with TreeAnnotator (both programs are part of the BEAST package). To speed up the computational process, the BI analysis was set up to run through the CIPRES Science Gateway (Miller et al., 2010). Nodes that received UFBoot ≥ 95, SH-aLRT ≥ 80, and Bayesian posterior probability (pp) ≥ 0.95 were considered strongly supported.

Inter- and intraspecific uncorrected p-distances with pairwise deletion were estimated using MEGA X (Kumar et al., 2018) for the COI marker only, as it is the only overlapping marker for all four species of the genus *Trigonodactylus* in our dataset. Intraspecific uncorrected p-distances between all samples of *Trigonodactylus arabicus* were estimated for all three markers.

3. Results

The newly collected specimens from Jordan and Saudi Arabia were identified as *Trigonodactylus arabicus* using available relevant literature (Arnold, 1980, 1986; Gardner, 2013; Metallinou and Carranza, 2013; Nazarov et al., 2018) based on the following features: Adults small of up to 40 mm from snout to vent, slender habitus, clearly webbed forefeet, and dark and slightly triangular-shaped transverse bar in front of the eyes across the snout. This morphological species assignment was also confirmed by the genetic results (Fig. 3).

The final dataset included 73 specimens sequenced for up to 1603 base pairs (bp; 399 bp of 12S, 547 bp of 16S, and 657 bp of COI). The number of variable and parsimony-informative positions, respectively, were as follows: 140 and 104 for 12S, 167 and 123 for 16S, 266 and 215 for COI.

Both phylogenetic analyses resulted in an identical topology at the deepest nodes. The ML results remained consistent regardless of the partitioning scheme applied, we thus report only those for the partitioned by genes scheme. According to the trees (Fig. 3), the *Trigonodactylus* clade is strongly supported (UFBoot = 100; SH-aLRT = 100; BI pp = 1.00, support values are given in this order hereafter) and consists of these four species: *T. pulcher*, *T. sharqiyanensis*, *T. arabicus*, and *T. persicus*. *Trigonodactylus pulcher* is supported as sister to the remaining three species (100; 100; 1.00). *Trigonodactylus sharqiyanensis* is supported as a sister taxon to the clade formed by *T. persicus* and *T. arabicus* (100; 100; 1.00). The new samples from Jordan and Saudi Arabia cluster within *T. arabicus*. The two samples from central Saudi Arabia are genetically close to samples from Qatar and central and southern Oman, albeit with low node support (93; 74.1; 0.89). The new sample from Jordan clusters with two samples from Kuwait (99; 95.8; 1.00). This group of samples from Jordan and Kuwait was in the BI analysis sister to a strongly supported clade formed by all remaining *T. arabicus* samples (pp = 1.00). Although the ML analysis resulted in a similar topology, the support for the clade of all remaining *T. arabicus* samples was not convincing (UFBoot = 84; SH-aLRT = 93.3).

Uncorrected p-distances between the new sample from Jordan (JIR 446) and the remaining *T. arabicus* samples range between 1.3–2.9% for the 12S, 1.8–2.7% for the 16S and 3.7–7% for the COI (Table S3). Mean intraspecific genetic variability within *T. arabicus* is 1.6% for the 12S, 1.8% for the 16S and 4.3% for the COI (Table 1).

Inter- and intraspecific genetic distances based on the COI gene for all four species of the genus *Trigonodactylus* in our dataset. Intraspecific uncorrected p-distances between all samples of *Trigonodactylus arabicus* were estimated for all three markers.

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Inter- and intraspecific genetic distances based on the COI gene for all four species are shown in Table 1.
4. Discussion

Despite several previous attempts to infer the phylogeny of *Trigonodactylus*, none of the studies had all species of the genus represented (Metallinou et al., 2012; Nazarov et al., 2018). The results of our phylogenetic analyses conclusively confirm *T. pulcher* to belong to *Trigonodactylus*, branching as sister species to the three remaining taxa (Fig. 3). The close relationship of *T. pulcher* and *T. arabicus* was first found by Metallinou et al. (2012), who also time-calibrated their tree. Their age estimate of the split between the two species, which corresponds to the crown node of *Trigonodactylus* as confirmed here, dates back to the Middle Miocene (17.3 million years ago [Mya], 95% highest posterior density interval: 11.3–23.6 Mya). This indicates that *Trigonodactylus* originated in Arabia at the time when the peninsula was already well separated from Africa (e.g. Šmíd et al., 2013; Tamar et al., 2016). The subsequent split between *T. arabicus* and *T. sharqiyanhensis*, which with our current understanding is the crown split between *T. arabicus*, *T. sharqiyanhensis* and *T. persicus*, took place 6.4 Mya (3.9–9.3 Mya) according to Metallinou et al. (2012).

The distribution of all *Trigonodactylus* species is strongly tied with the distribution of sandy habitats as a result of their strict psammophilous requirements and adaptations (Arnold, 1980; Gardner, 2013). Among Arabian geckos, it is the only genus with interdigital webbing, an adaptation that allows the animals to walk on loose sand. This unique pedal specialization is only known in two other gecko species, both of the genus *Pachydaactylus* from Namibia (Arnold, 1980; Bauer and Russell, 1991).

Sand deserts and dunes cover vast areas of Arabia. Most of southern Arabia is encompassed by the Rub Al Khali (also termed the Empty Quarter), the largest continuous sand field in the world. Sand fields extend from there through the Dahna desert, a corridor that stretches north–northwestward from the Rub Al Khali and connects it with another large sand field, the Nafud desert, located in northwestern Arabia (Edgell, 2006). The range of *T. arabicus* follows tightly this distribution, albeit the interior of the Rub Al Khali lacks, for the time being, records (Šmíd et al., 2021). By sequencing *T. arabicus* samples from the central part of the species range near Riyadh we confirm the genetic homogeneity of the species, suggesting high levels of gene-flow in the interior of the Arabian Peninsula.

The new record from Jordan reported here represents a considerable range extension (ca. 930 km) to the northwest from all previously reported localities of the species. It is surprising that its presence in Jordan has remained undetected until now despite the fairly extensive herpetological research being done (Sindaco 2013).
et al., 1995; Disi et al., 2001; Al Quran, 2010; Disi, 2011; Scholz et al., 2013). Delima and Al-Nasser (2007), who discovered T. arabicus in Kuwait commented that the species might have remained unknown from the country for the difficulty of spotting due to its small size and pinkish, almost translucent appearance. Its occurrence in Jordan could have been overlooked for similar reasons, or as a result of confusion with the sympatrically occurring Stenodactylus doriae or S. stelvini (pers. obs.), although we find this very unlikely for the unique morphology of Trigonodactylus geckos. Its discovery is, however, not that surprising in terms of biogeography, as some other Arabian psammophilous squamates reach up to southern Jordan (e.g. Cerastes gasperetti, Acanthodactylus schmidtii, Phrynocephalus arabicus, Stenodactylus doriae (Wittenberg, 1992; Disi et al., 2001).

Our findings highlight the need for more field surveys to be carried out in the underexplored deserts of southern Jordan and northern Saudi Arabia, as these difficult-to-access places still hold a potential for new discoveries and are crucial for understanding the biogeography of the Arabian herpetofauna.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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