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Taxonomy of Iranian *Asaccus* (Squamata: Phyllodactylidae) with description of a new species from southern Iran

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Abstract

We provide the first diversity assessment of Iranian species of the genus *Asaccus* based on *COI* DNA-barcoding. We analyzed 53 samples of Iranian *Asaccus* representing nine OTU corresponding to 10 currently recognzied nominal species, and evaluated both morphological and genetic data to support the recognition of a new species from Bandar-e Jask, Hormozgan Province, southern Iran—*Asaccus authenticus* **sp. nov**. The new species is characterized by medium body size (SVL max 55.5 mm), elongated limbs, and relatively small dorsal tubercles arranged in 12–14 regular rows. Morphologically *Asaccus authenticus* **sp. nov**. resembles both Arabian and Iranian representatives of the genus; phylogenetically it forms a highly divergent lineage with sister relationships to all other Iranian congeners. We applied the geometric morphometrics method to compare the position and shape of postmental plates for almost all members of *Asaccus* and evaluated the importance of this character in species diagnostics in this group. We also critically evaluate the recent phylogenetic data on *Asaccus* and discuss the most problematic questions on taxonomy of this genus. We also revalidate *Asaccus ingae* (Eiselt, 1973) as a full species; overall our work raises the total number of species of the genus *Asaccus* to 20.

Key words: systematics, phylogeny, COI, mtDNA, barcoding, distribution, Zagros Mountains, Persian Gulf, reptiles

Introduction

The genus *Asaccus* Dixon & Anderson, 1973 is one of the three most species-rich gekkotan genera occurring in the Western Palearctic: *Hemidactylus* Oken, 1817 (Gekkonidae) includes more than 30 species, *Pristurus* Rüppell, 1835 (Sphaerodactylidae) includes 26 species, and *Asaccus* (Phyllodactylidae) currently includes 19 species (Papenfuss *et al.* 2009; Carranza and Arnold 2012; Badiane *et al.* 2014; Uetz *et al.* 2023). The genus *Asaccus* was originally described by Dixon and Anderson (1973) who divided the genus *Phyllodactylus* Gray, 1828 *sensu lato*, which previously encompassed the leaf-toed geckos of the Old and New Worlds. Both in the scalation features and in the structure of the subdigital plates the two genera have indeed remarkably similar morphology. The main synapomorphy distinguishing the genus *Asaccus* is the absence of cloacal sacs and the postanal bone (Dixon and Anderson 1973; Anderson 1999).

For a long time after discovery, the genus *Asaccus* was comprised of only three species: two from the Zagros Mountains in Iran and one from the Hajar Mountains in Arabia (Anderson 1999). After 1994 studies on the taxonomy of this genus intensified, with 16 new species from Iran, United Arab Emirates (UAE), and Oman described since then (Rastegar-Pouyani *et al.*, 2006; Papenfuss *et al.* 2009; Torki, 2010; Torki *et al.*, 2011; Carranza *et al.*, 2016; Simó-Riudalbas *et al.* 2017a, 2017b; Fattahi *et al.* 2020).

At the current stage, the genus *Asaccus* includes the following 19 nominal species: *A. andersoni* Torki, Fathinia, Rostami, Gharzi & Nazari-Serenjeh, 2011; *A. arnoldi* Simó-Riudalbas, Tarroso, Papenfuss, Al-Sariri & Carranza, 2017; *A. barani* Torki, Ahmadzadeh, Ilgaz, Avci & Kumlutas, 2011; *A. caudivolvulus* Arnold & Gardner, 1994; *A. elisae* (Werner, 1895); *A. gallagheri* (Arnold, 1972); *A. gardneri* Carranza, Simó-Riudalbas, Jayasinghe, Wilms & Els, 2016; *A. granularis* Torki, 2010; *A. griseonotus* Dixon & Anderson, 1973; *A. iranicus* Torki, Ahmadzadeh, Ilgaz, Avci & Kumlutas, 2011; *A. kermanshahensis* Rastegar-Pouyani, 1996; *A. kurdistanensis* Rastegar-Pouyani, Nilson & Faizi, 2006; *A. margaritae* Carranza, Simó-Riudalbas, Jayasinghe, Wilms & Els, 2016; *A. montanus* Gardner, 1994; *A. nasrullahi* Werner, 2006; *A. platyrhynchus* Arnold & Gardner, 1994; *A. saffinae* Afrasiab & Mohamad, 2009; *A. tangestanensis* Torki, Ahmadzadeh, Ilgaz, Avci & Kumlutas, 2011 (Uetz *et al.* 2023). Type localities and sampling locations of these species are shown in Fig. 1.



FIGURE 1. Distribution of the genus *Asaccus*. Numbers indicate the type localities of all nominal species. The specimen IDs of all used samples given inside the boxes and associated to Table S2 for locality details.

Relatively few synonymized taxa among representatives of the genus *Asaccus* are known. *Phyllodactylus eugeniae* Nikolsky, 1907, was described from Iran, Khuzestan Province, Dizful [Dezful] and Abu-Garia, and has been subsequently synonymized with *Asaccus elisae* (Werner, 1895); the herpetological collection of the Zoological Institute of R.A.S. (ZISP) in Saint-Petersburg, Russia, houses a large type series of *A. eugeniae* which were collected by N. A. Zarudny in Persia (Ananjeva *et al.* 2020). Another synonymized taxon is *Phyllodactylus ingae* Eiselt, 1973 (Holotype NMW 20452), which was described from Malavi village, 60 km from Khorramabad, Lorestan Province, Iran. Just one month earlier Dixon and Anderson (1973) published the description of a new gecko genus and species from Iran—*Asaccus griseonotus* Dixon & Anderson, 1973 corresponding to the same population. Though *Phyllodactylus ingae* Eiselt, 1973 is considered as a junior subjective synonym of *A. griseonotus* Dixon & Anderson, 1973, at the present moment *P. ingae* is mentioned in the list of synonyms for both *A. eliase* and *A. gresionotus* in the Reptile Database (Uetz *et al.* 2023).

One of the most interesting problems associated with *Asaccus* taxonomy is the possible center of origin of this genus. Before the molecular era, Arnold and Gardner (1994) based on examination of morphological and anatomical

features, suggested that the basal radiation of the genus *Asaccus* most likely took place on the Arabian Peninsula, as morphologically the most distinct lineage occurs in Oman. Subsequent molecular studies confirmed this hypothesis and provided robust evidence for the localization of ancestral lineages among Arabian representatives of *Asaccus* (Papenfuss *et al.* 2009; Carranza *et al.*, 2016; Simó-Riudalbas *et al.* 2017a, 2017b). In contrast, based on the high diversity of *Asaccus* discovered in the Zagros Mountains of Iran, Rastegar-Pouyani *et al.* (2006) suggested that this area might be the center of origin of the genus. After the discovery of high cryptic diversity among Arabian *Asaccus* species (Carranza *et al.* 2016), studies of the putative underestimated diversity of the genus in the Zagros became more relevant.

The recent molecular study by Fattahi *et al.* (2020) reported on a high level of cryptic diversity in Iranian *Asaccus*, including at least nine undescribed lineages. Among other undescribed *Asaccus* lineages reported by Fattahi *et al.* (2020), two lineages from Zagros were characterized by especially deep levels of divergence (*Asaccus* sp. 8 and *Asaccus* sp. 9; Fattahi *et al.* 2020) and were reported to be more closely related to *A. montanus* than to the rest of Iranian *Asaccus*. This result is quite significant as, if confirmed by genomic data, it might change the current understanding of the phylogeography and origins of the genus *Asaccus*.

The Zagros Range is a vast mountainous region that runs from western to southern Iran. The Zagros Mountains separate the Mesopotamian lowlands from the Iranian Plateau; their complex geological history resulted in a high diversity of landscapes and habitats. The terrain of the Zagros Mountains is predominantly formed by parallel ranges oriented from northwest to southeast; the Alpine orogeny along with volcanic activity likely played the leading role in the formation of this complicated topography (Petrov 1955). Moreover, the Plio-Pleistocene climate oscillations which led to mountain glaciations have also deeply affected the distribution biodiversity in this region (Selivanov 1980). The existence of mosaic landscapes in the Zagros with numerous isolated habitats has led to high levels of both diversity and endemism in this region (Kazemi and Hosseinzadeh 2020).

During our fieldwork in southern Iran in 2018, our team discovered a new population of *Asaccus* in the coastal area of the Persian Gulf near Bandar-e Jask, Hormozgan Province, which we recognize as a new species. The locality where the new species was found lies away from the Zagros Range, and distant from all other known Iranian *Asaccus* species, representing the easternmost distribution limit of the genus in Iran (Fig. 1). The Bandar-e Jask population was included in the phylogenetic dataset of Fattahi *et al.* (2020) and was labeled there as *Asaccus* sp. 7 (see Supplementary Fig. S1). According to Fattahi *et al.* (2020), this new species occupies a sister position to most Iranian species of *Asaccus*; while some morphological features, such as elongated limbs and rostral part of the head, small and roundish dorsal tubercles, closely resemble the Arabian species of the *caudivolvulus—platyrhynchus* species complex. In the present paper, based on morphological differences, *COI*-barcoding data, and the previously published molecular results of Fattahi *et al.* (2020), we formally describe the Bandar-e Jask population as a new species of *Asaccus* and give some taxonomic comments regarding *Asaccus*.

Materials and methods

Sampling and specimen deposition

The materials for the present study were collected during fieldwork in Iran in 2018–2022 within the framework of the Russian–Iranian collaboration project (INSF 99003440 and RFBR 20-54-56033, see Acknowledgements for details). Geographic coordinates and elevations were obtained using a Garmin eTrax 20 GPS receiver and recorded in datum WGS 84. The information on geographic localities of the samples included in the morphological and molecular analyses in the present study is summarized in Supplementary Tables S1 and S2, respectively; and presented in Fig. 1.

Materials (preserved specimens, tissue samples, and photographs) from the following collections were used in this work: Zoological Institute of the Russian Academy of Science (ZISP, Saint-Petersburg, Russia), Zoological Museum of Moscow State University (ZMMU, Moscow, Russia), Zoological Museum Berlin (ZMB, Berlin, Germany), Alexander Koenig Zoological Research Museum (ZFMK, Bonn, Germany), Natural History Museum Vienna (NHW, Vienna, Austria), Museum of Vertebrate Zoology (MVZ, Berkeley, USA), Field Museum of Natural History (FMNH, Chicago, USA), and National Museum of Natural History, Tehran, Iran (MMTT). The type series of the new species was deposited in the Zoological Museum of Moscow State University (ZMMU) National Museum of Natural History, Tehran, Iran (MMTT) and Hakim Sabzavari University, Iran (ERP). Specimens were photographed in life, and then euthanized using MS-222 solution, fixed in 4% formalin and subsequently stored in 75% ethanol. Tissue samples (muscles, heart, or liver) were taken prior to preservation and stored in 96% ethanol for genetic analysis.

Morphological analyses

For the morphological study, we examined 53 adult specimens of seven species of the genus *Asaccus* (see Supplementary Table S1). The morphological features examined were selected based on previous taxonomic studies of this genus (Arnold 1972; Dixon and Anderson 1973; Arnold and Gardner 1994; Gardner 1994; Rastegar-Pouyani 1996; Rastegar-Pouyani *et al.* 2006; Werner 2006; Afrasiab and Mohamad 2009; Parsa *et al.* 2009; Torki 2010; Torki *et al.* 2011a. 2011b; Carranza *et al.* 2016; Simó-Riudalbas *et al.* 2016, 2017a, 2017b).

The following 24 measurements were taken on the right side of each specimen using a Mitutoyo digital caliper to the nearest 0.1 mm: snout-vent length (SVL), taken from the tip of the snout to the vent; tail length (TailL), taken from the posterior edge of the cloaca to the tip of the non-regenerated tail; head length (HL), taken from tip of the snout to the occipital sinus; head height (HH), the maximum depth of the head from the occiput to the throat; head width (HW), measured at the angle of the jaws; frontal width (WF), between the centres of the eyes; snout width (SW), measurement between the third supralabials; snout height (SH), measurement at the level of the third supralabials; the greatest orbit diameter (OrbD); distance from the nostril to anterior edge of the eye (NEye); distance from the tip of the snout to the anterior-most margin of the orbit (SnEye); distance from the anterior edge of the ear opening to the posterior edge of the orbit (EyeEar); distance from the nostril to anterior edge of the ear (NostEar); mental length (ML); mental width (MW); rostral height (RH); rostral width (RW); trunk length (TrunkL), taken from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hind limb at its insertion point on the body; humerus length (LHu), from elbow to the insertion of the fore limb; ulna length (LUn), taken on the dorsal surface from the posterior margin of the elbow while flexed 90° to the inflection of the flexed wrist; fourth finger length (F4L); femur length (FemurL), from knee to the insertion of the hind limb on the posterior side of body; tibia length (TibiaL) taken on the ventral surface from the posterior surface of the knee while flexed 90° to the base of heel; and the fourth toe length (T4L), taken from the base of the first phalanx to the claw.

We also examined 12 following meristic characters: number of ventral scales in a longitudinal row (GVA), counted along the middle line of the ventral surface between the mental scales and cloaca; interorbital scales (IOS), scales between the center of the eyes; number of scales from nostril to eye (NES), counted between the posterior edge of the nostril and the anterior edge of the eye; pairs of postmentals (PPM); number of small scales surrounding postmental plates (SPM); number of longitudinal rows of dorsal tubercles at midbody (DTubL) counted transversely across the middle of the dorsum; number of transversal rows of enlarged dorsal tubercles between the occipital sinus and the middle of the sacrum along the spine (DTubW); number of enlarged subdigital lamellae under the 4th finger (SLF4); number of small lamellae on 4th finger (FLT_2); number of supralabials (SL) and infralabials (IL)counted from the largest scale immediately posterior to the dorsal inflection of the upper jaw to the rostral and mental scales, respectively; and the number of enlarged tubercles in the fifth tail segment (TT).

During the initial analyses of this dataset, we found that from 36 features examined (see supplementary materials, Table S3), only 25 (14 morphometric and 11 meristic) were informative for distinguishing among the species; accordingly, only the 25 taxonomically significant characters were used in further analyses (see Table 3).

We have grouped the material collected from different localities for statistical processing of morphometric data because most localities were represented by single samples. Due to this reason, for comparative morphometric analyses, only four populations of *Asaccus* cf. *elisae* (n=30) were taken into account and compared to the new species (n=6) described herein (see Table 1). All morphometric measurements were adjusted to remove the effects of body size variation: we used the allometric formula: Xadj = log(X)–b[log(BL)–log(BLmean)] following Chan and Grismer (2021).

Species	Museum number	Locality	Latitude N	Longitude E
Asaccus authenticus sp. nov . (n=6)*	ZMMU R-17675–17677; MMTT 2269; MMTT 2270; ERP 10900	Iran, Hormozgan Prov., 25 km N from Jask	25.81	57.82
A. andersoni (n=1)	ZMMU R-16337	Iran, Khuzesran Prov., near Lali town	32.31	49.15
A. barani (n=1)	ZMMU R-16384	Syria, Prov. Khapab, south bank of the El Asad reservoir, vicinity Muskanakh	36.00	38.06
A. gardneri (n=1)	ZMMU R-15494	N. Oman, Musandam		
<i>A</i> . cf. <i>elisae</i> (n=6)*	ZMMU R-12702_1-6	Iran, Kermanshah Prov., Irano-Iraq border, near Qasr-e Shirin	34.49	45.65
A. cf. elisae (n=1)	ZMMU R-14250	Iran, Khuzestan Prov., vicinity of Haftgel	31.46	49.51
A. cf. <i>elisae</i> (n=4)*	ZMMU R-14978_1-4	Iran, Fars Prov., vicinity of Kazerun	29.71	51.63
A. cf. elisae (n=10)*	ZMMU R-13879_1-5	Iran, Ilam Prov., ~45 km, southeast Dehloran	32.55	47.55
A. cf. elisae (n=10)*	ZMMU R-16875-16884	Iran, Fars Prov., 15 km W from Basht	30.38	51.12
A. cf. elisae (n=8)	ZMMU SIR1-8	South Iran, with unknown exact locality		
A. cf. griseonotus (n=3)	ZMMU R-15418_1-3	Iran, Chahal Mahal Prov., road to Lordagan, near Ab Bidak, next to the dam	31.55	50.55
A. platyrhynchus (n=1)	ZMMU R-16871	Oman, Wadi Tanuf	23.07	57.49
A. montanus (n=1)	ZMMU R-13902	Oman, N. Oman, Al Akhpaz	23.16	57.28

TABLE 1. List of specimens and museum accession numbers used in morphological analyses. The asterisk marks the samples used in morphometric comparison.

The scalation features for 53 specimens, including six specimens of the new species and six populations tentatively identified as *Asaccus* cf. *elisae* were analyzed separately (see Table 1). The Kruskal-Wallis test was carried out due to the low number of individuals in the analysis. Principal Component Analysis (PCA) was performed to visualise the morphological variation between the examined specimens.

Geometric morphometrics

We used the geometric morphological method to assess the variation in the shape and position of the mental and postmental plates among the representatives of the genus *Asaccus*. To achieve this, we analyzed 65 digital photographs of the ventral surfaces of the heads, representing 12 nominal species of *Asaccus*, using MorphoJ software. The list of examined specimens and species is presented in Supplementary Table S1. To digitalize the geometric shape of the mental and postmental plates, 19 landmarks were placed on each image of the ventral surface of the head (see Fig. 2). The landmarks were mostly located at the junction of two or three plates. We also included in the analysis the exclusively geometric landmarks, position of which was calculated and defined as the external points on the outer edge of the scales using a reference line, for example, the medial point of the mental plate. Such landmarks were previously used to assess plate shapes (Rajabizadeh *et al.* 2016). Landmarks were digitized using tpsDig (version 2) to obtain two-dimensional coordinates of each landmark.

To prevent the spectator error, all images were digitized twice to evaluate any digitization-related errors. Landmarks with obvious errors were then removed from the dataset. Prior to the analysis, Generalized Procrustes analysis (GPA) was performed using PAST software (version 17.2) to even out the size of the image and eliminate image changes and rotations (Rohlf and Slice 1990; Rajabizadeh *et al.* 2015). To investigate the morphological variation among examined species of *Asaccus*, the obtained coordinates of all landmarks were later subjected to the PCA.



FIGURE 2. Principal component analysis (PCA) of the shape of mental scalation of 12 species of *Asaccus*. Location of 19 landmarks used in geometric morphometrics analysis is shown above. An asterisk marks the position of the type specimens. See the material and methods section for more details.

Molecular analyses

Overall, we included 53 samples of the members of the genus *Asaccus* in the molecular analyses. All newly obtained sequences were deposited in GenBank under the accession numbers OR267464–OR267515 and OR391921–OR391926; the information on GenBank Accession Numbers, specimen IDs and localities is detailed in Supplementary Table S2. Sequences of *Hemidactylus frenatus* Duméril & Bibron, 1836 were used as an outgroup within the phylogenetic analyses.

DNA extraction, amplification, and sequencing

We analyzed a 634 bp fragment of cytochrome oxidase I subunit (*COI*) mitochondrial DNA gene. Molecular analysis was conducted at the Department of Biology, Faculty of Science, Hakim Sabzevari University, Sabzevar, Iran. The total genomic DNA was extracted using the standard phenol-chloroform extraction protocol (Sambrook *et al.* 1989), and PCR amplification was performed using MyCycler BioRad under conditions described elsewhere (Rastegar-Pouyani *et al.* 2014). Two primer pairs were used for PCR and sequencing: Rep-COI-F (5'-TNTTMTCAACNAACCACAAAGA-3', forward) and Rep-COI-R (5'-ACTTCTGGRTGKCCAAARAATCA-3', reverse) (Nagy *et al.* 2012). The PCR reaction volume was 25 µl and contained ca. 100 ng of template DNA, 0.3 pM/µl of each PCR primer, 1xTaq-buffer with 25 mM of MgCl2, 0.2 mM dNTPs, and 1 unit of Taq-polymerase (5 units/µl). The results of the amplification were examined using electrophoresis in 1% agarose gel in the presence of ethidium bromide.

Phylogenetic analyses

The final alignment used for phylogenetic analysis contained 634 bp of the COI gene for 56 specimens representing ten species of Asaccus and three sequences of Hemidactylus frenatus (see Supplementary Table S2). Sequences were aligned by eye using BioEdit Sequence Alignment Editor 5.0.9 (Hall 1999). Phylogenetic analyses were conducted using the maximum likelihood (ML) and Bayesian Inference (BI) methods. Uncorrected genetic distances (pdistance) between the sequences were calculated in MEGA7 (Kumar et al. 2016). JMODELTEST (v.0.1.1) (Posada 2008) was used to estimate the optimal evolutionary models to be used for the dataset analysis. ML-analysis was performed using RaxML 7.4.2 (Stamatakis 2006) and was implemented in RaxMLGUI 1.3 (Silvestro and Michalak 2012) under the model GTR + G + I with heuristic search and 1,000 bootstrap replicates (ML BS, see Felsenstein 1985). BI-analysis was performed with MrBayes 3.2.5 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The likelihood settings corresponded to the general time-reversible model with rate heterogeneity (GTR + I + G), which was the closest approximation of the best-fit substitution models selected by the AIC criterion. The analysis was performed with four chains for 10 million generations and sampling every 100th tree. First 25,000 trees were discarded as a burn-in. A majority-rule consensus tree was subsequently produced from the remaining trees after discarding the burn-in trees, and the posterior probabilities (BI PP) were calculated as the frequency of trees recovering any particular clade (Huelsenbeck and Ronquist 2001). Each analysis was repeated four times with random starting trees, and the results were compared to assess the convergence.

In ML analysis, branches with bootstrap values of 75% or greater were regarded as sufficiently supported (Huelsenbeck and Hillis 1993). In BI analysis, branches with Bayesian posterior probabilities (BPP) of 0.95 and above were considered strongly supported; we considered branches with values of 0.90–0.94 as well-supported (Huelsenbeck *et al.* 2001; Wilcox *et al.* 2002).

Results

Molecular differentiation

The ML and BI analyses recovered trees with very similar topologies, with minor topological differences associated with only a few deeper nodes with insufficient nodal support (see Fig. 3; Supplementary Fig. S1-S2). Our mtDNAgenealogy suggests that the Bandar-e Jask population of Asaccus occupies a sister position with respect to all other Iranian species of Asaccus included in our analysis, however monophyly of the latter clade was not significantly supported in both analyses (53/50, hereafter node support values are given for BI PP / ML BS, respectively). The remaining species of Iranian Asaccus were grouped into two main clades, corresponding to the A. griseonotus species complex (99/78) and the A. elisae species complex (99/99). The first clade included A. nasrullahi, A. granularis, A. andersoni, A. kurdistanensis and A. griseonotus which is characterized by rounded, small and slightly keeled dorsal tubercles, rounded and short rostral part of head.; and the second clade included A. iranicus, A. tangestanensis, A. cf. elisae and A. zagrosicus characterized by large dorsal tubercles, elongated rostral part of the head and low morphological differentiation between species. Moreover, according to our data, A. iranicus and A. tangestanensis formed a single clade with shallow differentiation (100/100; inter-group genetic differentiation p = 1.0%, see Fig. 3 and Table 2). However, analyses of other loci (12S rRNA and cyt b) show the validity of these taxa (Fig. S2). The same results were obtained by Fattahi et al. 2020 (Fig. S1). Genetic differentiation of the Bandar-e Jask population of Asaccus from its congeners was significant with uncorrected genetic p-distance in COI gene sequences ranging from 23.7% (with A. zagrosicus) to 26.6% (with A. griseonotus, see Table 2), this also is comparable with that calculated by Fatahi et al 2020 for Cyt b, in which the genetic distance of Jask population with other Iranian Asaccus range from 20.5% to 27.5%.



FIGURE 3. Phylogenetic relationships and diversity of the genus *Asaccus*. A: Phylogenetic tree of the genus *Asaccus* based on analyses of 1857 bp of *12S* rRNA and *cytochrome b* mtDNA genes and *MC1R* nuDNA genes form Fattahi *et al.* (2020); B: The Bayesian phylogenetic tree of *Asaccus* species based on analysis of 634 bp of *COI* gene (generated in the present study). Values at nodes indicate posterior probabilities/bootstrap support for BI/ML analyses, respectively. Colors indicating the main lineages of *Asaccus* correspond to those in Figs. 1 and 2. For voucher specimen information and GenBank accession numbers see Supplementary Table S2.

TABLE 2. Uncorrected p-distances for sequences of mtDNA COI gene for groups (below the diagonal).	Values on the
diagonal correspond to average uncorrected intra-group <i>p</i> -distances.	

Species	1	2	3	4	5	6	7	8	9
1. A. granularis	0.02								
2. <i>A. kurdistanensis</i>	0.226	0.00							
3. A. nasrullahi	0.125	0.204	0.01						
4. A. griseonotus	0.220	0.122	0.206	0.00					
5. A. andersoni	0.162	0.220	0.158	0.217	0.00				
6. A. iranicus/ A. tangestanensis	0.260	0.261	0.280	0.253	0.276	0.01			
7. A. zagrosicus	0.270	0.260	0.255	0.262	0.271	0.212	0.00		
8. <i>A</i> . cf. <i>elisae</i>	0.269	0.252	0.247	0.278	0.281	0.199	0.193	0.03	
9. A. authenticus sp. nov.	0.245	0.260	0.257	0.266	0.261	0.251	0.237	0.242	0.00

Morphometric comparison of the Bandar-e Jask population of Asaccus with the other populations of the A. elisae species complex

Samples of four different populations from southwestern Iran belonging to the *A. elisae* species complex were available in suitable number to permit morphometric comparison with *Asaccus authenticus* **sp. nov** (Fig. 4a). Due to the limited sample sizes examined, the differences reported below must be considered preliminary and require further clarification in future studies utilising a larger dataset. The proportions of the head made the greatest contribution to the differentiation between the Bandar-e Jask population and the members of the *A. elisae* species complex. The head was relatively taller and more elongated in the Bandar-e Jask population, with a noticeably elongated rostrum, and the body had relatively more elongated fore- and hindlimbs.

The results of PCA analysis of the meristic features of specimens belonging to the six recognized species and five unrecognized populations of the *A. elisae* species complex are presented in Fig. 4b. Based on scalation characters, the Bandar-e Jask population was clearly separated from all other examined *Asaccus* species, including *A. caudivolvulus*, *A. andersoni* and *A. montanus*, while *A. cf. griseonotus*, *A. barani* and the members of the *A. elisae* species complex expectes complex were poorly differentiated in the morphospace (Fig. 4b).

Though the population of *A*. cf. *elisae* from the vicinity of Qasr-e Shirin differed from other studied specimens in the lower number of ventral scales along the midbody (GVA 137–150 *vs*. 147–176), we did not find any significant differences in this feature among all other examined populations, including the Bandar-e Jask population. The contribution of morphometric and meristic features to the distinction among the studied species and population is present in Table 3.

TABLE 3. Loadings, eigenvalues, proportion, and cumulative proportion of variance explained by the first three components selected from the PCA performed on shape residuals for each morphological variable. The component loadings in bold indicate a remarkable difference between species. See abbreviations of morphological variables in the Materials and Methods section.

Metric characters	Factor 1	Factor 2	Factor 3
HL	-0.478469	-0.067194	-0.635593
HH	-0.883604	-0.001772	-0.154526
SW	-0.823074	0.087551	0.004825
SH	0.011360	0.721221	-0.251806
OrbD	-0.063523	0.795518	-0.234837
Neye	-0.877242	-0.066947	-0.053214
SynEye	-0.968621	-0.147636	0.023510
EyeEar	-0.477855	-0.379019	-0.614207
Nost Ear	-0.883846	-0.127742	-0.069070
Trunk	0.010951	0.852539	-0.047754
Lhu	-0.864416	0.245457	0.351465
Lun	-0.944171	0.091052	0.227758
FemurL	-0.891564	0.167241	0.132247
TibiaL	-0.922246	-0.024776	0.205923
Eigenvalue	8.536778	2.287632	1.699781
Total variance (%)	47.42654	12.70906	9.44323
Cumulative (%)	47.4265	60.1356	69.5788
Meristic characters			
GVA	0.206875	0.240091	-0.262938
IOS	0.215631	0.262016	0.002166
NES	0.262934	-0.039104	-0.010709

.....continued on the next page

TABLE 3 (Continued)

Metric characters	Factor 1	Factor 2	Factor 3
SPM	0.014530	0.385077	0.013674
DTubL	0.111520	-0.188272	0.367973
DTubW	0.243864	-0.142630	0.042038
FLT_1	0.142939	-0.132443	0.397223
FLT_2	0.023934	-0.249380	-0.506124
HLT_1	0.082245	-0.163184	0.008123
HLT_2	0.125312	-0.349904	-0.228653
SLS	0.143821	0.253546	-0.079421
Eigenvalue	3.393261	1.600056	1.472282
Total variance (%)	30.84783	14.54596	13.38438
Cumulative (%)	30.8478	45.3938	58.7782

Geometric morphometrics analyses

The geometric morphometric analysis best distinguished the representatives of the Arabian lineages of *Asaccus*, namely *A. platyrhynchus* and *A. gardneri* (Fig. 2). The Bandar-e Jask population of *Asaccus* also was quite well separated from its congeners in the morphospace of the PCA, although one specimen of *A. zagrosicus* fell into the dispersion of the Jask population. Moreover, the dispersion cloud of *A. tangestanensis* also closely bordered the dispersion cloud of the Bandar-e Jask population. *Asaccus andersoni* and *A. montanus* also occupied a distant position in the morphospace, and the rest of the examined species formed a weakly differentiated cloud (Fig. 2).

Variation in the arrangement of mental and postmental plates among different species of *Asaccus* is presented in Fig. 5. Among the members of the *A. elisae* species complex, two major morphotypes can be distinguished based on the position and shape of the mental scalation. The population of *A.* cf. *elisae* from the environs of Kazerun City (Fig. 5d) closely resembles the Bandar-e Jask population (Fig. 5i) in the arrangement of mental plates. The population of *A.* cf. *elisae* from the vicinity of Qasr-e Shirin City is characterized by fully separated first pair of postmentals (Fig. 5c), however the diagnostic value of this character remains unclear.

Within the *A. griseonotus* species complex, *A. andersoni* is clearly distinct from other species by the fully separated first pair of postmentals (Fig. 5t). No obvious differences in mental scalation were recorded between the holotypes of *Phyllodactylus ingae* Eiselt, 1973 (Fig. 5q) and *A. granularis* (Fig. 5r). The relative position of the first pair of postmentals (in contact or separated), the ratio of the area of the first and the second pair of postmentals, and the orientation along the longest axis of the first pair of postmentals make the most significant contribution to the morphological differentiation among these species.

Taxonomy

Though based on a limited molecular data (partial *COI* gene sequences) our mtDNA-based genealogy agrees with the earlier phylogenetic hypothesis of Fattahi *et al.* (2020), which was based on two mtDNA genes (12S rRNA and cyt b) and one nuclear DNA gene (MC1R). According to Fattahi *et al.* (2020), the population of *Asaccus* from Bandar-e Jask represents the sister clade with respect to all other Iranian *Asaccus* and likely diverged from the most recent common ancestor of this group around 23 million years ago (see Supplementary Fig. S1). For the first time we provide *COI* DNA-barcoding data for Iranian *Asaccus* species, and according to our data, the population from Bandar-e Jask clearly represents a highly divergent lineage warranting taxonomic recognition. Overall, the results of the *COI*-barcoding of Iranian *Asaccus* (Fig. 3) fully agree with the previously obtained data of Fattahi *et al.* (2020).



FIGURE 4. Morphometric comparisons of *Asaccus authenticus* **sp. nov.** with Iranian *Asaccus elisae* complex and position of some other representatives of this genus. (a) PCA based on morphometric data for the new species and four Iranian populations of the *Asaccus elisae* species complex; (b) PCA based on meristic (scalation) features of the new species and 12 *Asaccus* representatives, see Table 1 for details.

In the present study we also report on the morphological differences between the Bandar-e Jask population and other congeners. According to our data, this population is clearly different from all currently recognized species of the genus *Asaccus* both in morphometric and scalation features. Recognizing the limitations of the analysis of concatenated mtDNA + nuDNA datasets in reconstruction of phylogenetic relationships (see, e.g., Hillis *et al.* 2021; Gallego-Garcia *et al.* 2023; Dufresnes *et al.* 2023), we nevertheless consider the results presented in the phylogenetic study of Fattahi *et al.* (2020) along with the concordant data on morphological differentiation and divergence in diagnostic *COI* mtDNA gene presented in the present paper, as strong evidence for a full species status of the Bandar-e Jask population of *Asaccus*. These results support the hypothesis that the Bandar-e Jask population represents a previously unknown species of *Asaccus*, which we formally describe below.

Family Phyllodactylidae Gamble, Bauer, Greenbaum & Jackman, 2008

Genus Asaccus Dixon & Anderson, 1973

Asaccus authenticus sp. nov.

(Fig. 5i, Fig. 6, Fig. 7a; Fig. 9b, Table 4).

Chresonymy:

Asaccus sp. 7-Fattahi et al. (2020).

Holotype: ZMMU R-17675 (field number RAN 3400), adult male, collected on April 26, 2018 from a sandstone cliff ca. 25 km northwards from Bandar-e Jask, Hormozgan Province, southern Iran (25.8088° N; 57.8188° E, elevation 74 m a.s.l.) by Roman A. Nazarov, Daniel A. Melnikov, Hossein Nabizadeh, and Mehdi Rajabizadeh.

Paratypes: ZMMU R-17676 (field number RAN 3401, adult female), ZMMU R-17677 (field number RAN 3402 adult male), MMTT 2269 (field RAN 3399 subadult), MMTT 2270 (field number RAN 3404, adult male) and ERP10900 (field number RAN 3403 adult female). Altogether, five specimens (two adult males, two adult females, one subadult) with the same collection data as the holotype.

Diagnosis: A member of the genus *Asaccus* with the following combination of morphological characters: body size medium (SVLmax: 55.5 mm); limbs elongated; two pairs of postmentals, the anterior pair in broad contact; fine scales across the supraorbital region; 12–14 regular longitudinal rows of whitish, enlarged, weakly keeled, oval dorsal tubercles; small pointed tubercles on occiput, neck, and lateral surfaces of head; enlarged keeled tubercles scattered on the hindlimbs and the distal part of forelimbs; 2–3 small tubercles present on the upper arms; terminal lamellae on digits paired, extending beyond claws on 1/3 of the total length; cloacal tubercles weakly developed; ventral surface of the tail with transverse expanded plates; tip of tail laterally compressed and expanded; general background color light-grey with whitish dorsal tubercles; dorsal pattern consisting of five narrow transverse orange-brown bands: one on the neck, three on the body, and one on the sacrum; the interspaces between the dorsal bands wider than the bands themselves; five or six wide transverse bands on the tail, usually brownish or orange-brownish at the base, black in the middle, getting less distinct from the middle to the tip of the tail; tail tip white.

Description of the holotype: Adult male ZMMU R- 17675 (RAN 3400) in a good state of preservation (see Fig. 6). Snout-vent length 51.1 mm, tail 64.4 mm; other measurements of the holotype presented in Table 4. Head relatively elongated (SVL/HL ratio 2.89), not wide (HeadL/HW ratio 1.82), high (HL/HH ratio 2.85), distinct from slender neck. Rostral part not elongated (HL/SnEye 2.6), larger than the diameter of the eye (HL/OrbD ratio 4.31) and the occipital part of the head (HL/EyeEar ratio 5.53), scales on the lateral surface of the snout twice the size of the granular scales on the medial part of the snout and the occipital region. Eyes big, pupils vertical with crenelated margins; supraciliary scales with tiny conical spines posteriorly. External ear opening elliptical, obliquely oriented, and small in size (HL/EarL ratio 9.07); eye-to-ear distance less than the diameter of the eye (OrbD/EyeEar ratio 0.94). Rostral plate shorter (0.9 mm) than wide (2.31 mm) and weakly depressed in the middle. Two large supranasals in broad contact with each other; rostral in contact with the first pair of supralabials and two supranasals (Fig. 6b,c); each nostril surrounded by supranasal, rostral, first supralabial, and two postnasals, about two times smaller than the supranasals. One row of small granular scales separating the orbit from the supralabials; mental plate triangular, higher (3.1 mm) than wider (2.8 mm); two pairs of enlarged postmentals, first pair in broad contact with each other, second pair divided by one enlarged rounded scale; 12 supralabials and 11 infralabials.



FIGURE 5. The arrangement of the mental scalation in *Asaccus* species. Drawings are based on photographs of type specimens and illustrations from the original descriptions of the examined *Asaccus* species. For details see Supplementary Table S1.



FIGURE 6. *Asaccus authenticus* **sp. nov.**: a—general view of the holotype ZMMU R-17675 (RAN 3400) in preservative; b, c, d—dorsal, lateral, and ventral aspects of the head of the holotype; e—general view of the type series in preservative.

Character	Holotype					
Specimen ID	ZMMU R-17675 (RAN 3400)	ZMMU R-17675 (RAN 3401)	ZMMU R-17675 (RAN 3402)	ERP 10900 (RAN 3403)	MMTT 2270 (RAN 3404)	MMTT 2269 (RAN 3399)
Sex	male	female	male	female	male	subadult
SVL	51.1	47.6	55.5	51.8	54.7	39.4
TL	64.4	44.4	-	-	60.9	-
HL	15.8	15.5	17	16.8	16.8	12.6
HW	9.7	9	10.7	9.5	9.2	7.8
HH	6.2	5.5	6.2	5.6	6.2	4.3
WF	1.80	1.80	1.72	1.77	1.72	1.16
SW	5.4	5.2	6.2	6.4	6.3	4.5
SH	2.61	1.66	2.3	2.04	2.63	1.74
OrbD	4.1	4.3	5.2	5.2	5.8	3.8
NEye	5.9	4.2	6	5.5	6	4
SnEye	6.8	6.5	7.3	7.4	7.3	5.4
EyeEar	3.2	3.2	3.8	3.2	3.4	3.8
NostEar	13.6	13.2	14.7	14.2	14	10.6
TrunkL	21.3	17.9	24	23.5	25.9	16.6
FLL	25	23.4	27.7	28.3	28.2	19.8
LHu	10.3	10.4	11.7	12	12	8.6
LUn	10.4	9.3	11.3	11.6	11.6	8
F4L	4.5	4.5	4.8	4.5	4.5	3.5
HLL	34.1	33.7	38.2	35.6	35.8	27.6
FemurL	14.3	13.8	15.8	15.5	15.8	11.3
TibiaL	12.8	11.4	14	13.4	13.5	9.8
T4L	6.6	5.3	6.9	6.2	6	5
GVA	150	150	163	157	155	167
IOS	26	20	24	24	21	24
NES	15	16	15	15	15	14
PPM	2	2	2	2	2	2
SPM	18	16	19	16	16	17
DTubL	13	14	12	12	13	13
DTubW	29	29	30	34	29	29
SLF4	9	8	7	8	7	7
FLT_2	3	4	4	4	5	4
SLT4	9	9	10	9	9	9
HLT_2	5	6	5	6	5	5
SL	12	13	13	14	13	13
IL	11	12	10	11	9	11
TT	6	6	6	6	6	6

TABLE 4. Measurements and counts of the type series of Asaccus authenticus sp. nov. (all in mm).

Trunk slender, slightly flattened, elongated (SVL/TrunkL 2.39), with no ventrolateral folds. Dorsal trunk surface covered by small granular scales and relatevly small conical keeled tubercles (5–6 times larger than the adjacent scales), forming 12 regular longitudinal rows running from the base of head to the middle of sacrum, 29 keeled tubercles along the mid-dorsum. Ventral scales larger than the scales on dorsum, smooth, subimbricate with rounded margins; no femoral and precloacal pores; scales on the ventral surface of femur large, approximately the same size as the ventral scales; two subfemoral tubercles on each side of the tail base; approximately 38 abdominal scales across the middle of the belly; 151 midventral scales along the belly (between the mental scales and cloaca); gular region covered by homogeneous small roundish and smooth scales.

Fore- and hindlimbs elongated and thin (SVL/forelimb 2.04; SVL/hindlimb 1.49); digits moderately long, with two enlarged marginal lamellas; 12 (nine proximal and three distal) subdigital lamellae on the 4th finger and 14 (nine paroxysmal and five distal) subdigital lamellae on the 4th toe. Enlarged keeled tubercles present on the dorsal surfaces of hindlimbs and distal part of forelimbs and 2–3 smaller tubercles present on the upper arm.

Tail slender, somewhat longer than body (SVL/TailL 0.79); segments of tail well-developed, fifth tail segment formed by a ring of 6 keeled tubercles; subcaudals in a single median row of transverse enlarged scales; tail tip laterally compressed and expanded.

Coloration: Background coloration light-grey with whitish dorsal tubercles (Fig. 7a). The pattern on dorsum consists of five narrow transverse orange-brown bands: one on the neck, three on the body, and one on the sacrum. The interspaces between the dorsal bands are wider than the bands themselves (Fig. 7a). Five to six wide transverse bands on the tail, brownish or orange-brownish closer to the tail base, black in the middle, getting less distinct from the middle to the tip of the tail. Tail tip white. The ventral surfaces of the body white, with some dark wide crossbands visible on the ventral surface of the tail.

After five years in preservative, the background coloration faded to light-brown, and the dorsal pattern became almost indistinct (Fig. 6a).

Variation: Measurements of the type series are presented in Table 4. Due to the limited sample size examined, we did not find any obvious dimorphism between the sexes.

Etymology: The species name '*authenticus*' is a Latin adjective in nominative singular (masculine gender), meaning 'genuine' or 'original'. The name is given in reference to the distant phylogenetic position of *Asaccus authenticus* **sp. nov.** with respect to other Iranian congeners, as revealed by the latest phylogenetic studies (Fattahi *et al.*, 2020). We propose "*Bandar-e Jask Leaf-toed Gecko*" as a common name of the new species.

Distribution and natural history: To date, the new species is known only from the type locality in 25 km northwards from Bander-e Jask (25.8088° N; 57.8188° E), Hormozgan Province, southern Iran, and was recorded on elevation of 74 m a.s.l. The new species was recorded on sandstone cliffs within the dry river canyon during a night excursion approximately at 21:00 h. These geckos were observed perching on the vertical surfaces of sandstone outcrops and sometimes were recorded on the ground under the *Acacia* sp. trees and bushes which densely grow on the sides of the canyon (Fig. 7b). The population density of the new species appears to be locally high: during 3 hours of night observation, we counted 12 specimens on a ca. 500 m long sandstone wall. The reptile species recorded syntopically with the new species include: *Cyrtopdion* cf. *hormozganum*, *Cyrtopodion* cf. *agamuroides*, *Laudakia melanura*, *Hemidactylus* cf. *persicus*, and *Acanthodactylus* cf. *khamirensis*.

Comparison with closely related species (see Figs. 8–10): The members of the genus *Asaccus* can be classified in three groups based on their maximal body size (SVLmax). The small-bodied group with SVLmax up to 45 mm, includes: *A. arnoldi* (33.6 mm), *A. gallagheri* (40 mm), *A. montanus* (40 mm), and *A. iranicus* (41.4 mm); these species can be readily distinguished from the new species, which has a much larger body size (SVLmax 55.5 mm). The large-bodied group with SVLmax 65–71 mm includes five species: *A. andersoni* (66.2 mm), *A. gardneri* (70.7 mm), *A. granularis* (70.2 mm), *A. griseonotus* (71 mm), and *A. nasrullahi* (70 mm); they can be also easily diagnosed from a much smaller *Asaccus authenticus* **sp. nov.** (SVLmax 55.5 mm). Finally, the medium-sized group with SVLmax 55–63 mm includes most members of the genus: *A. barani* (56 mm), *A. caudivolvulus* (63.2 mm), *A. elisae* (57 mm), *A. kermanshahensis* (55.7 mm), *A. margaritae* (58.7 mm), *A. platyrhynchus* (63 mm), *A. saffinae* (57 mm), *A. tangestanensis* (57.8 mm), *A. zagrosicus* (55 mm), and *Asaccus authenticus* **sp. nov.** (55.5 mm).



FIGURE 7. Asaccus authenticus sp. nov. (a) in situ, and (b) typical biotope with Acacia sp. trees and sandstone outcrops.



FIGURE 8. The type specimens of some representatives of the *Asaccus*, '*elisae*' complex (a, c, e, g) and '*griseonotus*' complex (b, d, f, h): a—*A. elisae* syntype NHW 17525; b—*Phyllodactylus ingae* Eiselt, 1973 holotype NMW 20452; c—*A. iranicus* holotype ZFMK 91933; d—*A. griseonotus* holotype FMNH 170824; e—*A. tangestanensis* holotype ZFMK 91934; f—*A. granularis* holotype ZMB 75010; g—*A. zagrosicus* holotype ZFMK 91935; h—*A. andersoni* holotype ZMB 75015.



FIGURE 9. A new species of *Asaccus authenticus* **sp. nov.** *in situ* (b) with the some other representatives of the *A. elisae* species complex: *A. iranicus* (a), *A.* cf. *elisae*, Qasr-e Shirin (c-d); *A.* cf. *elisae* Basht (e-f); *A. tangestanensis* (g-h).



FIGURE 10. The representatives of other phylogenetic lineages of *Assacus: A. platyrhynchus* (a) wadi Tanuf, Oman; *A. gardneri*, Oman (b); *A. kurdistanensis*, type locality, vicinity of Marivan, Iran; *A. cf. griseonotus* ZMMU R-15418-1 (d), Iran; *A. andersoni*, ZMMU R-16337, vicinity of Lali, Iran (e); *A. montanus* ZMMU R-13902, Al Akhpaz, Oman.

Morphologically, *Asaccus authenticus* **sp. nov.** combines the features typical for the Arabian and Iranian *Asaccus* species. Therefore, below we will compare the morphological characteristics of the new species with the representatives of both geographic groups of *Asaccus*. The new species can be distinguished from *A. platyrhynchus* by a relatively smaller maximal body size (SVL max. 55.5 mm, compared to 63 mm); laterally compressed and vertically expanded tail tip (*vs.* tail tip rounded, not laterally compressed or vertically expanded); and by the absence of sexual dimorphism in tail coloration compared to clearly dimorphic tail coloration (white tail with black crossbars in females and yellowish tail in males of *A. platyrhynchus*).

Asaccus authenticus **sp. nov.** differs from *A. caudivolvulus*, *A. margaritae*, and *A. gardneri* by a relatively smaller maximal body size (SVL max. of 55.5 mm vs. 58.7 mm, 63.2 mm, and 70.7 mm, respectively), by 12–14 relatively small oval dorsal tubercles (vs. 14–16 large keeled trihedral dorsal tubercles), and by the smaller size of the tubercles on the occiput, neck, and head sides (vs. large pointed keeled tubercles on occiput, neck and head sides).

The new species can be distinguished from most members of A. elisae species complex by a greater number of scales between nostril and the eye (NSE 15–16 vs. 10–13). However, the populations of the A. elisae species complex from Qasr-e Shirin (Fig. 9c,d), Dehloran, Basht, and Kazerun are not different from Asaccus authenticus **sp. nov.** in this trait. Torki et al. (2011b) noted that the size, shape, and localization of the enlarged dorsal tubercles play an important role in taxonomy of this group. The members of A. elisae species complex are characterized by relatively larger keeled tubercles, located in a smaller number of longitudinal and transverse rows than in the new species (8–12, 22–28 vs. 12–14, 29–34 in Asaccus authenticus **sp. nov.**).

Asaccus elisae sensu stricto can be distinguished from Asaccus authenticus **sp. nov.** by having 8–12 longitudinal rows of large strongly keeled trihedral dorsal tubercles (*vs.* 12–14 rows of comparatively smaller oval dorsal tubercles in the new species); by the presense of large pointed keeled tubercles on the occiput, neck, and head sides (*vs.* small and smooth tubercles on the occiput, neck, and head sides in the new species), by claws extending somewhat beyond the digital scansors (*vs.* digital scansors extending well beyond the claws in the new species), and by 2–12 enlarged tubercles on the upper forelimb above the elbow (*vs.* lacking of enlarged tubercles on the shoulders or only 2–3 enlarged scales in the new species).

Finally, *A. iranicus* (Fig.9a), occurring on the Iranian coast of Persian Gulf in Bushehr Province, southern Iran, is geographically most closely distributed to *Asaccus authenticus* **sp. nov.** among all other Iranian representative of the genus *Asaccus*. The two species can be easily distinguished from each other by the presence of large pointed keeled tubercles on the dorsum, occiput, neck, and head sides in *A. iranicus* (*vs.* small oval tubercles on the dorsum, occiput, neck, and by claws extending somewhat beyond the digital scansors in *A. iranicus* (*vs.* wide digital scansors extending well beyond claws in the new species).

Discussion

The territory of origin of the genus *Asaccus* was a subject of debate in the phylogenetic studies of this group of geckos. Arnold and Gardner (1994) based on examination of morphological characters suggested that the genus most likely originated from the Arabian Peninsula. However later Rastegar-Pouyani *et al.* (2006) based on a high diversity of *Asaccus* in the Zagros Mountains, hypothesized the Iranian origin of the genus with subsequent dispersal and colonization of Arabia. One of the first molecular phylogenetic studies of this group by Papenfuss *et al.* (2010) demonstrated that *A. montanus*, occurring in Arabia, represents a sister lineage to all other species included in their analysis. Further molecular studies demonstrated that the Arabian species of *Asaccus* do not form a single clade and are paraphyletic with respect to the Iranian members of the genus (Simó-Riudalbas *et al.* 2017a). According to the latest phylogenetic study by Fattahi *et al.* (2020) which also has a quite complete taxon sampling, *A. montanus* together with *A. platyrhynchus* and *A. gallagheri* and two undescribed lineages from Iran (*Asaccus* sp. 8 and *Asaccus* sp. 9) form a clade with sister relationships to all other *Asaccus* species. The remaining species occurring in the Arabian Peninsula include *A. margaritae*, *A. caudivolvulus* and *A. gardneri*; these taxa form a sister clade to all species of Iranian *Asaccus* (Simó-Riudalbas *et al.* 2017a; Fattahi *et al.* 2020). Therefore, the hypothesis of origin of the genus *Asaccus* in Arabia with subsequent radiation and dispersal to Iran is strongly supported by the available phylogenetic data.

In most of the previous studies, the Iranian clade of *Asaccus* was represented by a limited dataset; for example, the study by Papenfuss *et al.* (2010) only included three species: *A. elisae* (MVZ 234514), *A. griseonotus* (MVZ 234326) and *A. nasrullahi* (MVZ 234330). The most comprehensive analysis of Iranian *Asaccus* was recently presented by Fattahi *et al.* (2020); based on their study Irainian *Asaccus* are also not monophyletic and include four main clades, corresponding to the (1) *A. elisae* and (2) *A. griseonotus* species complexes, (3) *Asaccus* sp. 8 and *Asaccus* sp. 9, which are closely related to *A. montanus*, and (4) the lineage from Bandar-e Jask with sister relationships to all remaining Iranian species; in the present study we describe this lineage as *Asaccus authenticus* **sp. nov.** (*Asaccus* sp. 7 in Fattahi *et al.* 2020). The split between the *A. elisae* and *A. griseonotus* species complexes

is also reflected in difference in external morphology between their members. It should be noted that in this species complex, we observe a deep genetic divergence along with poor morphological differentiation among the lineages (see Fig. 9); overall the species of the *A. elisae* species complex are generally phenotypically poorly differentiated and their taxonomy requires further studies.

Asaccus authenticus **sp. nov.** is not only phylogenetically distant from all other Iranian congeners; this species inhabits a coastal area of the Strait of Hormuzin 1,500 km southeast of the area of highest diversity of Iranian *Asaccus* in Zagros Mountains, and just in 100–150 km from Arabian species which occur on the opposite side of the strait in Oman and UAE (Fig. 1). These data suggest that *Asaccus authenticus* **sp. nov.** represents a population, which probably reflects the process of ancient colonization of Iran by *Asaccus* from the Arabian Peninsula. The preliminary divergence time estimates by Fattahi *et al.* (2020) indicate that the split between *Asaccus authenticus* **sp. nov.** and the remaining Iranian *Asaccus* species likely took place in the late Oligocene (ca. 28 MYA). The present data suggest that the dispersal of *Asaccus* to the Zagros Range occurred several times independently by representatives of different phylogenetic lineages of the genus. Thus, the two Iranian lineages (*Asaccus* sp. 8 and *Asaccus* sp. 9 of Fattahi *et al.* 2020) belong to one clade with *A. montanus*, *A. platyrhynchus* and *A. gallagheri*, while the basal split of the genus *Asaccus* was dated as the late Eocene (ca. 36 MYA) (Fattahi *et al.* 2020). Further studies including examination of a larger number of taxa and loci and, perhaps, genomic data, are required for a better understanding of evolutionary and biogeographic history of the genus *Asaccus*.

Below, we will discuss the main controversial questions in taxonomy of the genus *Asaccus* in scope of recent phylogenetic data. A big challenge in taxonomic studies of *Asaccus* geckos is the correct identification and attribution of the lineages and populations to the available names proposed in this group. We provide our considerations which result from interpretation of the recently published phylogenetic data and examination of the available type material of *Asaccus* species (see Table 1, Supplementary Table S1).

(1) Asaccus griseonotus species complex. The type series of Asaccus griseonotus Dixon & Anderson, 1973 includes the holotype FMNH 170824 (Fig. 8d; collected from a locality 38.5 miles from Shahabad, Kermanshah Province, Iran, 29.08.1968 by Dan Womochel and Anthony F. De Blasé), seven paratypes FMNH 170817–170823 (form the same locality as the holotype), and one paratype FMNH 74553 (collected on 19.04.1955 by C. A. Reed in Palegawra Cave, Sulaimaniyah Liwa, Iraq). At present, *Phyllodactylus ingae* Eiselt, 1973 (Fig. 8b) is recognized as a subjective junior synonym of Asaccus griseonotus Dixon & Anderson, 1973 (Uetz et al. 2023). However, the type localities of both species are located quite far from each other and given the high diversity of Asaccus lineages in Zagros along with low morphological differentiation among them, we consider that the proposed synonymy may be premature; further studies are required to clarify the taxonomic status of *Phyllodactylus ingae* Eiselt, 1973.

Another species of the *A. griseonotus* species complex was described from Lorestan Province of Iran as *A. granularis* Torki, 2010 (holotype ZMB 75010, Fig. 8f, 5 km NW from Poledokhtar, Khers-Dar vill., mt. Makhmalekoh, 29° 50' N, 59° 53' E, 1100–1800 m a.s.l.). It is noteworthy that the type locality of *A. granularis* is situated less than 50 km from the type locality of *A. ingae* (see Fig. S3). Comparison of the main morphological features of the type specimens of these species (see Table 5) demonstrates that the differences between *A. ingae* and *A. griseonotus* are minor; further studies including molecular analysis of the topotypic materials of these two taxa are required to verify the full species status of *A. granularis*.

The specimen MVZ 234326 originally identified as 'Asaccus griseonotus' was mentioned in Fattahi et al. (2020) and included in the phylogenetic analyses, where it clustered together with A. granularis (see Supplementary Fig. S1). This specimen was collected from Lorestan Province of Iran (99 km SW from Khorram Abad), what is near to the type locality of Asaccus ingae (see Fig. S3). However, additional morphological and molecular studies are required to clarify the status of this specimen. The topology where a member of the A. griseonotus species complex is placed deep within the radiation of the A. elisae species complex seems problematic and is likely based on a misidentification. The specimen MVZ 234326 was also used in an earlier phylogenetic study on Asaccus (Papenfuss et al. 2010), where the authors noted its unexpected position within the A. elisae species complex. Most likely, this results from a misidentification or a technical mistake during the sampling process; this inaccuracy has led to misinterpretation of the results of subsequent studies.

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Species	A. granularis	A. ingae
Type locality	Iran: Lorestan Province: 5 km northwest of Poledokhtar (town): Khers-Dar (village): Mt. Malekoh. 29°50'N. 59°53'E. 1100–1800 m a.s.l.	Iran. Lorestan Province. 110 km by road SW Khoramabad, W junction with road to Malavi.
Tubercles on head	no tubercles on head or neck	no tubercles on head or neck
Dorsum tubercles rows	12–16	14
Ventral side	ventral sides of the fore limbs covered with granular scales	The abdominal scales about the same size as the dorsal tubercles (smaller in <i>A. elisae</i>), flat and tuberous.
PPM	2–3	2
Mental	slightly longer than wide	wedge-shaped
number of enlarged lamellas on toes	8 (8–10) lamellae under the fourth toe	6/4, 6/7, 8/8, 8/9 , 10/10
SVL	66.9 (60.0–70.2)	70.5
HW	13.6 (11.3–14.1)	14.7
HL	19.6 (19.1–21.2)	19.8
НН	8.6 (7.0–9.3)	9.1
EyeD	4.2 (4.0–5.1)	4.2
EarD	2.6 (2.2–3.1)	2.8
Scales surrounding nostril	5: 1st supralabial, rostral and 3 granular scales behind	5: internasale, 2 postnasalia, 1st supralabiale and rostral
number of scales between nostril and eye	12 (10–12)	9/10 + 2/3 granules between the inferior postnasal and the anterior orbital margin
number of interorbital scales	28 (18–29)	23
number of scales across the snout between the two 3rd supralabials	16–22	15
Supralabialis	10–13	12/13

TABLE 5. Morphological comparisons of two species of the genus *Asaccus—A. ingae* and *A. granularis*, according to the original descriptions of these taxa (Eiselt 1973; Torki 2010).

Based on morphological examination of specimens included in the study of Fattahi *et al.* (2020), we suggest that '*A. granularis*' (2413, 2418, 6535–6539, 6541) were misidentified and actually belong to the representatives of the *A. elisae* species complex. Therefore, we regard the clade identified as '*A. granularis*' in the work of Fattahi *et al.* (2020) (see Supplementary Fig.3, Fig. S1–S2) as one of the members of the *A. elisae* species complex, which likely represents a yet unnamed lineage. Correspondingly, one of the unnamed clades in the the *A. griseonotus* species complex likely represents the true *A. granularis* sensu stricto (Supplementary Fig. S1).

Torki *et al.* (2011) have recently suggested that *A. saffinae* Afrasiab & Mohamad, 2009 described from Iraq represents a subjective junior synonym of *A. griseonotus*. Given the deep genetic divergence and high level of endemism within this group, we consider this taxonomic act to be premature and consider this taxon as a valid species.



FIGURE 11. Type series of Asaccus eugeniae (A, a-ZISP 10261; B, b-ZISP 10270).

(2) Asaccus elisae species complex. Asaccus eugeniae (Nikolsky, 1907) clearly belongs to the A. elisae species complex (Fig. 9, 11), and preliminary estimates indicate that this complex hosts a rich cryptic diversity consisting of at least three or four yet unnamed lineages (Fattahi et al. 2020). The type locality of Asaccus elisae (Werner, 1895) lies at the ruins of Niniveh, near Mosul, Iraq (syntype NHW 17525 shown in Fig. 8a), which is over 700 km from the known Iranian populations of the A. elisae species complex. It is likely that the distribution of A. elisae sensu stricto is limited to upper Mesopotamia, and this species does not occur in Iran. As mentioned by Papenfuss et al. (2010), "The taxonomy of A. elisae awaits comparison with samples from the type locality in Iraq". Morphological and molecular analisis of material from the type locality of A. elisae s.s. can clarify the identity and taxonomic status of the A. elisae species complex (in particular A. elisae, A. eugeniae, A. zagrosicus, and Asaccus sp. 2, Asaccus sp. 3, Asaccus sp. 4 in Fattahi et al. 2020).

Representatives of this complex often inhabit anthropogenically modified environment. We found populations of *A*. cf. *elisae* on concrete vaults of drainage tunnels under roads, under bridges, and on old buildings. This probably favours faster dispersal of representatives of this complex. Thus, near Dehloran city (Iran), we found a population with high density living in old abandoned military dugouts of the Iran-Iraq war times. In addition, we noted collective clutches of this species on the ceilings of these dugouts (Fig. 12).

FIGURE 12. Collective oviposition of *A*. cf. *elisae* near Dehloran city, Iran, inside an old military dugout from the Iran-Iraq War.

Conclusions

Summarizing our research, we can make the following conclusions:

(1) Our work raises the total number of species of the genus *Asaccus* to 20. The new species *Asaccus authenticus* **sp. nov.** described herein can be recognized from its congeners by both morphological and genetic characters. This species represents a lineage highly divergent to the most Iranian species of *Asaccus*.

(2) *Asaccus iranicus* and *Asaccus tangestanensis* are closely related species and further study is necessary to clarify the taxonomic status and the extent of distribution of these taxa.

(3) *Asaccus ingae* (Eiselt, 1973) represents a valid species, while *A. granularis* Torki 2010 should most likely be considered as its junior synonym; further studies including examination of topotypic material are required for final determination.

(4) The specimen MVZ 234326 was likely misidentified as *A. griseonotus*, in fact this specimen belongs to the *A. elisae* species complex.

(5) The members of the clade identified as '*A. granularis*' in Fattahi *et al.* 2020 were likely also misidentified and also belong to the *A. elisae* species complex.

(6) The synonymy of *A. saffinae* with *A. griseonotus* as previously proposed by Torki *et al.* (2011) seems to be unjustified; we consider *A. saffinae* as a valid species (see Fig.5).

(7) In the present study we have applied the methods of geometric morphometrics for the purpose of taxonomic diagnostics in *Asaccus* geckos. The performed analysis of a limited material demonstrated pronounced differentiation between the main clades of *Asaccus* in the shape and proportions of the mental and postmental plates. However, within the *A. elisae* species complex, neither geometric morphometrics, nor the comparison of other metric and meristic morphological characters provided a sufficient level of discrimination between the examined groups; this result can be explained by a limited dataset used in our study.

Further studies on the diversity and evolutionary relationships of *Asaccus* geckos is important both for achieving a better understanding of speciation and phylogeography patterns in the region, as well as for the environmental and conservation issues. The high level of endemism in the genus *Asaccus* indicates the existence of yet underestimated diversity and lineages that need to be protected.

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