Additions to the phylogeny of colubrine snakes in Southwestern Asia, with description of a new genus and species (Serpentes: Colubridae: Colubrinae)

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Reptiles are still being described worldwide at a pace of hundreds of species a year. While many discoveries are from remote tropical areas, biodiverse arid regions still harbor many novel taxa. Here, we present an updated phylogeny of colubrid snakes from the Western Palearctic by analyzing a supermatrix of all available global snake species with molecular data and report on the discovery of a new genus and species of colubrine snake from southeastern Iran. The new taxon, named *Persiophis fahimii* **Gen. et sp. nov.**, is nested within a clade containing Middle Eastern and South Asian ground racers (*Lytorhynchus*, *Rhynchocalamus, Wallaceophis,* and *Wallophis*). This species has a derived morphology including an edentulous pterygoid and occurrence of short and blunt teeth on the palatine, maxillae and dentary bones, an elongated snout and a relatively trihedral first supralabial scale that is slightly bigger than the second, and elongated toward the tip of rostral. We also report on the osteology and phylogenetic placement of several poorly studied colubrines: *Hierophis andreanus* (reassigned to *Dolichophis*) and *Muhtarophis barani.*

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RUNNING TITLE: A new snake genus from Iran

ABSTRACT

Reptiles are still being described worldwide at a pace of hundreds of species a year. While many discoveries are from remote tropical areas, biodiverse arid regions still harbor many novel taxa. Here, we present an updated phylogeny of colubrid snakes from the Western Palearctic by analyzing a supermatrix of all available global snake species with molecular data and report on the discovery of a new genus and species of colubrine snake from southeastern Iran. The new taxon, named *Persiophis fahimii* **Gen. et sp. nov.**, is nested within a clade containing Middle Eastern and South Asian ground racers (*Lytorhynchus*, *Rhynchocalamus, Wallaceophis,* and *Wallophis*). This species has a derived morphology including an edentulous pterygoid and occurrence of short and blunt teeth on the palatine, maxillae and dentary bones, an elongated snout and a relatively trihedral first supralabial scale that is slightly bigger than the second, and elongated toward the tip of rostral. We also report on the osteology and phylogenetic placement of several poorly studied colubrines: *Hierophis andreanus* (reassigned to *Dolichophis*) and *Muhtarophis barani.*

SUBJECTS: Biodiversity, Biogeography, Evolutionary Studies, Taxonomy, Zoology

KEYWORDS: phylogeny, supermatrix, colubrinae, *Rhynchocalamus*, *Eirenis*, parallel evolution

INTRODUCTION

The family Colubridae is the most speciose group of snakes, inhabiting a diverse array of ecosystems worldwide except Antarctica and some remote oceanic islands *(Vitt & Caldwell 2013).* While at least 1,959 species of colubrid snakes have been described *(Uetz 2019)*, there are undoubtedly many new species remaining to be discovered. Colubrid phylogeny has been recently studied at higher levels *(Lawson et al., 2005; Nagy et al., 2004; Pyron et al., 2011;*

Vidal et al., 2007; Zaher et al., 2019) and with species-level sampling *(Figueroa et al., 2016; Pyron et al., 2013; Zheng & Wiens 2016)*, but many nodes remain poorly supported. One of the possible reasons is the absence of unsampled or undescribed taxa, hampering the estimation of a complete phylogeny *(see Pyron et al., 2013)*. This emphasizes the importance of studying the biodiversity of colubrid snakes, not only from a conservation point of view *(Böhm et al., 2013)*, but also to shed light on the phylogeny of the whole group.

In phylogenetics, extensive sampling may increase accuracy *(Zwickl & Hillis 2002)*. New methods and data may help in studying the biodiversity of rare colubrids, whether it be the discovery of new species, or the placement of enigmatic taxa. Thus, densely-sampled supermatrices of all available gene sequences are desirable to improve phylogenetic estimations *(Pyron et al., 2011)*, both to cement the placement of sampled species as well as the recognition of new taxa. Furthermore, integrative taxonomy can help in accommodating different data sources and provide new avenues for delimiting species using different organismal properties (Padial et al., 2010).

Of Western Palearctic colubrid snakes in southwestern Asia (including Iran and adjacent countries), the phylogenetic relationships of a considerable number of rare or narrowly endemic taxa are unknown (*Rajabizadeh, 2018*). Here, we present an updated phylogeny of colubrid snakes from the Western Palearctic by analyzing a supermatrix of all available global snake species (*Figueroa et al., 2016*). To this matrix, we have added data from two rare and poorly known species from Iran. The first is Andreas' Racer, *Hierophis andreanus* (*Werner, 1917*), an endemic colubrid snake from Iran with ambiguous phylogenetic placement *(Figueroa et al., 2016; Schätti & Monsch 2004),* currently classified in the genus *Hierophis (Wallach et al., 2014)*. The second is a previously unknown taxon, discovered by some of us during a 2008 field survey in southeastern Iran, which shows unique morphological adaptations and represents a new genus

and species of colubrid snakes. In addition to the molecular phylogeny, we provide osteological data for consideration in taxonomic evaluations.

MATERIALS AND METHODS

Nomenclatural acts

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone (see Articles 8.5-8.6 of the Code). This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information can be viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is as follows: urn:lsid:zoobank.org:pub:4EAACC14-8FC8-46B9-830C-4AEC8A42A562. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Specimen Collection

During one month of fieldwork in southern and western Iran (Fig. 1) in May 2008, two specimens of rare colubrid snakes were collected by R. Nazarov and M. Rajabizadeh: a sample of *Hierophis andreanus*, and a specimen of Colubridae **Gen. et sp. nov.** superficially resembling snakes of the genera *Rhynchocalamus* or *Lytorhynchus.* Voucher specimens were preserved and deposited in the International Center for Science, High Technology and Environmental Sciences Herpetological Collection (ICSTZM), Kerman, Iran, along with tissue samples (muscle tissue, preserved in 100% ethanol) for molecular phylogenetic analysis. The skulls of both specimens

were examined using micro-CT scanning. Specimen information are as follows:

1. *Hierophis andreanus*, collected from around Darreh Shahr City, western Iran, Ilam Province (Fig. 1), preserved in 75% ethanol and cataloged as ICSTZM.7H.1154.
2. Colubridae **Gen. et sp. nov.**, ICSTZM.7H.1151, collected from around Orzueeyeh City, southern Iran, Kerman Province (Fig. 1), preserved in 75% ethanol.

Field work, including collection of the samples and animals in the field, was performed outside of any protected area, in the framework of a project contract signed by International Center for Science, High Technology and Environmental Sciences, Kerman, Iran (contract number 1.87, issued at 11.04.2008). The contract bears a permission to collect the reptile samples outside of any protected area of Department of the Environment (specified in www.doe.ir) that needed extra permissions. Specimen collection protocols and animal operations followed the Institutional Ethical Committee of International Center for Science, High Technology and Environmental Sciences, Kerman, Iran (certificate number 1.87-1).

Molecular Phylogeny

We used the species-level supermatrix from *Figueroa et al. (2016)*, which is currently the largest such dataset available for snakes (A dataset comprising 1745 taxa representing 1652 snake species and 7 outgroup taxa, and 9523 base pairs from 10 loci, accessible in https://doi.org/10.1371/journal.pone.0161070.s002). First, we removed the chimeric representative of "*Lytorhynchus diadema*" and added several newly-sequenced specimens from this clade derived from recent publications (Table 1). For our two new samples, we then added sequences for the mitochondrial genes 12S, ND4, and CYTB (sequencing details as in *Pyron et al., 2011*), accessioned in GenBank under numbers MN531564, MN531565, MN531566, MN531567, MN536808, MN536809 (Table S1). We used the same partitioning and analytical strategy as *Figueroa et al. (2016)*. With their model-partitions file (by gene and codon), we first

used RAxML version 8.2.9 *(Stamatakis 2014)* with the rapid-bootstrapping function to estimate a ML topology from 200 independent searches from every 5th bootstrap replicate, with support from the 1000 total bootstraps. Then, we performed a secondary search on this topology to generate an NNI-optimal topology with SHL support values, for which 85% is considered strong support (see *Pyron et al., 2011*). While we re-estimated the entire snake phylogeny, we only report results from the clade of interest containing our focal taxa and other Western Palearctic Colubrids.

Osteology

The skull osteology of *Hierophis andreanus* was compared with that of closely related genera, including *Hierophis* (*H. gemonensis* - MNHN 1937-454) and *H. viridiflavus* - MNHN 1967-79, 1869-806), loaned from the Muséum national d'Histoire naturelle in Paris), *Dolichophis* and *Eirenis* from published reports *(Hosseinian Yousefkhani & Rajabizadeh, 2014; Mahlow et al., 2013)*. Additionally, we gathered novel osteological observations regarding Colubridae **Gen. et sp. nov.**, for a thorough description of the new taxon. The micro-CT scans of the heads of two snake specimens were performed at the Centre for X-ray Tomography of Ghent University *(Vlassenbroeck et al., 2007)*. The setup was a transmission head of a dual-head X-ray tube (Feinfocus FXE160.51) and an a-Siflat panel detector (PerkinElmer XRD 1620 CN3 CS). The focal spot size was 900 nm at a tube voltage of 130 kV for high resolution. Number of projections and voxel size of the scanned specimen is presented in Table S2. Exposure time was 2 seconds per projection, resulting in a 360° output CT Scan. The raw data were processed and reconstructed using the in-house CT software Octopus (http://www.octopusreconstruction.com) *(Vlassenbroeck et al., 2007)* and rendered using Amira V. 5.4.1 (Mercury Systems of Visage Imaging GmbH). The CT-rendered images were color coded to distinguish separate ossified units, where stiff and rigidly interconnected bones were given a single color.

144 **Morphological evolution**

145 We used phylogenetic comparative methods to test for possible convergence in size and shape
146 within the focal clade. We used the Parsimony Ancestral State Estimation Method in Mesquite
147 ver. 2.75 *(Maddison & Maddison 2011)* to reconstruct the evolutionary history of morphological
148 traits across the western Palearctic racers, whip snakes and dwarf snakes. Morphological data
149 were extracted from the literature *(Kharin & Akulenko, 2008; Mahlow et al., 2013;*
150 *Rajabizadeh, 2018; Schätti, 1987)*. The cladogram is a pruned subtree of our large-scale
151 phylogeny, comprising the Western Palearctic whip snakes (genera *Hierophis* and *Dolichophis*),
152 Slender Racer (*Orientocoluber*), *Hierophis andreanus*, and dwarf snakes of the genus *Eirenis*.
153 We examined several pholidotic traits related to overall body-size and head size, to test the
154 hypothesis that dwarfism has evolved convergently at least twice in the group. We based this on
155 our phylogenetic hypothesis for *Hierophis andreanus*, which is a dwarf species that is estimated
156 outside of *Eirenis* (see Results). Morphological examination was performed following to
157 Dowling (1951). Pileus length was measured as the maximum distance from tip of snout to
158 posterior margin of parietals. Dorsal scales rows were counted at the level of one head length
159 posterior to the head (anterior body), midbody and one head length anterior to the anus (posterior
160 body).

161

162 **RESULTS**

163 **Phylogeny**

164 The ML tree (see Fig. 2) is overall highly similar to many recent estimates of colubroid
165 snake phylogeny *(Figueroa et al., 2016; Pyron et al., 2011; Zaher et al., 2019)*, with a few major
166 exceptions highlighted in part by our new sampling. Our results confirm the occurrence of a
167 monophyletic lineage (SHL = 88) of Western Palearctic colubrids including 17 genera and

Colubridae **Gen. et sp. nov.** However, phylogenetic placement of all genera within this clade is not fully resolved, due to low support values for some nodes. Our results strongly support a sister-group relationship of *Muhtarophis barani* and *Scaphiophis albopunctatus* (SHL = 89), which together form a clade that is the sister group to all above mentioned genera of Western Palearctic and South Asian colubrids with high support (SHL = 88). There are two main subclades of western Palearctic and South Asian colubrines that we highlight here for further attention.

The first involves a small radiation of colubrine ground-snakes endemic to southwestern Asia (including Colubridae **Gen. et sp. nov.**), and the second involves colubrines from the Old-World racer lineage. In the first sub-clade the genera *Wallaceophis* and *Wallophis* share a sister-group relationship that is strongly supported (SHL = 100), and a lineage that is the sister group (SHL = 100) to the genera *Lytorhynchus*, *Rhynchocalamus* and Colubridae **Gen. et sp. nov.** The phylogenetic relationship between the latter genera is poorly supported (SHL < 50). The new colubrid lineage is moderately supported (SHL = 80) as the sister lineage to *Rhynchocalamus*, though both are genetically distant. The monophyly of both *Lytorhynchus* and *Rhynchocalamus* is strongly supported, which combined with the morphological distinctiveness of the new lineage necessitates a novel generic assignment.

The second sub-clade is divided into several groups. In the first lineage, *Mopanveldophis zebrinus* is the sister group (SHL = 86) to the genera *Bamanophis* and *Macroprotodon*. This lineage is sister to other remaining genera in the Western Palearctic colubrine clade (SHL = 99). The second lineage contains *Hemorrhois* as the sister group to the genera *Spalerosophis* and *Platyceps* with strong support (SHL = 98). Relationships in the latter genus are poorly resolved (Fig. 2). It must also be noted that the recent cranial osteology and molecular phylogeny data from *Argyrogena fasciolata* indicate placement of *A. fasciolata* as the sister lineage of *Platyceps*

192 (*Das et al., 2019*).

193 Among the remaining lineages, the Western Palearctic whip snakes (genera *Hierophis*
194 and *Dolichophis*), the Slender Racer (*Orientocoluber*), *Hierophis andreanus*, and dwarf snakes
195 of the genus *Eirenis* are confirmed in our tree as a monophyletic group (SHL = 100). This clade
196 comprises one lineage including the genera *Orientocoluber* and *Hierophis* (sister relationship
197 strongly supported; SHL = 97), and a second lineage including the genera *Dolichophis* and
198 *Eirenis*. Although the monophyly of each of the latter genera is confirmed, their phylogenetic
199 relationships are weakly supported. Furthermore, *Hierophis andreanus* is placed within the
200 genus *Dolichophis* as the sister group to *D. jugularis* with strong support (SHL = 90), and to
201 which we formally reassign it, with *D. jugularis* as the sister species. Based on our tree,
202 monophyly of the genus *Dolichophis* is confirmed (SHL = 100), and a basal divergence within
203 the genus is supported (SHL = 100) between a sub-group comprising *D. schmidti* and *D. caspius*
204 (SHL = 100), and another sub-group of *D. jugularis* and *Hierophis andreanus*. The genus
205 *Hemerophis* is also placed in this clade, but its position is not clear.

206

207 **Systematics**

208 Phylogenetic results indicate that Colubridae **Gen. et sp. nov.** is nested within the
209 subfamily Colubrinae, and we estimate strong support for a sister group relationship with snakes
210 of the genus *Rhynchocalamus*, while both clades are distantly diverged. From an osteological
211 point of view, Colubridae **Gen. et sp. nov.** lacks teeth on the premaxilla and proteroglyphous or
212 solenoglyphous teeth on the maxilla, a coronoid bone in the mandible, girdle or limb elements,
213 and valvular dorsal nostrils (see Osteology, below), and so belongs to the family Colubridae *(Vitt*
214 *& Caldwell 2013)*. The occurrence of a broad articulation between snout bones and the lack of
215 numerous and closely-set teeth, as well as the fact that the specimen was found on an arid

mountain side and does not have an aquatic or semiaquatic lifestyle confirms that Colubridae **Gen. et sp. nov.** belongs to the subfamily Colubrinae rather than the related subfamily Natricinae *(Vitt & Caldwell, 2013; Zaher et al., 2012)*. Although the occurrence of an edentulous pterygoid is observed in the genera *Dasypeltis*, *Lytorhynchus* and *Rhynchocalamus* as well *(Avcı et al., 2015; Gans, 1952; Gans & Williams, 1954; Leviton & Anderson, 1970)*, the combination of osteological traits of Colubridae **Gen. et sp. nov.** is unique within the subfamily, indicating that this single specimen represents a new genus as well as a new species of colubrid snakes, which are described herein as follows:

***Persiophis fahimii* Gen. et sp. nov.**

(Figs. 3–5 and S1)

Holotype. Adult female, ICSTZM.7H.1151 (field number: RAN 2948). Iran, Kerman province, 19 km Northwestern Orzueeyeh City, 1350 meters ASL; coll. R. Nazarov, May 2008 (Figs. 3-5 and S1). The specimen originally preserved in 96% ethanol and then moved to 75% ethanol for long term preservation. Since the authors are concerned about the conservation of the species, the exact geographic coordinates of the type locality are not given here.

Etymology. The genus name derives from the Greek words "*Persi-*" (*Persís*) = Persia (old name of Iran) and "*ophis*" = serpent. The species is named after Dr. Hadi Fahimi, a young naturalist and herpetologist who dedicated his life to studying the biodiversity and conservation of reptiles and mammals of Iran. As a young nature lover, Hadi joined the rangers of the Department of Environment in Kerman province for two years and served partly in Khabr National Park where is close to the type locality of *Persiophis fahimii.* He was a PhD student in IAU, Tehran, studying on the conservation of black bears in southeastern Iran, but sadly passed

240 away in an aircraft crash in Dena Mountain in central Zagros in February 2018.

241 **Diagnosis.** For the genus and species, *Persiophis fahimii* is distinguished within the
242 subfamily Colubrinae by a combination of distinct osteological characters, including the
243 occurrence of vestigial teeth on the palatine; a thin, edentulous pterygoid; short and blunt teeth
244 on the maxillae and dentary, occurrence of edentulous parts on the anterior and middle region of
245 the maxillae; a fully fused basioccipital and basisphenoid; the occurrence of a highly oblique
246 quadrate bone attached to the posterior tip of a somewhat elongated supratemporal. The genus
247 and species are also distinguished within the subfamily Colubrinae by a combination of
248 morphological characters, including an elongated snout; occurrence of a rostral scale that is
249 visible from above and wedged between the internasals; a relatively trihedral first supralabial
250 that is slightly bigger that the second and elongated toward the tip of rostral; 15 longitudinal
251 rows of dorsal scales on midbody; and an edentulous pterygoid.

252 **Comparisons.** The above mentioned anatomical traits are in contrast to those observed in
253 the genus *Rhynchocalamus*, including a small, thin, down and backward directed premaxilla; a
254 broad, edentulous pterygoid; relatively elongated, posteriorly curved teeth on the maxillae and
255 dentary; a closed suture between basioccipital and basisphenoid; a short and nearly vertical
256 quadrate bone on each side of cranium, and a broad attachment surface for a short supratemporal
257 (*Avcı et al., 2015*). Also, *Persiophis fahimii* differs from *Rhynchocalamus* and *Lytorhynchus* in
258 having maxillae that anteriorly and medially are edentulous and in between, bear small and
259 vestigial teeth except for the last two, in contrast to relatively elongated, posteriorly curved teeth
260 over most of the maxillar length in *Rhynchocalamus* and *Lytorhynchus* (*Avcı et al., 2015;*
261 *Leviton & Anderson, 1970)*. *Persiophis* differs from *Dasypeltis* in having smooth edges on the
262 anterior frontal and posterior nasals (compared to small premaxilla and a serrated anterior free
263 edge of frontals and posterior edges of nasals (Gans 1952).

Description of the holotype. Body and tail slender and elongate. Head small, oblong-shaped, slightly distinct from neck; snout elongated. Snout-vent length 380 mm, tail length 115 mm, head length 12.9 mm, head width 7.6 mm, pileus length 9.6 mm, parietal length 4.5/4.8 mm, (right/left), frontal length 3.0 mm, frontal width 2.2 mm, prefrontal suture length 1.2 mm, eye diameter 1.3 mm, distance between nostrils, 2.2 mm, interocular distance 3.2 mm.

Head scalation. Tip of rostral scale visible from above and wedged between the internasals. Internasal slightly shorter in length than the prefrontal scale. Width of the frontal scale is smaller than its length, shorter than parietals. Supraoculars are smaller in length and width than the frontals. Parietals elongated, medial suture between scales crooked-shaped giving an asymmetrical appearance. Nasal scale elongated and rectangular, the nostril situated upward, approximately mid length of the nasal. Loreal is small, longer than wide. 8/8 (hereafter values given in right/left order) supralabials , the first supralabial is relatively trihedral, slightly bigger that the second scale and elongated toward the tip of rostral, the fourth and fifth bordering the eye. A single presubocular on each side of the head, 1/2 postoculars; 3/2 anterior and 3/3 posterior temporals. 8/8 infralabials bordering the mouth on each side of the head, the first through fifth bordering the anterior genials. On the underside of the head, the mental small and triangular. Anterior genials small, in contact with each other, obliquely elongated towards the border of mouth, median suture between the anterior genials about the length of mental scale. Posterior genials contacting each other, elongated and larger than the anterior genials, median suture between them slightly more than twice the length of suture between the anterior genials.

Body scalation. Dorsal scales smooth, having a single apical pit. Dorsal scales at the anterior body, midbody and posterior body are in 19, 15, and 15 longitudinal rows, respectively. Dorsal scale reduction happens at the level of 22 (DSR 19 to 18), 25 (DSR 18 to 17), 34 (DSR 17 to 16) and 38 (DSR 16 to 15) ventral scales. On the underside of the body, two preventral scales,

288 followed by 206 ventral scales. The anal plate divided, followed by 83 pairs of subcaudal scales,
289 ending to a single terminal scale.
290 *Coloration.* The dorsal head ground color grayish-white, with a blackish blotch on the posterior
291 prefrontals and anterior frontal, and a parenthesis-shaped blackish blotch on the parietals. Dorsal
292 head scale sutures with irregular feebly blackish dots. On the sides of head, irregular blackish
293 blotches scattered around eye, a blackish stripe running from posterior eye edge along the margin
294 of the parietal on each side of the head. Snout and labial region whitish with irregular blackish
295 dots adjacent to the eye. The underside of the head whitish. Dorsal body and tail ground color
296 grayish white. Three blackish longitudinal stripes on the dorsal and lateral sides of the nape,
297 changing to continuous black blotches on dorsal surfaces of body and tail. Dorsum with nearly
298 parallel blackish dorsal bands, having irregular margins, the width of each band about one and a
299 half of dorsal scale length, separated by a grayish-white interspace of about the length of one
300 scale. Body sides with continuous blackish blotches alternating with dorsal bands. Dorsal
301 blotches fade to scattered blackish spots posteriorly on dorsal surfaces of the tail. The ventral
302 surface of the body whitish.

303 **Cranial Osteology.** The skull in *Persiophis* is long and elliptical and well ossified. At the
304 tip of the snout, the single, pyramid-shaped premaxilla is deeply wedged in the space between
305 the septomaxillae and the nasals. The nasals are directed downward. Left and right articulated
306 nasals form a median septum between the nasal cavities and cover it dorsally. Ventrally the
307 nasals form a process which lies in between the two frontals. Left and right septomaxillae are
308 plate-like, bifurcate anteriorly and in contact medially. They form the floor of nasal cavity.
309 Septomaxillae contact the nasal septum medially and posteriorly form a process that contact the
310 frontals. The septomaxillae are partly fused with the vomers. The toothless vomers lie beneath
311 the two septomaxillae and form a pair of spherical cavities in which lies the vomeronasal organs.

312 The vomeronasal organs open by paired orifices into the buccal cavity. On each side of the head,
313 a cone-shaped prefrontal borders the orbit anteriorly. Dorsally, the prefrontals have a tight
314 articulation with the anterolateral surface of the frontals, and ventrally they bear a rather loose
315 articulation with the maxillae.

316 The neurocranium is composed of compactly ossified bones, fully fused to each other by
317 to form a complete enclosure of the brain. Left and right frontals are well separated at the tip but
318 joined together along the rest of their length. Parietals are ovally shaped, fused together to form a
319 single bone (largest cranial element) that dorsally roofs the braincase, bearing no elaborated
320 crests. Laterally it extends far down either side of the brain, reaching the basisphenoid and the
321 prootics. Left and right postorbitals articulate with the anterolateral surfaces of the parietal and
322 form the dorsoposterior boundary of each orbit.

323 Left and right prootics are quadrate shaped bones, partly fused with the parietal and
324 forming the anterior walls of each internal otic capsule. They also constitute the anterior half of
325 each fenestra ovalis and the posterolateral wall of the braincase. Left and right supraoccipitals
326 are fused together to form a single bone. Externally it roofs the posterior brain cavity, internally
327 it expands to form the posterior part of each otic capsule. A pair of diagonal crests extend
328 transversally along the posterior part of the supraoccipitals. Left and right exoccipital bones form
329 the posterolateral wall of the braincase, as well as part of its roof. They are fused with the
330 opisthotics and together surround the jugular foramen and extend forward to form the posterior
331 border of the fenestra ovalis. They form the entire oval foramen magnum, except for a small
332 ventral portion of the occipital condyle. The basioccipital forms the floor of the posterior part of
333 the brain cavity and the ventral portion of the occipital condyle. It completes the foramen
334 magnum and creates a big, thick and raised occipital condyle. The basioccipital forms the
335 posterior braincase floor. The basisphenoid and parasphenoid are fused to each other to form a

single, long bone. It forms the posterior snout and anterior braincase floor.

In the palatomaxillary arches, the palatines are long and narrow, articulate with the prefrontal process of the maxilla laterally and with the pterygoid posteriorly. There are three small sized teeth at the mid-length of each palatine. The pterygoids are edentulous, long and bent bars that are narrow anteriorly, flattened posteriorly, and extend from the posterior palatines to the posterior mandibles. The ectopterygoids are flat, bifurcate anteriorly, notched posteriorly and connect the maxillae to the pterygoids. Left and right maxillae are curved, anteriorly thin, posteriorly somewhat broadened and connect to the flattened ventral surface of the ectopterygoid by a mesial process. The maxilla medially articulates with the ventral surface of the prefrontal. Each maxilla is edentulous anteriorly, bears three small teeth, and after another edentulous medial region, bears 6/5 small teeth. Finally, after a small space (equal to the length of one socket) two big, elongated, posteriorly curved teeth are present. In the medial, edentulous region of the left maxilla, a small socket is observed.

The mandibular units are composed of compactly ossified bone elements. Left and right supratemporals are narrow, flattened, dermal elements, connected to the proximal end of quadrates and the posterolateral part of braincase by fibrous connective tissue. Each supratemporal is long, slightly bent upward, and overlays the exoccipital, prootic and even reaches the edge of the parietal. Left and right quadrates are long, tick, rectangular shaped, having a flattened proximal end aligned along the posterolateral border of each supratemporal. The distal articulating surface of each quadrate is extended transversely and directed backward. Left and right mandibles are long, dorsally concave, connected to each other anteriorly by an elastic ligament. Each mandible unit is composed of two major bones, a compound bone and dentary. The dentary is somewhat dorsally curved and bears sockets for closely set 18/19 (L/R) small teeth that decrease in size posteriorly. Left and right stapes (columella) are slender, rod like

bones, proximally enlarged and form a footplate that fit into the fenestra ovalis, distally connect to the inner surface of the quadrate at about mid length level.

Natural history. Our data on biology of *Persiophis fahimii* is based on the one specimen collected. The holotype was collected at elevation of 1350 meters ASL on a bare mountainside, while climbing on a vertical rocky wall, at late night (2.30 AM). The mountain is composed of Devonian limestone marbles, at the southeastern edge of the central mountains of Iran, ranging from 1050 to 1600 meters ASL. Dominant vegetation on the plain in front of the mountain is *Calligonum* and annual forbs and grasses. At the base of the mountain, the vegetation changes to *Calligonum* and *Ziziphus nummularia*. At the type locality, the vegetation is dominated by sparse woody, thorny or aromatic shrubs, including *Periploca* sp. (Apocynaceae), *Dichanthium* sp. (Poaceae), *Fagonia* sp. (Zygophyllaceae), *Ephedra foliata* (Ephedraceae), *Teucrium* sp. (Lamiaceae), *Lophochloa* sp. (Poaceae), *Lycium* sp. (Solanaceae), *Tribulus* sp. (Zygophyllaceae), *Pulicaria* sp. (Asteraceae), *Reseda* sp. (Resedaceae), *Heliotropium* sp. (Boraginaceae), *Gymnocarpos decander* (Caryophyllaceae), *Convolvulus* sp. (Convolvulaceae), *Heliantemum* sp. (Cistaceae), and *Diceratella persica* (Apiaceae).

Conservation. Since the first field expedition in 2008 and two more field expeditions in spring 2017 and 2018 in the type locality of *Persiophis fahimii* failed to find any additional specimens of this snake, we assume that this snake is a very rare species with a limited local distribution. Currently, there is not enough data to evaluate the conservation status of *Persiophis fahimii*; hence, further expeditions are needed to shed light on the distribution and ecology of this snake. We suggest it be considered to have the IUCN Red List status 'DD – Data Deficient.' But researchers should take care in studying the species, avoiding over collecting or disturbing the habitat. We suggest that the local conservation management around the type locality of the species is urgently required.

DISCUSSION

Additional information on *Dolichophis andreanus* (*Werner, 1917*) comb. nov.

Though Andreas' Racer was originally described as *Zamenis andreana* by *Werner (1917)*, it was an unknown and forgotten snake not listed in regional checklists *(Latifi, 1991; Leviton et al., 1992)* until researchers in the first decade of 21st centaury shed light on its distribution *(Rajabizadeh & Rastegar-Pouyani, 2006; Rajabizadeh & Rastegar-Pouyani, 2009; Schätti, 2001)*. Since the genetic proximity of the species to dwarf snakes (genus *Eirenis*) and morphologic proximity to whip snakes (genera *Hierophis* and *Dolichophis*) were in contrast *(Schätti & Monsch, 2004)*, its taxonomy was obscure and authors referred to it as *Coluber* (s. l.) *andreanus (Rajabizadeh & Rastegar-Pouyani, 2006)*. *Rastegar-Pouyani et al. (2008)* erroneously listed Andreas' Racer in the genus *Zamenis*. *Torki (2010)* assigned the species to the genus *Hierophis* without any taxonomic justification. Surprisingly, other authors followed this classification without further questioning its taxonomic status *(Chefaoui et al., 2018; Wallach et al., 2014)*. Recent phylogenetic studies on snakes cast doubt on the taxonomic placement of *Hierophis andreanus* within the genus *Hierophis (Figueroa et al., 2016)*. Our molecular phylogenetic results clearly indicate placement of *Hierophis andreanus* within the genus *Dolichophis* (Fig. 2), hence we suggest the new combination *Dolichophis andreanus* (Werner, 1917) comb. nov.

From a comparative point of view, the overall shape of skull and neurocranium in *Dolichophis andreanus* generally resembles that of *Eirenis* more than *Hierophis* and *Dolichophis*. In both *D. andreanus* and *Eirenis*, the neurocranium is wide, ovally shaped, bearing no elaborated V-shaped pair of crests on the parietal bones, and the braincase is large. The skull is

long and elliptical, well ossified and composed of relatively thick bones. On the tip of the snout, there is a single, pyramid-shaped bone (premaxilla), that is dorsally wedged between the nasals, and like *Eirenis*, it is projected less anteriorly than in *Hierophis* and *Dolichophis*. Compared to whip snakes, the neurocranium in *Dolichophis andreanus* is wider, bearing a less-elaborated V-shaped pair of crests on the parietal bones, again resembling *Eirenis*. The CT-scanned *Dolichophis andreanus* specimen has 10/10, 9/9, 10/9, 15/13 curved teeth on maxilla, palatine, pterygoid and dentary bone.

Based on the head and body scalation data, *Schätti & Monsch (2004)* inferred a sister-group relationship between *Dolichophis andreanus* and dwarf snakes of the genus *Eirenis*, especially based on similar traits including the low number of supralabial, infralabial, anterior temporal and dorsal scale rows. Morphological similarity between *Dolichophis andreanus* and *Eirenis* is striking. The evolutionary history of head and dorsal body scales, as well as total size shows that the most parsimonious state for the common ancestor of Western Palearctic racers, whip snakes and dwarf snakes is a large-size snake (total size more than one meter) having two anterior temporals, 8 supralabials, 9-10 infralabials and 19 dorsal scales. Total size of less than one meter, a single anterior temporal as well as 15, 17 and 18 dorsal body scales evolved independently in both *Eirenis* and *D. andreanus*. The number of supralabials and infralabials is not totally unique in dwarf snakes, hence 7-8 supralabials and 7-9 infralabials are present in the genus *Eirenis* and in *D. andreanus* too (Figs. 6-9).

Additional information on *Muhtarophis barani* (Olgun et al., 2007)

Although previous phylogenetic studies did not unambiguously resolve the phylogenetic position of Baran's Black-headed Dwarf Snake (*Avcı et al., 2015*; *Šmíd et al., 2015*; *Tamar et al., 2016*), our tree surprisingly places it strongly as the sister group to the genus *Scaphiophis*.

African Shovel-nosed Snakes (*S. albopunctatus* Peters, 1870 and *S. raffreyi* Bocourt, 1875) are large-sized snakes, maximum total length around 150 centimeters *(Broadley, 1994)*, distributed around the periphery of the Central African rain forest from Ghana to western Ethiopia and adjacent Sudan *(Largen & Rasmussen, 1993)*. In contrast, *Muhtarophis* is a dwarfed ground snake with maximum total length around 40 centimeters, reported from Hatay Province, Southern Turkey (*Avcı et al., 2015*).

The skull in *Scaphiophis* is robust, the premaxilla is large, beak shaped and divides the nasals, and each lateral projection of premaxilla is actually indeed divided into two lobes, the posterior nasals are articulated to the middle of the anterior frontal, the quadrate is not oblique nor slanting backward, dentition in a sample of *S. albopunctatus* is maxillary 15, palatine 9, pterygoid 8, dentary 18, and in a sample of *S. raffreyi* is 13, 7, 7, 16 respectively *(Bourgeois, 1968; Broadley, 1994)*. In *Muhtarophis*, the skull is also robust, having a large pyramid shaped premaxilla that is wedged between the anterior nasals. The posterior nasal is broadly articulated to the anterior frontal, the quadrate is more or less vertical, and the dentition in two examined samples consists of six maxillary 6 heterogeneous teeth (5 same size anterior teeth and one about two times larger rear tooth), palatine 4, pterygoid 8, dentary 9 (*Avcı et al., 2015*). Though there are some shared osteological traits between *Scaphiophis* and *Muhtarophis*, the obvious differences in osteology of these genera makes a sister group relationship doubtful, despite the strong support estimated here. The variable placement among the phylogenetic analyses may result from a lack of taxon sampling, or more likely, inadequate sampling of independent loci and phylogenetically informative molecular characters. Hence, further research is needed to identify the phylogenetic position of *Muhtarophis*.

The challenge of monotypy

Since currently only one species is known in *Persiophis*, the genus is monotypic. Moreover, the sole species is known only from a single specimen, which is a common problem in squamate taxonomy *(Meiri et al., 2018)*. Two scenarios exist which may, in the future, avoid the challenge of monotypy and demonstrate monophyly of the genus based on cladistic theory, which generally demands that a genus is a monophyletic group of species; thus, monotypic genera are not phylogenetically informative *(Platnick, 1976)*. First, since the reptile fauna (especially snakes) of southwestern Asia is not sufficiently studied and many undescribed taxa still likely remain (*Rajabizadeh, 2018*), it is possible that other species within the genus *Persiophis* exist that have not been discovered to date, either extant or in the fossil record. Regardless, since the species *Persiophis fahimii* is strongly supported as a lineage distinct from any existing snake genera, based on the molecular phylogeny and osteological analyses, we here accept it as a representative of a distinct genus *Persiophis* that is currently monotypic.

Miniaturization in Old World racers

Our phylogenetic data indicate proximity in morphological and anatomical traits between *Dolichophis andreanus* and the genus *Eirenis*, which we suggest is an example of parallel evolution. Parallel evolution is a particular type of convergent evolution defined as a similarity that has appeared independently in different closely related taxa *(McGhee, 2011)*. In the monophyletic clade of the genera *Orientocoluber*, whip snakes (genera *Hierophis* and *Dolichophis*), and dwarf snakes of the genus *Eirenis*, reduction in body size (to less than one meter in maximum adult size), temporal and dorsal scale numbers, as well as reduction in labial scale number took place in two different, but closely related lineages, *D. andreanus* and the genus *Eirenis* (Fig. 7-9). Hence, our tree suggests that the similar morphological and anatomical traits among *D. andreanus* and genus *Eirenis* are homoplastic traits (or convergent), not

480 secondary homologous traits (or synapomorphic). A hypothesis is that in *D. andreanus* and the
481 genus *Eirenis* morphological and anatomical homoplastic traits appeared as a result of overall
482 size reduction.

483 This hypothesis is supported by neural anatomy of these snakes as well. Several studies in
484 various groups of vertebrates demonstrated that brain size does not reduce isometrically with
485 body size *(Roth et al., 1995; Weston & Lister, 2009; Yeh, 2002)*. Allometric decrease in brain
486 size vs. body size may reflect a higher size-threshold for the brain compared to the body of
487 smaller organisms, in order to maintain all required neuronal activities *(Hanken, 1984)*. Thus,
488 negative allometry of the brain size relative to body size is observed in many dwarfed vertebrates.
489 Since brain size directly affects the size of the neurocranium, relatively bigger neurocrania are
490 observed in dwarfed vertebrates, including *Dolichophis andreanus* and *Eirenis*. Our suggested
491 hypothesis that needs to be tested is that, bigger neurocrania may induce a spatial constraint to
492 other head elements including size of the snout. Thus, smaller head elements may be
493 accompanied by a lower number of head scales including labials and temporals. Reduced head
494 scalation is also observed in other dwarfed colubrid snakes, *e.g.* dwarf snakes of the genus
495 *Tantilla* having maximum total size 71.1 cm, supralabials 6-7, infralabials 6, anterior temporals 1
496 and dorsal scales 15 *(Koch & Venegas, 2016; Wilson & Mata-Silva, 2014)*.
497

498 **CONCLUSIONS**

499 Here, we present new molecular sequence data and a new phylogenetic analysis of snakes,
500 focusing primarily on Colubrinae from southwestern Asia. We find continued uncertainty in the
501 placement of the enigmatic Turkish genus *Muhtarophis* based on osteological comparisons,
502 despite strong support in the phylogenetic analysis. On the basis of the tree and morphology, we
503 confidently reassign *Hierophis andreanus* from *Hierophis* to *Dolichophis*, hereafter referred to

504 *Dolichophis andreanus*. Our morphological and molecular data also suggest a potential instance
505 of convergent miniaturization in these Old-World racers. Finally, we report on the discovery of a
506 new genus and species of ground snake, *Persiophis fahimii*, from southeastern Iran. Our data
507 highlight the importance of broad phylogenetic sampling and ground-level field research to
508 gather an accurate picture of global biodiversity, phylogenetic relationships, and evolutionary
509 patterns in groups such as snakes.
510

511 **ACKNOWLEDGMENTS**

512 We are grateful to Eskandar Rastegar-Pouyani for his kind assistance in the field and reviewing
513 the manuscript. Thanks to Firouzeh Bordbar (Bahonar University, Kerman) for identification of
514 plant species. We are also grateful to Jens Vindum and Lauren Scheinberg (CAS) and Ted
515 Papenfuss (MVZ) for their assistance. Also we thank Daniel Melnikov, Hossein Nabizadeh and
516 Morteza Moaddab for their help in the field.
517

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Table 1(on next page)

Additional specimens added to the matrix of *Figueroa et al. (2016).*

Species	Locality	Voucher	Reference
Muhtarophis barani	-	ZMHRU2014/60-5	*Tamar et al., 2016*
Wallaceophis gujaratensis	-	NCBS HA-105	*Mirza et al., 2016*
Wallophis brachyura	-	-	*Mirza & Patel, 2018*
Lytorhynchus maynardi	Iran	MVZ234499	*Tamar et al., 2016*
Lytorhynchus maynardi	Pakistan	MVZ248463	*Tamar et al., 2016*
Lytorhynchus gaddi	Iran	MVZ234500	*Tamar et al., 2016*
Lytorhynchus diadema	Oman	CN4093	*Tamar et al., 2016*
Lytorhynchus diadema	Morocco	IBES1329	*Tamar et al., 2016*
Lytorhynchus diadema	Egypt	SPM002589	*Tamar et al., 2016*
Rhynchocalamus satunini	Iran	CAS228723	*Tamar et al., 2016*
Rhynchocalamus satunini	Turkey	ZMHRU2015/0	*Tamar et al., 2016*
Rhynchocalamus arabicus	Oman	CN4780	*Tamar et al., 2016*
Rhynchocalamus dayanae	Israel	TAU.R17093	*Tamar et al., 2016*
Rhynchocalamus melanocephalus	Israel	HUJ.R22054	*Tamar et al., 2016*

1

Figure 1

Distribution map of *Persiophis fahimii* Gen. et sp. nov. (star) and *Hierophis andreanus* (circle) in Iran.

Localities of *Hierophis andreanus* are based on *Rajabizadeh (2018)* . Arrows indicate the locality of *Hierophis andreanus* specimens for which genetic data were included in the molecular phylogenetic analysis, along with *Persiophis fahimii* **Gen. et sp. nov.**

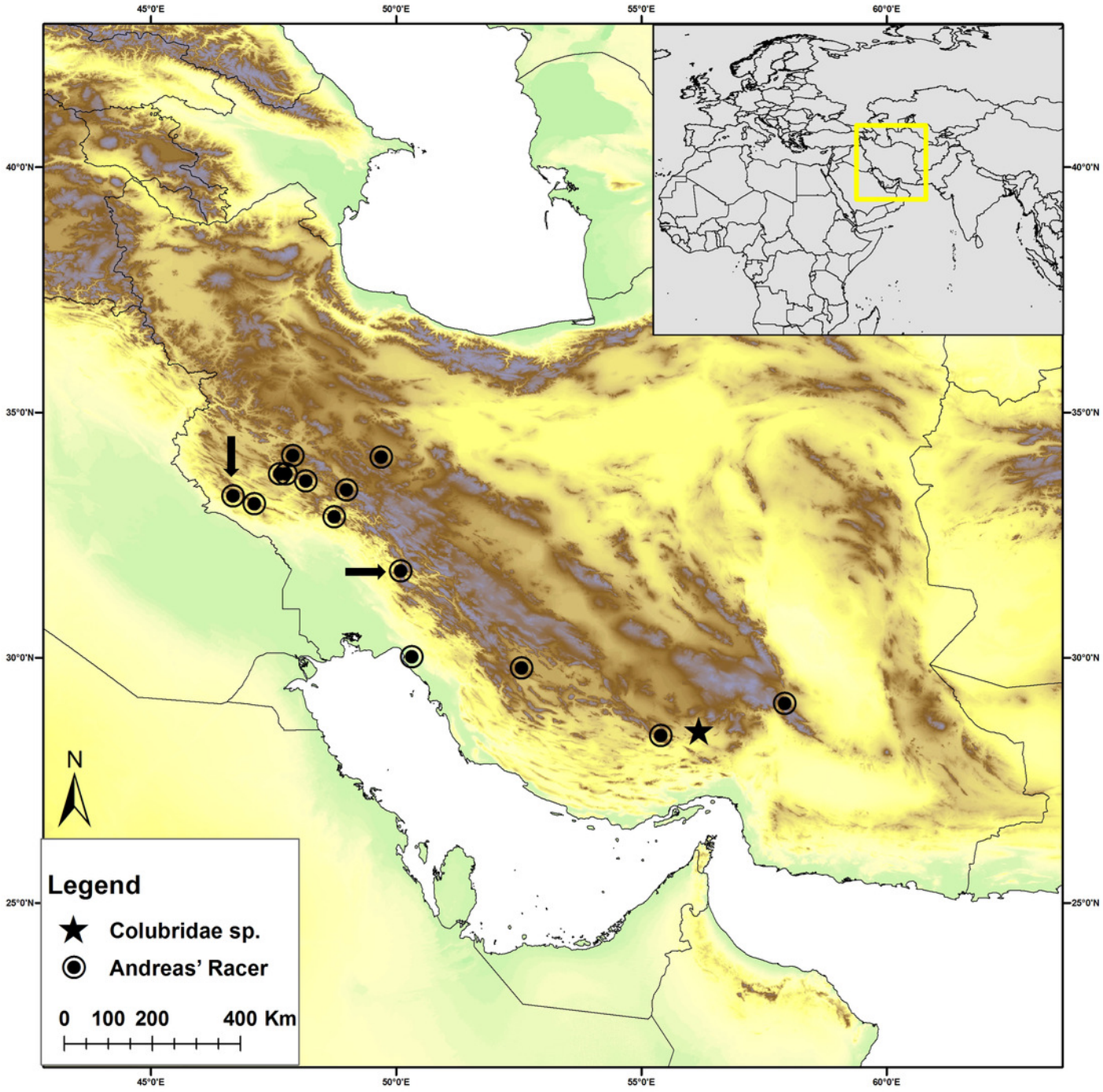

45°0'E
50°0'E
55°0'E
60°0'E
40°0'N
35°0'N
30°0'N
25°0'N
N
Legend
Colubridae sp.
Andreas' Racer
0 100 200 400 Km

Figure 2

Resulting topology and SHL-support values from reanalysis of the matrix of (Figueroa et al., 2016) with additional colubrines from SW Asia.

The species *Hierophis andreanus* is nested within *Dolichophis* with strong support, while *Persiophis fahimii* **Gen. et sp. nov.** forms a distinct lineage as the sister group to *Rhynchocalamus* and clearly represents a new genus and species.

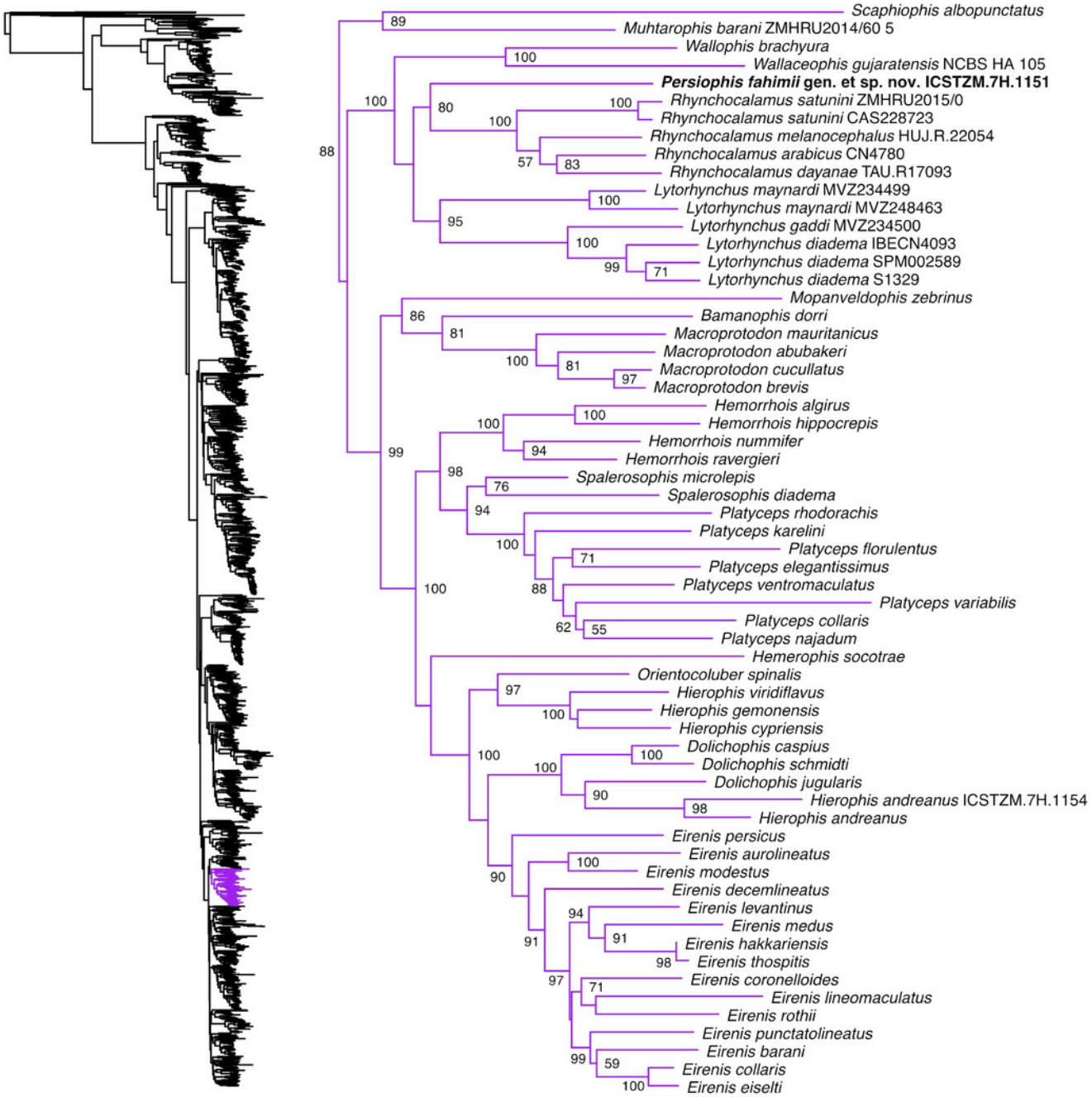

Scaphiophis albopunctatus
Muhtarophis barani ZMHRU2014/60 5
Wallophis brachyura
Wallaceophis gujaratensis NCBS HA 105
Persiophis fahimii gen. et sp. nov. ICSTZM.7H.1151
Rhynchocalamus satunini ZMHRU2015/0
Rhynchocalamus satunini CAS228723
Rhynchocalamus melanocephalus HUJ.R.22054
Rhynchocalamus arabicus CN4780
Rhynchocalamus dayanae TAU.R17093
Lytorhynchus maynardi MVZ234499
Lytorhynchus maynardi MVZ248463
Lytorhynchus gaddi MVZ234500
Lytorhynchus diadema IBECN4093
Lytorhynchus diadema SPM002589
Lytorhynchus diadema S1329
Mopanveldophis zebrinus
Bamanophis dorri
Macroprotodon mauritanicus
Macroprotodon abubakeri
Macroprotodon cucullatus
Macroprotodon brevis
Hemorrhois algirus
Hemorrhois hippocrepis
Hemorrhois nummifer
Hemorrhois ravergieri
Spalerosophis microlepis
Spalerosophis diadema
Platyceps rhodorachis
Platyceps karelini
Platyceps florulentus
Platyceps elegantissimus
Platyceps ventromaculatus
Platyceps variabilis
Platyceps collaris
Platyceps najadum
Hemerophis socotrae
Orientocoluber spinalis
Hierophis viridiflavus
Hierophis gemonensis
Hierophis cypriensis
Dolichophis caspius
Dolichophis schmidti
Dolichophis jugularis
Hierophis andreanus ICSTZM.7H.1154
Hierophis andreanus
Eirenis persicus
Eirenis aurolineatus
Eirenis modestus
Eirenis decemlineatus
Eirenis levantinus
Eirenis medus
Eirenis hakkariensis
Eirenis thospitis
Eirenis coronelloides
Eirenis lineomaculatus
Eirenis rothii
Eirenis punctatolineatus
Eirenis barani
Eirenis collaris
Eirenis eiselti

Figure 3

The holotype of *Persiophis fahimii* Gen. et sp. nov., live specimen *in situ.*

Details of head scalation in close-up (a) lateral, (b) ventral and (d) dorsal views; (s) lateral view of the fore body, and (e) dorsal view of the whole body. Photos by Roman A. Nazarov.

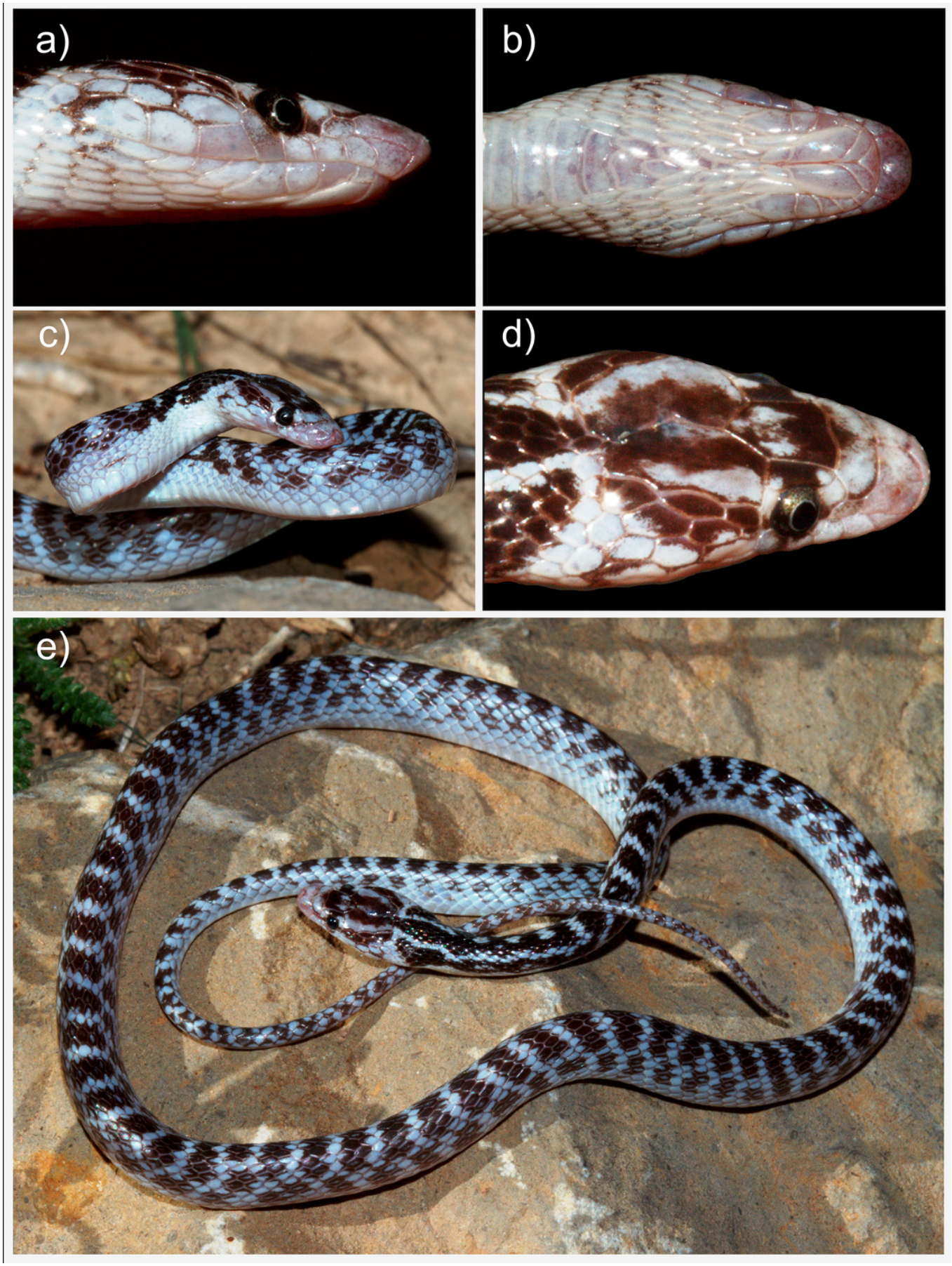

a)
b)
c)
d)
e)

Figure 4

Micro-CT reconstruction of the skull of *Persiophis fahimii* Gen. et sp. nov.

(a) Lateral, (b) dorsal, (c) ventral and (d) sagittal views of the skull of the holotype. Visualization by Mahdi Rajabizadeh.

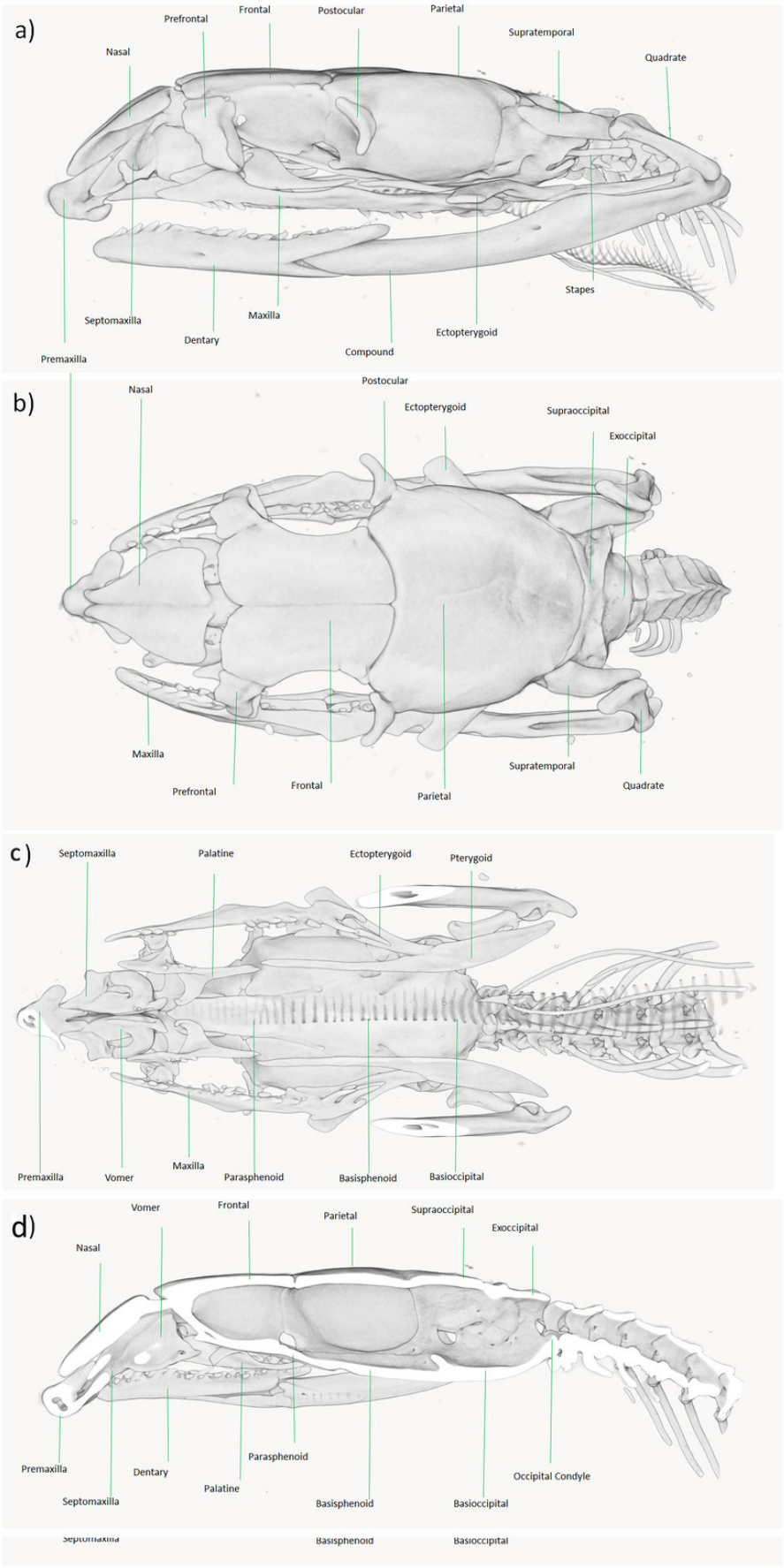

a)
Prefrontal
Frontal
Postocular
Parietal
Supratemporal
Quadrate
Nasal
Stapes
Septomaxilla
Maxilla
Dentary
Ectopterygoid
Compound
Premaxilla
b)
Nasal
Postocular
Ectopterygoid
Supraoccipital
Exoccipital
Maxilla
Prefrontal
Frontal
Parietal
Supratemporal
Quadrate
c)
Septomaxilla
Palatine
Ectopterygoid
Pterygoid
Premaxilla
Vomer
Maxilla
Parasphenoid
Basisphenoid
Basioccipital
d)
Vomer
Frontal
Parietal
Supraoccipital
Exoccipital
Nasal
Premaxilla
Dentary
Parasphenoid
Palatine
Occipital Condyle
Septomaxilla
Basisphenoid
Basioccipital

Figure 5

Habitat of *Persiophis fahimii* Gen. et sp. nov. at the type locality in vicinity of Orzueeyeh City, Kerman Province, Southern Iran.

(a) Macrohabitat, arrow indicates the place where the snake was collected; (b) microhabitat at the site of collection of the type specimen. Photos by Mahdi Rajabizadeh.

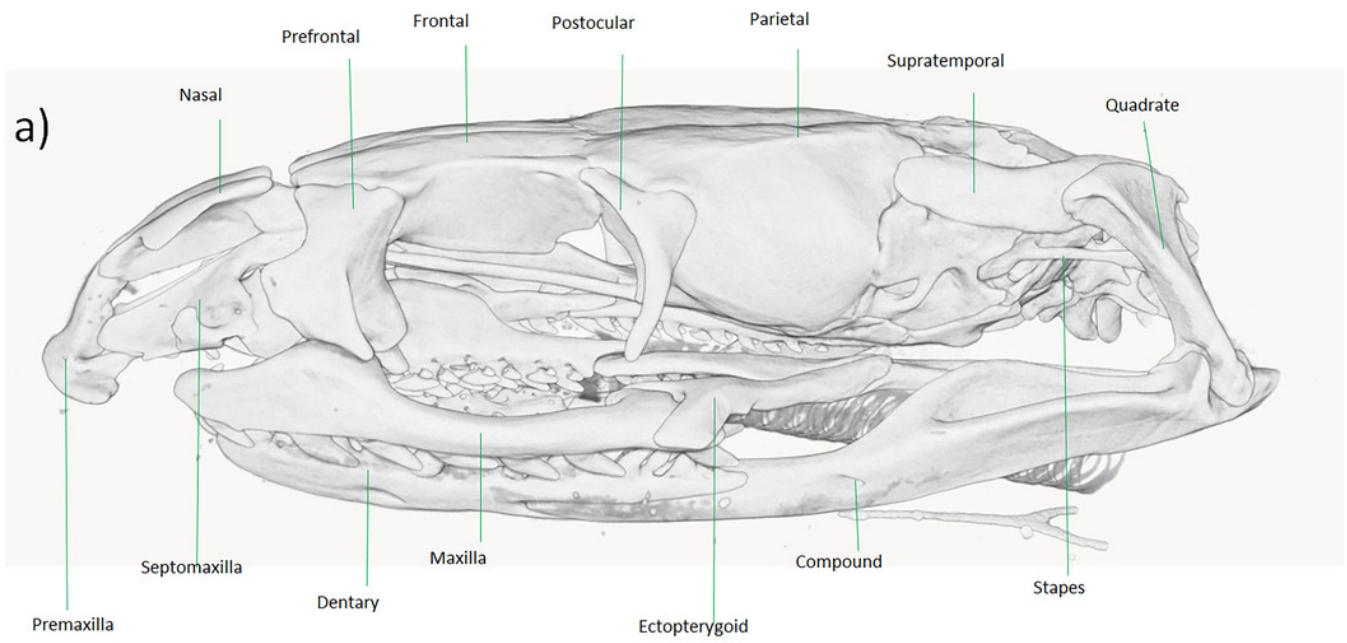
a)

b)

Figure 6

Micro-CT reconstruction of the skull cranial osteology of *Dolichophis andreanus* comb. nov.

(a) Lateral and (b) dorsal views of the skull. Visualization by Mahdi Rajabizadeh.


a)
Nasal
Prefrontal
Frontal
Postocular
Parietal
Supratemporal
Quadrate
Premaxilla
Septomaxilla
Dentary
Maxilla
Ectopterygoid
Compound
Stapes

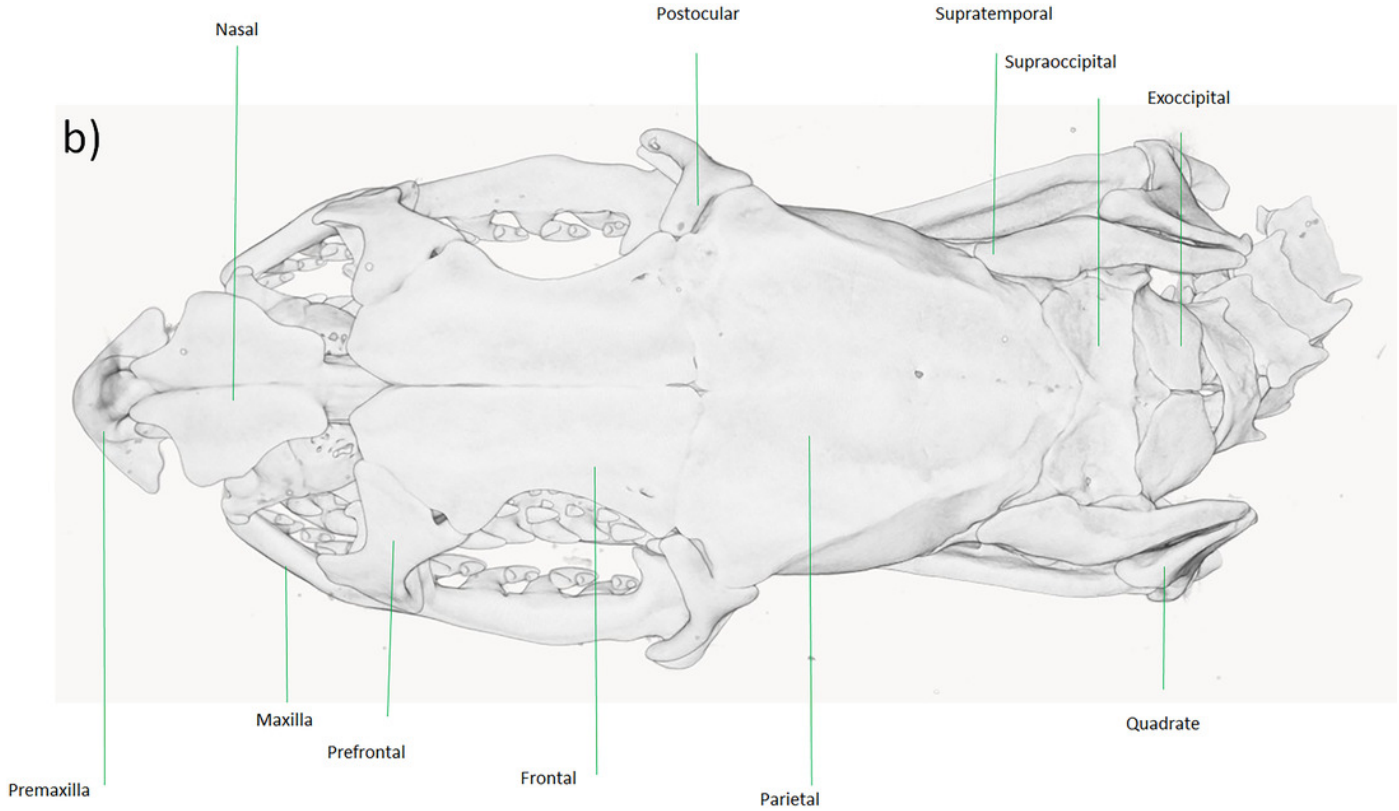

b)
Nasal
Postocular
Supratemporal
Supraoccipital
Exoccipital
Premaxilla
Maxilla
Prefrontal
Frontal
Parietal
Quadrate

Figure 7

Character history of the anterior temporal compared to dorsal scales across the Western Palearctic racers, whip snakes and dwarf snakes.

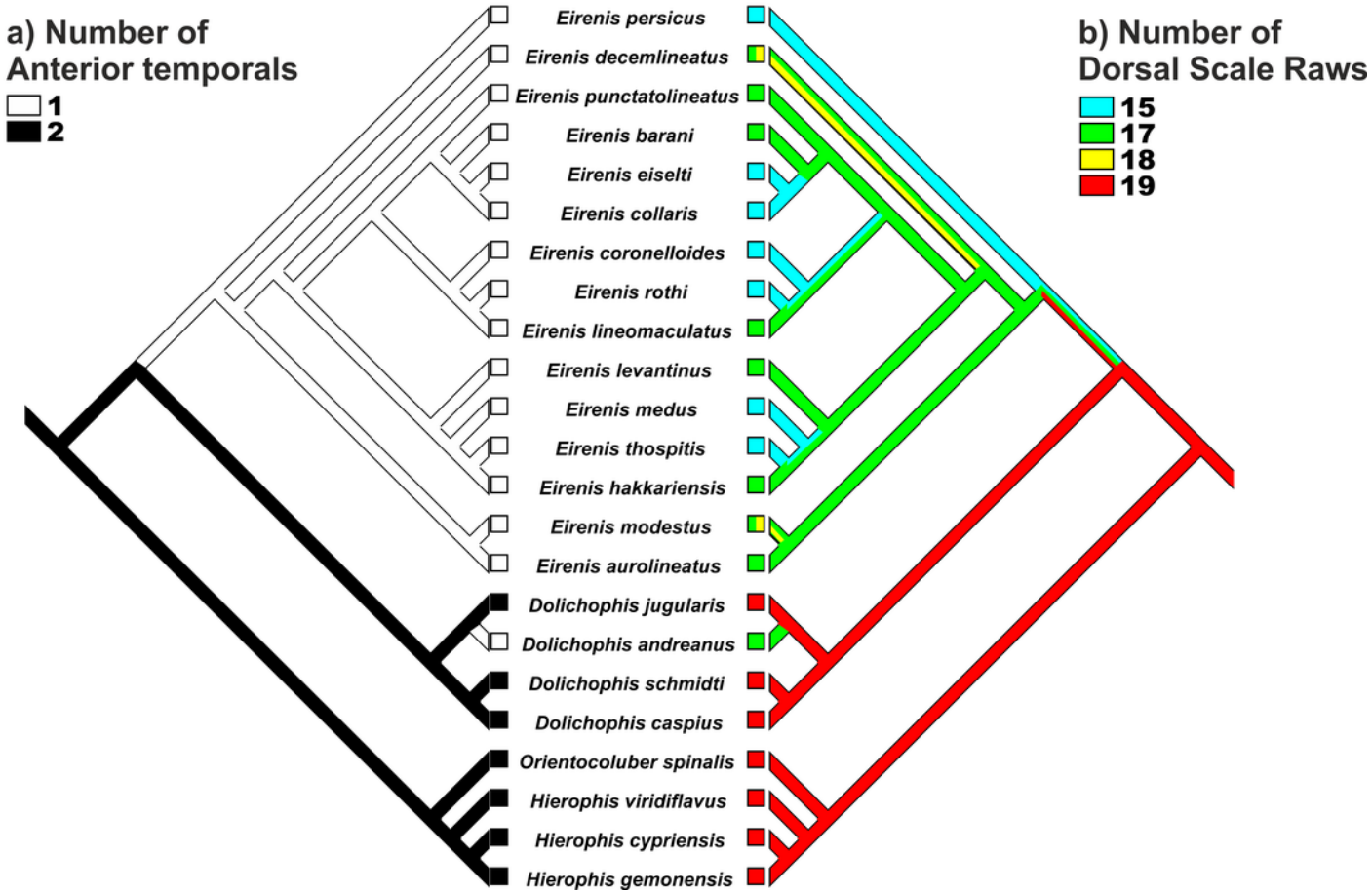


Figure 8

Character history of the labial scales across the Western Palearctic racers, whip snakes and dwarf snakes.

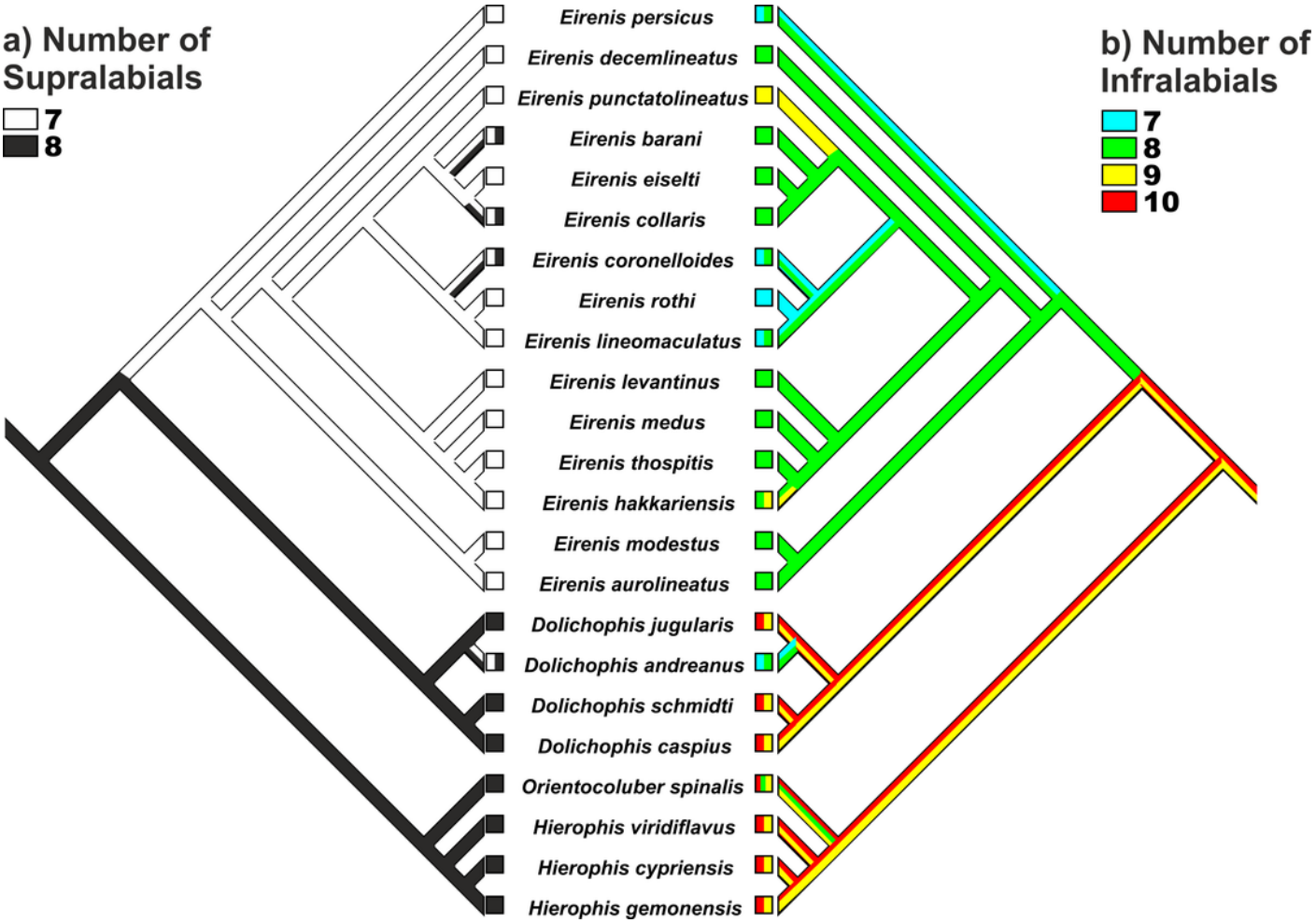
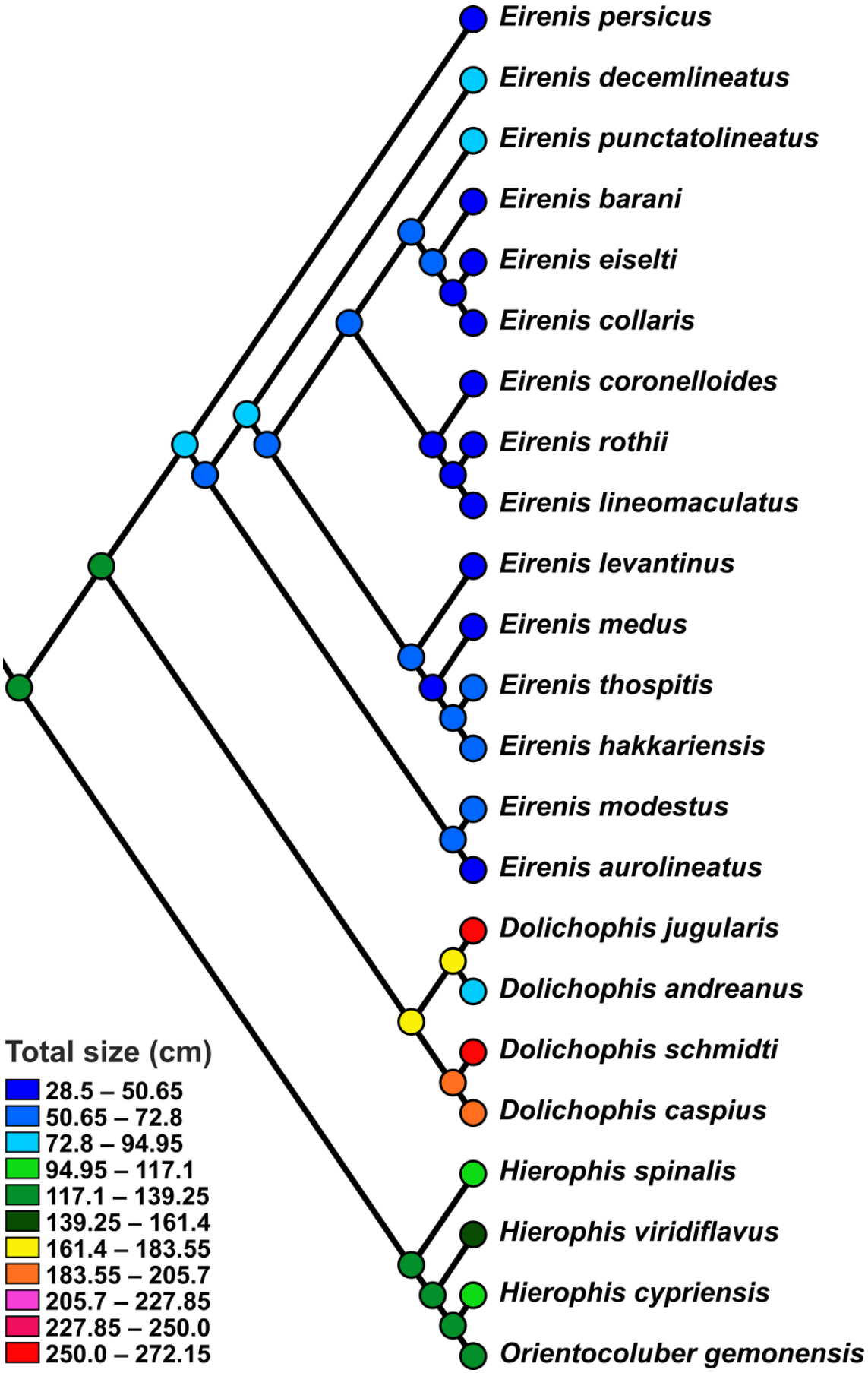


Figure 9

Character history of total body size across the Western Palearctic racers, whip snakes and dwarf snakes.


Eirenis persicus
Eirenis decemlineatus
Eirenis punctatolineatus
Eirenis barani
Eirenis eiselti
Eirenis collaris
Eirenis coronelloides
Eirenis rothii
Eirenis lineomaculatus
Eirenis levantinus
Eirenis medus
Eirenis thospitis
Eirenis hakkariensis
Eirenis modestus
Eirenis aurolineatus
Dolichophis jugularis
Dolichophis andreanus
Dolichophis schmidti
Dolichophis caspius
Hierophis spinalis
Hierophis viridiflavus
Hierophis cypriensis
Orientocoluber gemonensis
Total size (cm)
28.5 – 50.65
50.65 – 72.8
72.8 – 94.95
94.95 – 117.1
117.1 – 139.25
139.25 – 161.4
161.4 – 183.55
183.55 – 205.7
205.7 – 227.85
227.85 – 250.0
250.0 – 272.15