

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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RUNNING TITLE: A new genus of Colubrinae

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25 ABSTRACT

26 Reptiles and amphibians are still being described worldwide at a pace of hundreds of species a
 27 year. While many discoveries are from remote tropical areas, biodiverse arid regions still harbor
 28 many novel taxa. Here, we present an updated phylogeny of colubrid snakes from the Western
 29 Palearctic by analyzing a supermatrix of all available global snake species and report on the
 30 discovery of a new genus and species of colubrine snake from southeastern Iran. The new taxon,
 31 named *Persiophis fahimii* **Gen. et sp. nov.**, is nested within ~~the clade of~~ Middle Eastern and
 32 South Asian ground racers (*Lytorhynchus*, *Rhynchocalamus*, *Wallaceophis*, and *Wallophis*). This
 33 species has a derived morphology including a projected premaxilla, an edentulous pterygoid and
 34 occurrence of short and blunt teeth on the palatine, maxillae and dentary bones. We also report
 35 on the osteology and phylogenetic placement of several poorly studied colubrids: *Coluber* (s. l.)
 36 *andreas* (reassigned to *Dolichophis*) and *Muhtarophis barani*. The biodiversity in colubrine
 37 snakes is likely much higher than previously realized, particularly in southwestern Asia.

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39 **SUBJECTS:** Biodiversity, Evolutionary Studies, Taxonomy, Zoology

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41 **KEYWORDS:** *Persiophis*, supermatrix, Squamata, Iran, *Rhynchocalamus*, *Eirenis*,
 42 *Muhtarophis*, parallel evolution, *Coluber*, *Dolichophis*

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44 INTRODUCTION

45 The family Colubridae is the most speciose group of snakes, inhabiting a diverse array of
 46 ecosystems worldwide except Antarctica and some remote oceanic islands (*Vitt & Caldwell*
 47 2013). While at least 1,959 species of colubrid snakes have been described (*Uetz et al. 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*) and with species-level sampling (*Figuerola 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 (*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 ~~phylogeny of the whole group~~.

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. In phylogenetics, extensive sampling may increase accuracy (*Zwickl & Hillis 2002*). Thus, densely-sampled supermatrices of all available gene sequences are proposed 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 resources and ~~providing new concepts and methods for species delimitations~~ 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 (*Figuerola et al. 2016*). To this matrix, we have added data from two rare and poorly known colubrid snakes from Iran. The first is Andreas' Racer, *Coluber (s. l.) andreanus* (*Werner, 1917*), an endemic colubrid snake from Iran with ambiguous phylogenetic placement (*Figuerola et al. 2016; Schätti & Monsch 2004*), currently classified in the genus *Hierophis* (*Wallach et al.*

2014). The second one is a previously unknown taxon, discovered by us during our recent field surveys 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 fieldwork in southern and western Iran (Fig. 1) in 2008, two specimens of rare colubrid snakes were collected by R. Nazarov and M. Rajabizadeh: a sample of Andreas' Racer, and a specimen of Colubridae **Gen. sp.** 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 for molecular phylogenetic analysis. The skulls of both specimens were examined using micro-CT scanning. Specimen information are as follows:

1. *Andreas' Racer*, 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. sp.**, ICSTZM.7H.1151, collected from around Orzuieh City, southern Iran, Kerman Province (Fig. 1), preserved in 75% ethanol.

Field works, 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. 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 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 *Andreas' Racer* 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. sp.**, 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 (*Masschaele et al. 2007*). The setup was a transmission head of a dual-head X-ray tube (Feinfocus FXE160.51) and an a-Si flat 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.

Morphological evolution

We used phylogenetic comparative methods to test for possible convergence in size and shape

within the focal clade. We used the Parsimony Ancestral State Reconstruction Method in Mesquite ver. 2.75 (Maddison & Maddison 2011) to reconstruct the evolutionary history of morphological traits across the western Palearctic racers, whip snakes and dwarf snakes. Morphological data were extracted from the literature (Mahlow *et al.* 2013; Rajabizadeh 2018a; Schätti 1987; Kharin & Akulenko 2008). The cladogram is a pruned subtree of our large-scale phylogeny, comprising of the Western Palearctic whip snakes (genera *Hierophis* and *Dolichophis*), Slender Racer (*Orientocoluber*), Andreas' Racer, and dwarf snakes of the genus *Eirenis*. We examined several traits related to overall body-size and head size, to test the hypothesis that dwarfism has evolved convergently at least twice in the group. We based this on our phylogenetic hypothesis for Andreas' racer, which is a dwarf species that is estimated outside of *Eirenis* (see Results).

RESULTS

Phylogeny

The ML tree (see Fig. 2) is overall highly similar to many recent estimates of colubroid snake phylogeny (Pyron *et al.*, 2011; Figueroa *et al.*, 2016), with a few major exceptions highlighted in part by our new sampling. Our results confirm the occurrence of a monophyletic lineage (SHL = 88) of Western Palearctic colubrids including 17 genera and Colubridae **Gen. sp.** However, phylogenetic placement of all genera within this clade is not fully resolved, due to low supporting values of some inter-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 colubrids that we highlight here for further attention.

The first involves a small radiation of colubrine ground-snakes endemic to southwestern Asia (including Colubridae **Gen. sp.**), and the second involves colubrids from the Old-World racer lineage (*Coluber sensu lato*). In the first sub-clade (see Tamar et al., 2016), the genera *Wallaceophis* and *Wallophis* share a sister-group relationship that is strongly supported (SHL = 100), and ~~which forms~~ a lineage that is the sister group (SHL = 100) to the genera *Lytorhynchus*, *Rhynchocalamus* and Colubridae **Gen. sp.** The phylogenetic relationship between the latter genera is poorly supported. 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.

Among the remaining lineages, the Western Palearctic whip snakes (genera *Hierophis* and *Dolichophis*), the Slender Racer (*Orientocoluber*), Andreas' Racer, and dwarf snakes of the genus *Eirenis* are confirmed in our tree as a monophyletic group (SHL = 100). This clade comprises one lineage including the genera *Orientocoluber* and *Hierophis* (sister relationship strongly supported; SHL = 97), and a second lineage including the genera *Dolichophis* and *Eirenis*. Although the monophyly of each of the latter genera is confirmed, their phylogenetic relationships are weakly supported. Furthermore, Andreas' Racer is placed within the genus *Dolichophis* as the sister group to *D. jugularis* with strong support (SHL = 90), and to which we formally reassign it, with *D. jugularis* as the sister species. Based on our tree, monophyly of the

genus *Dolichophis* is confirmed (SHL = 100), and a basal divergence within the genus is supported (SHL = 100) between a sub-group comprising *D. schmidtii* and *D. caspius* (SHL = 100), and another sub-group of *D. jugularis* and **Andreas' Racer**. The genus *Hemerophis* is also placed in this clade, but its position is not clear.

Systematics

Phylogenetic results indicate that Colubridae **Gen. sp.** is nested within the subfamily Colubrinae, and we estimate strong support for a sister group relationship with snakes of the genus *Rhynchocalamus*, while both clades are distantly diverged. From an osteological point of view, Colubridae **Gen. sp.** lacks teeth on the premaxilla and proteroglyphous or solenoglyphous teeth on the maxilla, a coronoid bone in the mandible, girdle or limb elements, and valvular dorsal nostrils (see Osteology, below), and so belongs to the family Colubridae (*Vitt & Caldwell 2013*). The occurrence of a broad articulation between snout bones and the lack of 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. sp.** 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 *Elachistodon*, *Dasypeltis*, *Lytorhynchus* and *Rhynchocalamus* as well (*Avci et al. 2015; Gans 1952; Gans 1954; Leviton & Anderson 1970*), the combination of osteological traits of Colubridae **Gen. sp.** 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)

Holotype. Adult female, ICSTZM.7H.1151 (field number: RAN 2948). Iran, Kerman province, 19 Km, Northwestern Orzuieh Region, 1350 meters ASL; coll. R. Nazarov, May 2008 (Figs. 3-5).

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* **Gen. et sp. nov.**. He started his scientific career in herpetology in 1999 with T. Papenfuss (University of California, Berkeley), and during 18 years of professional activities, he managed and contributed to many biodiversity and conservation projects *e.g.* conservation of sea turtles in Qeshm Island, Euphrates Softshell Turtle and Kaiser's spotted newt in Kuzestan Province, Latifi's Viper in Tehran Province, Mugger Crocodile in Sistan & Baluchestan Province, as well studying the herpetofauna of Iran and Iraqi Kurdistan. He contributed to several ISI publication including the checklist of reptiles of Iran (*Safaei-Mahroo et al. 2015*), a distribution note on *Rhinogecko misonnei* (*Moradi et al. 2011*) and data on *Lytorhynchus maynardi* (*Shafiei et al. 2015*). He was a PhD student in IAU, Tehran, studying on the conservation of black bears in southeastern Iran, but sadly passed away in an aircraft crash in Dena Mountain in central Zagros in February 2018. We suggest the common name “Fahimi’s Ground Snake” in English, and (مار زمینی فهیمی) in Farsi (pronounced as “mare zæminə fæhimi:” according to International Phonetic Alphabet)

Diagnosis. For the genus and species, *Persiophis fahimii* **Gen. et sp. nov.** is

distinguished within the subfamily Colubrinae by a combination of distinct osteological characters, including a projected premaxilla; the occurrence of three vestigial teeth on the palatine; a thin, edentulous pterygoid; short and blunt teeth on the maxillae and dentary, occurrence of edentulous parts on the anterior and middle region of the maxillae; a fully fused basioccipital and basisphenoid; the occurrence of a highly oblique quadrate bone attached to the posterior tip of a somewhat elongated supratemporal.

Comparisons. The above mentioned anatomical traits are in contrast to those observed in the genus *Rhynchocalamus*, including a small, thin, down and backward directed premaxilla; the occurrence of 0-2 vestigial teeth on the palatine; a broad, edentulous pterygoid; relatively elongated, posteriorly curved teeth on the maxillae and dentary; a closed suture between basioccipital and basisphenoid; a short and nearly vertical quadrate bone on each side of cranium, and a broad attachment surface for a short supratemporal (Avci et al. 2015). Also, *Persiophis fahimii* **Gen. et sp. nov.** differs from *Rhynchocalamus* and *Lytorhynchus* in having maxillae that anteriorly and medially are edentulous and in between, bear small and vestigial teeth except for the last two, in contrast to relatively elongated, posteriorly curved teeth over most of the maxillary length in *Rhynchocalamus* and *Lytorhynchus* (Avci et al. 2015; Leviton & Anderson 1970). *Persiophis* differs from *Dasypeltis* in having a well projected premaxilla and having smooth edges on the anterior frontal and posterior nasals (compared to small premaxilla and a serrated anterior free edge of frontals and posterior edges of nasals (Gans 1952). The new genus differs from the rest of known genera of Colubrinae in having an edentulous pterygoid.

Description of the holotype. Body and tail slender and elongated. Head small and elongated, not distinct from neck. Snout-vent length 380 mm, tail length 115 mm, head length 12.9 mm, head width 7.6 mm.

Head scalation. The rostral scale anteriorly projected, the tip of rostral 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, ~~frontal~~ shorter than parietals. ~~Supralabials~~ are smaller in length and width than the frontals. Parietals ~~elongated and asymmetric, median suture between them not straight~~. On the side of the head, the nasal elongated and rectangular, the nostril situated ~~upward~~, about mid length of the nasal. Loreal is small, longer than ~~deep~~. ~~Eight~~ supralabials ~~bordering the mouth on each side of the head~~, the fourth and fifth bordering the eye. A single preocular and ~~a single anterior subocular~~ on each side of the head, 1/2 (hereafter values given in right/left order) postoculars; 3/2 anterior and 3/3 posterior temporals. ~~Eight~~ infralabials bordering the mouth on each side of the head, ~~the first and second~~ bordering the ~~posterior~~ genials. On the underside of the head, the mental small and triangular. Anterior **chin shields** small, in contact with each other, obliquely elongated towards the border of mouth, median suture between the anterior chin shields about the length of mental scale. Posterior chin shields contacting each other, elongated and larger than the anterior chin shields, median suture between them slightly more than twice the length of suture between the anterior chin shields.

Body scalation. Dorsal scales smooth, generally having a single apical pit. **Dorsal scales** at the level of one head length posterior to the head, midbody and one head length anterior to the **anus**, in 19, 15, and 15 longitudinal rows, respectively. On the underside of the body, two **gular** scales (counted following Dowling, 1951), followed by 206 ventral ~~plates~~. The anal plate divided, followed by **83 pairs of subcaudal scales**.

Coloration. The dorsal head ground color ~~grayish white~~, with a blackish blotch on the posterior prefrontals and anterior frontal, and a parenthesis-shaped blackish blotch on the parietals. Dorsal head scale sutures with irregular feebly blackish dots. On the sides of head, irregular blackish blotches scattered around eye, a ~~blackish stripe running~~ from posterior eye edge ~~along~~ the margin of ~~parietal~~ on each side of the head. ~~Supralabials and infralabials~~ whitish with irregular blackish

dots adjacent to the eye. The underside of the head whitish. Dorsal body and tail ground color grayish white. Three blackish longitudinal stripes on the dorsal and side of the nape, changing to continuous black blotches on dorsal surfaces of body and tail. Dorsum with nearly parallel blackish dorsal bands, having irregular margins, the width of each band about one and a half of dorsal scale length, separated by a grayish-white interspace of about the length of one scale. Body sides with continuous blackish blotches alternating with dorsal bands. Dorsal blotches fade to scattered blackish spots posteriorly on dorsal surfaces of the tail. The ventral side of the body whitish.

Cranial Osteology. The skull in *Persiophis* is long and elliptical and well ossified. At the tip of the snout, the single, pyramid-shaped premaxilla is deeply wedged in the space between the septomaxillae and the nasals. The nasals are directed downward. Left and right articulated nasals form a median septum between the nasal cavities and cover it dorsally. Ventrally the nasals form a process which lies in between the two frontals. Left and right septomaxillae are plate-like, bifurcate anteriorly and in contact medially. They form the floor of nasal cavity. Septomaxillae contact the nasal septum medially and posteriorly form a process that contact the frontals. The septomaxillae are partly fused with the vomers. The toothless vomers lie beneath the two septomaxillae and form a pair of spherical cavities in which lies the vomeronasal organs. The vomeronasal organs open by paired orifices into the buccal cavity. On each side of the head, a cone-shaped prefrontal borders the orbit anteriorly. Dorsally, the prefrontals have a tight articulation with the anterolateral surface of the frontals, and ventrally they bear a rather loose articulation with the maxillae.

The neurocranium is composed of compactly ossified bones, fully fused to each other by to form a complete enclosure of the brain. Left and right frontals are well separated at the tip but joined together along the rest of their length. Parietals are ovally shaped, fused together to form a

single bone (largest cranial element) that dorsally roofs the braincase, bearing no elaborated crests. Laterally it extends far down either side of the brain, reaching the basisphenoid and the prootics. Left and right postorbitals articulate with the anterolateral surfaces of the parietal and form the dorsoposterior boundary of each orbit.

Left and right prootics are quadrate shaped bones, partly fused with the parietal and forming the anterior walls of each internal otic capsule. They also constitute the anterior half of each fenestra ovalis and the posterolateral wall of the braincase. Left and right supraoccipitals are fused together to form a single bone. Externally it roofs the posterior brain cavity, internally it expands to form the posterior part of each otic capsule. A pair of diagonal crests extend transversally along the posterior part of the supraoccipitals. Left and right exoccipital bones form the posterolateral wall of the braincase, as well as part of its roof. They are fused with the opisthotics and together surround the jugular foramen and extend forward to form the posterior border of the fenestra ovalis. They form the entire oval foramen magnum, except for a small ventral portion of the occipital condyle. The basioccipital forms the floor of the posterior part of the brain cavity and the ventral portion of the occipital condyle. It completes the foramen magnum and creates a big, thick and raised occipital condyle. The basioccipital forms the 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* **Gen. et sp. nov.** is very scarce. 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), *Gymnocarpus decander* (Caryophyllaceae), *Convolvulus* sp. (Convolvulaceae), *Helianthemum* sp. (Cistaceae), and *Diceratella persica* (Apiaceae).

Conservation. Since several field expeditions in the type locality of *Persiophis fahimii* **Gen. et sp. nov.** 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* **Gen. et sp. nov.**; 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)

Though Andreas’ Racer was originally described as *Zamenis andreanus* by Werner (1917), it was an unknown and forgotten snake not listed in regional checklists (Latifi 1991; Leviton et al. 1992) until researchers in first decade of 21th century 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 it to *Coluber* (s. l.) *andreas* (Rajabizadeh & Rastegar-Pouyani 2006). Rastegar-Pouyani et al. (2008) erroneously listed Andreas' Racer in the genus *Zamenis*. Torki (2010) assigned Andreas' Racer 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 Andreas' Racer within the genus *Hierophis* (Figueroa et al. 2016). Our molecular phylogenetic results clearly indicate placement of Andreas' Racer within the genus *Dolichophis* (Fig. 2), hence it must be referred to as *Dolichophis andreas* (Werner, 1917).

From a comparative point of view, the overall shape of skull and neurocranium in *Dolichophis andreas* generally resembles that of *Eirenis* more than *Hierophis* and *Dolichophis*. In both *D. andreas* 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 Andreas' Racer is wider, bearing a less-elaborated V-shaped pair of crests on the parietal bones, again resembling *Eirenis*. The CT-scanned Andreas' Racer 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 Andreas' Racer 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 ~~the genus *Eirenis* as well as in~~ *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 definitely there are shared osteological traits between *Scaphiophis* and *Muhtarophis*, the obvious differences in osteology of these genera makes the sister group relationship of them 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* **Gen. nov.**, the genus is monotypic. Moreover, the sole species is known only from a single specimen, ~~what~~ 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 **Gen. nov.** exist that have not been discovered to date, either extant or in the fossil record. Regardless, since the species *Persiophis fahimii* **Gen. et sp. nov.** 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* **Gen. nov.** that is currently monotypic.

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

This hypothesis is supported by neural anatomy of these snakes as well. Several studies in various groups of vertebrates demonstrated that brain size does not reduce isometrically with body size (Roth et al. 1995; Weston & Lister 2009; Yeh 2002). Allometric decrease in brain size vs. body size may reflect a higher size-threshold for the brain compared to the body of smaller

organisms, in order to maintain all required neuronal activities (*Hanken & Wake 1993*). Thus, negative allometry of the brain size relative to body size is observed in many dwarfed vertebrates. Since brain size directly affects the size of the neurocranium, relatively bigger neurocrania are observed in dwarfed vertebrates, including *Dolichophis andreanus* and *Eirenis*. Bigger neurocrania may induce a spatial constraint to other head elements including size of the snout. Thus, smaller head elements may be accompanied by a lower number of ~~covering~~ scales including ~~labial and temporal scales~~. Reduced head scalation is also observed in other dwarfed colubrid snakes, e.g. dwarf snakes of the genus *Tantilla* having maximum total size 71.1 cm, supralabials 6-7, infralabials 6, anterior temporals 1 and dorsal scales 15 (*Koch & Venegas 2016; Wilson & Mata-Silva 2014*).

CONCLUSIONS

Here, we present new molecular sequence data and a new phylogenetic analysis of snakes, focusing primarily on Colubrinae from southwestern Asia. We find continued uncertainty in the placement of the enigmatic Turkish genus *Muhtarophis* based on osteological comparisons, despite strong support in the phylogenetic analysis. On the basis of the tree and morphology, we confidently reassign *Coluber* (s. l.) *andreanus* from *Hierophis* to *Dolichophis*. Our morphological and molecular data also suggest a potential instance of convergent miniaturization in these Old-World racers. Finally, we report on the discovery of a new genus and species of ground snake, *Persiophis fahimii* **Gen. et sp. nov.**, from southeastern Iran. Our data highlight the importance of broad phylogenetic sampling and ground-level field research to gather an accurate picture of global biodiversity, phylogenetic relationships, and evolutionary patterns in groups such as snakes.

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658

Table 1 (on next page)

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

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

Figure 1

Distribution map of *Persiophis fahimii* Gen. et sp. nov. (star) and Andreas' Racer (circle) in Iran

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

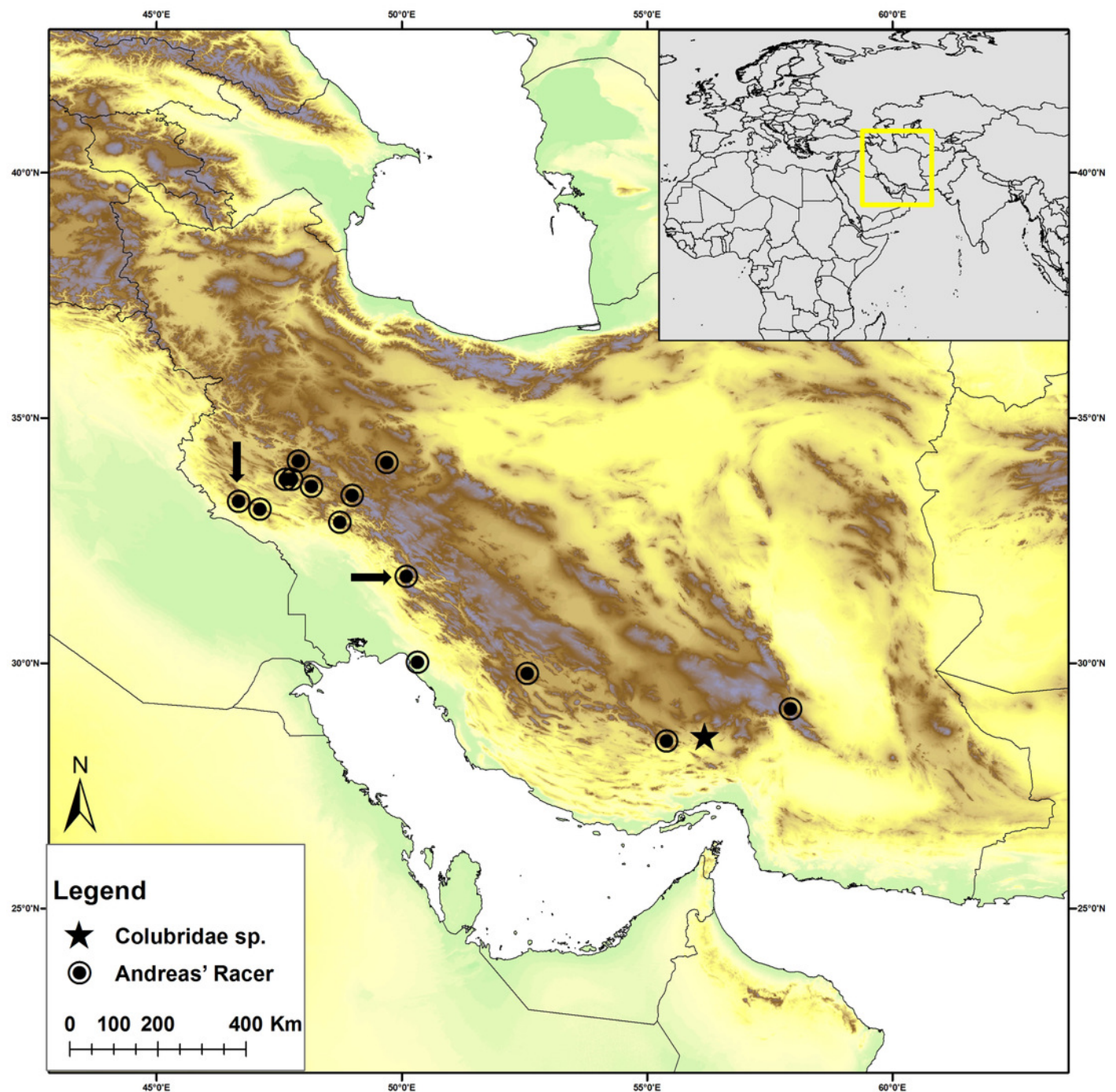


Figure 2

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

The species *Coluber (s. l.) 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 represents a clearly new genus and species.

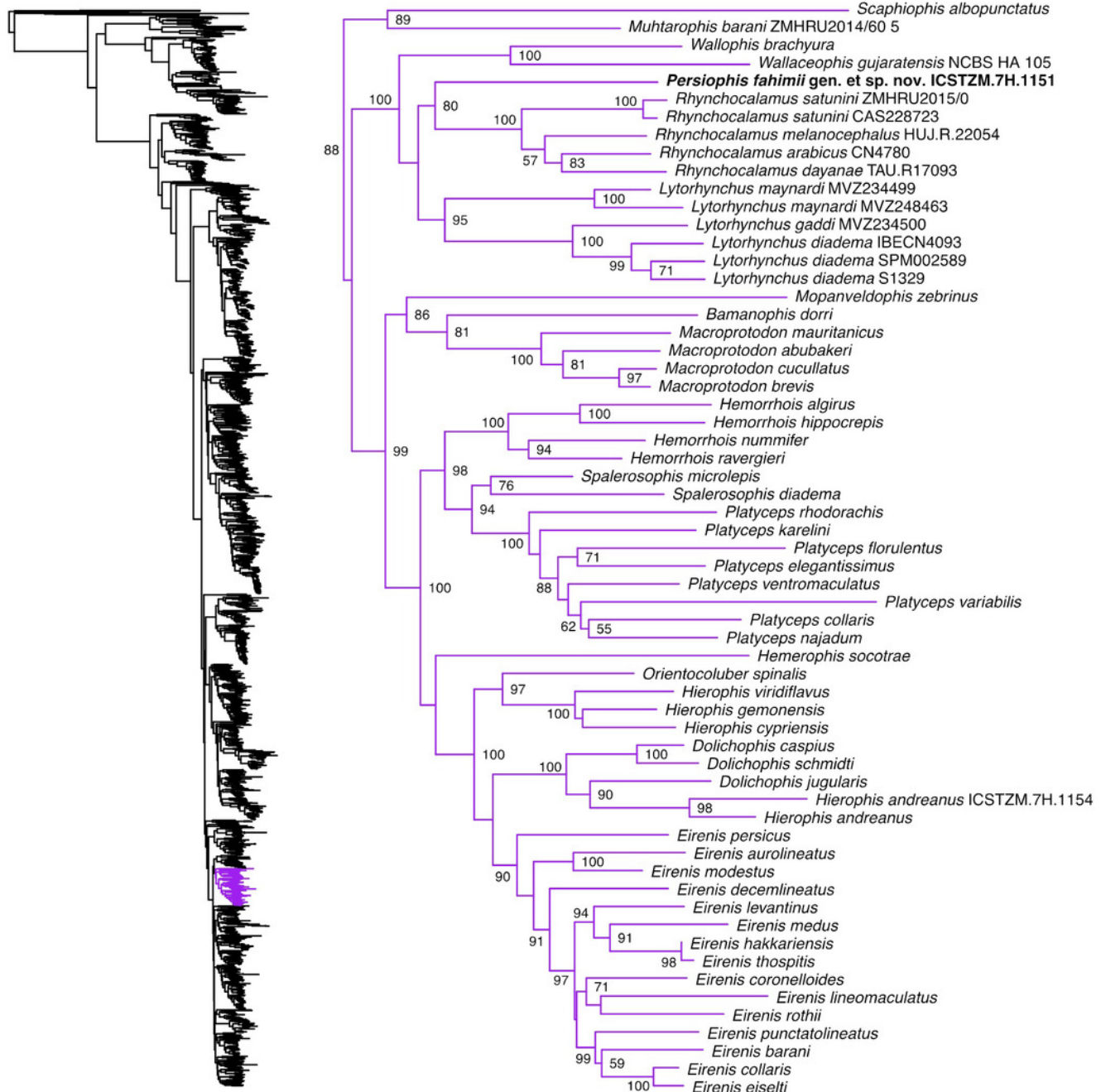


Figure 3

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

Details of head scalation in close-up lateral, ventral and dorsal view (a, b, d) ; lateral view of the fore body (c) as well as dorsal view of the whole body (e). Photos by R. Nazarov.

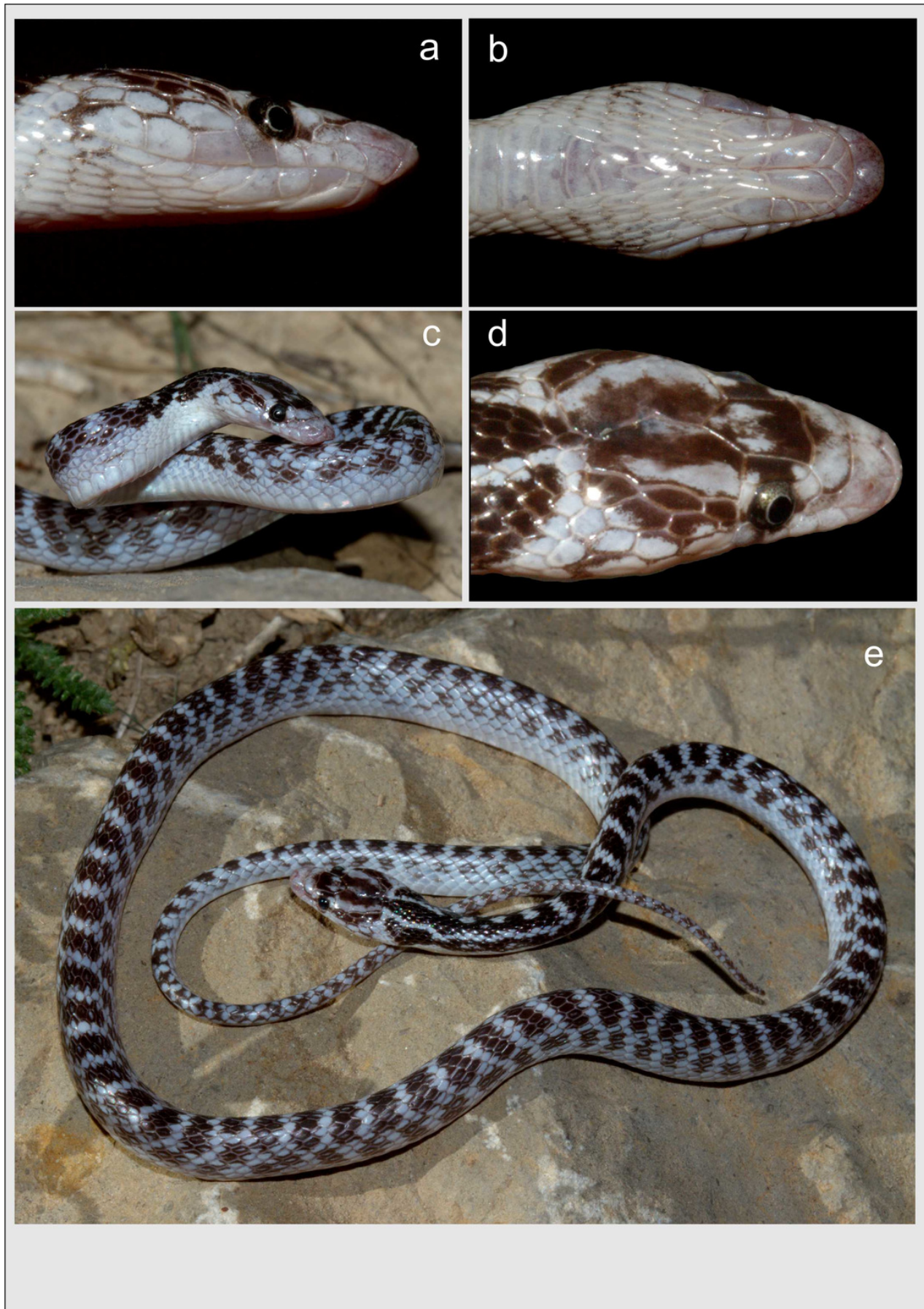


Figure 4

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.

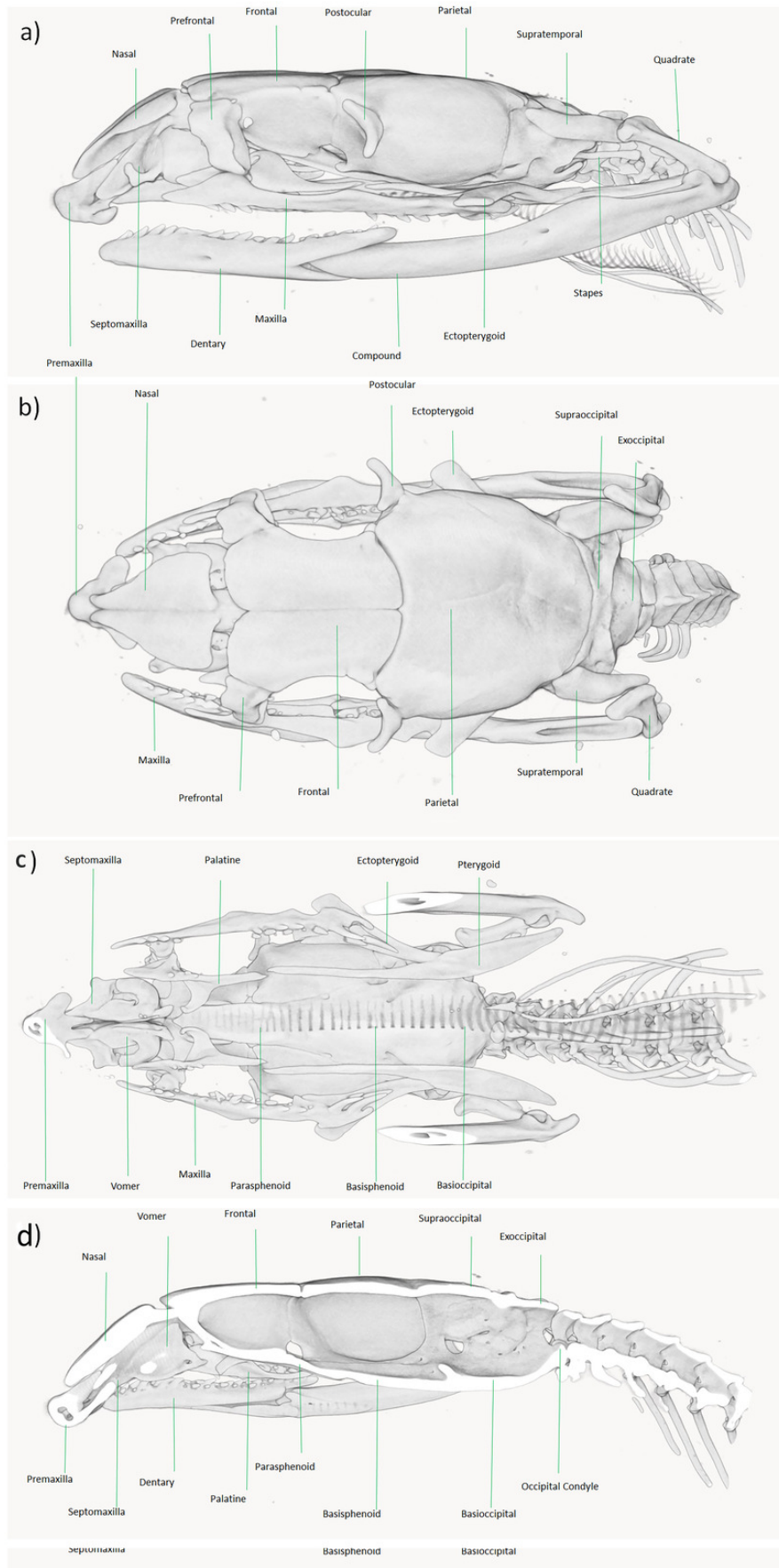


Figure 5

Habitat of *Persiophis fahimii* Gen. et sp. nov. at the type locality in vicinity of Orzuieh 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 M. Rajabizadeh.



Figure 6

Micro-CT reconstruction of the skull cranial osteology of *Coluber* (s. l.) *andreas*

(a) Lateral and (b) dorsal views of the skull.

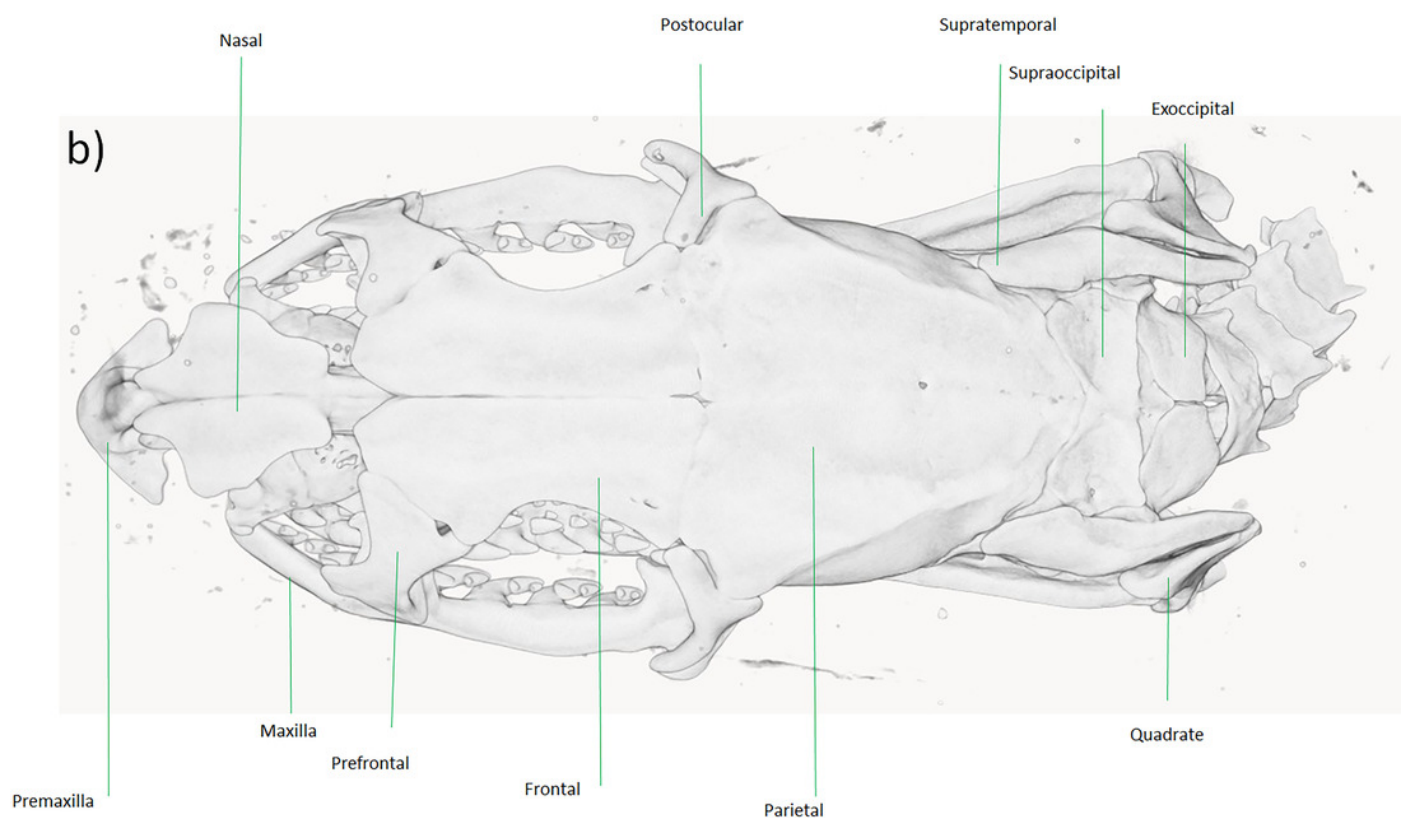
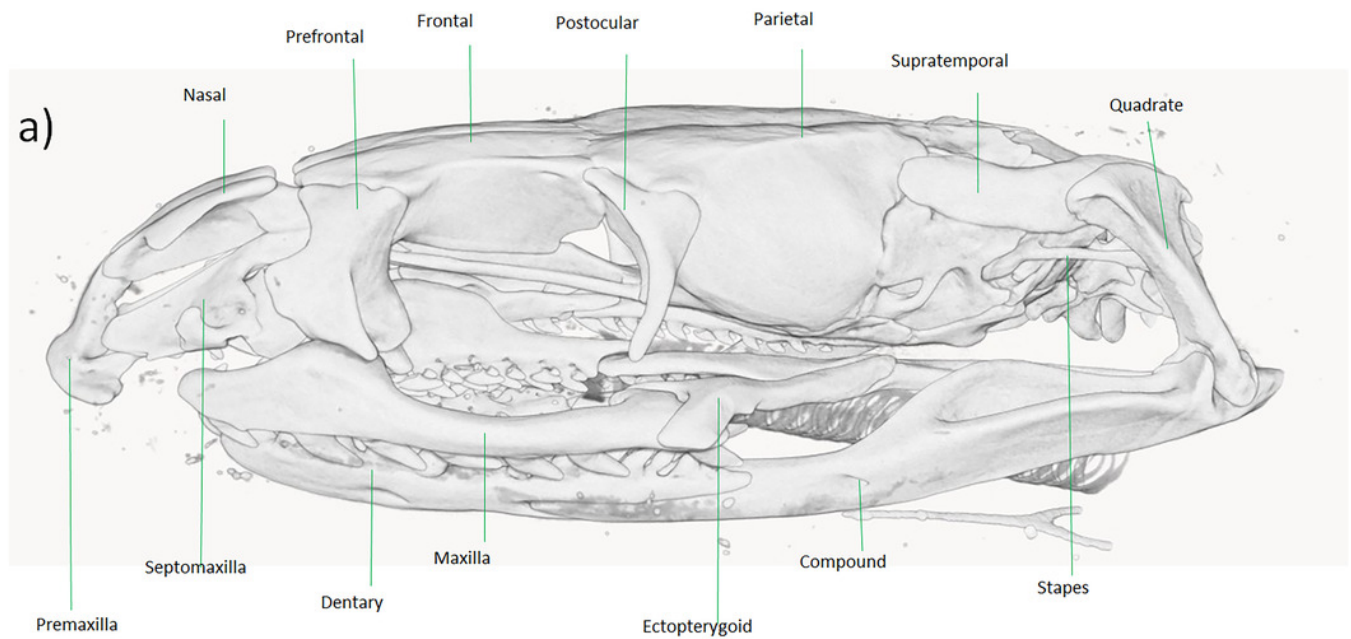


Figure 7

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

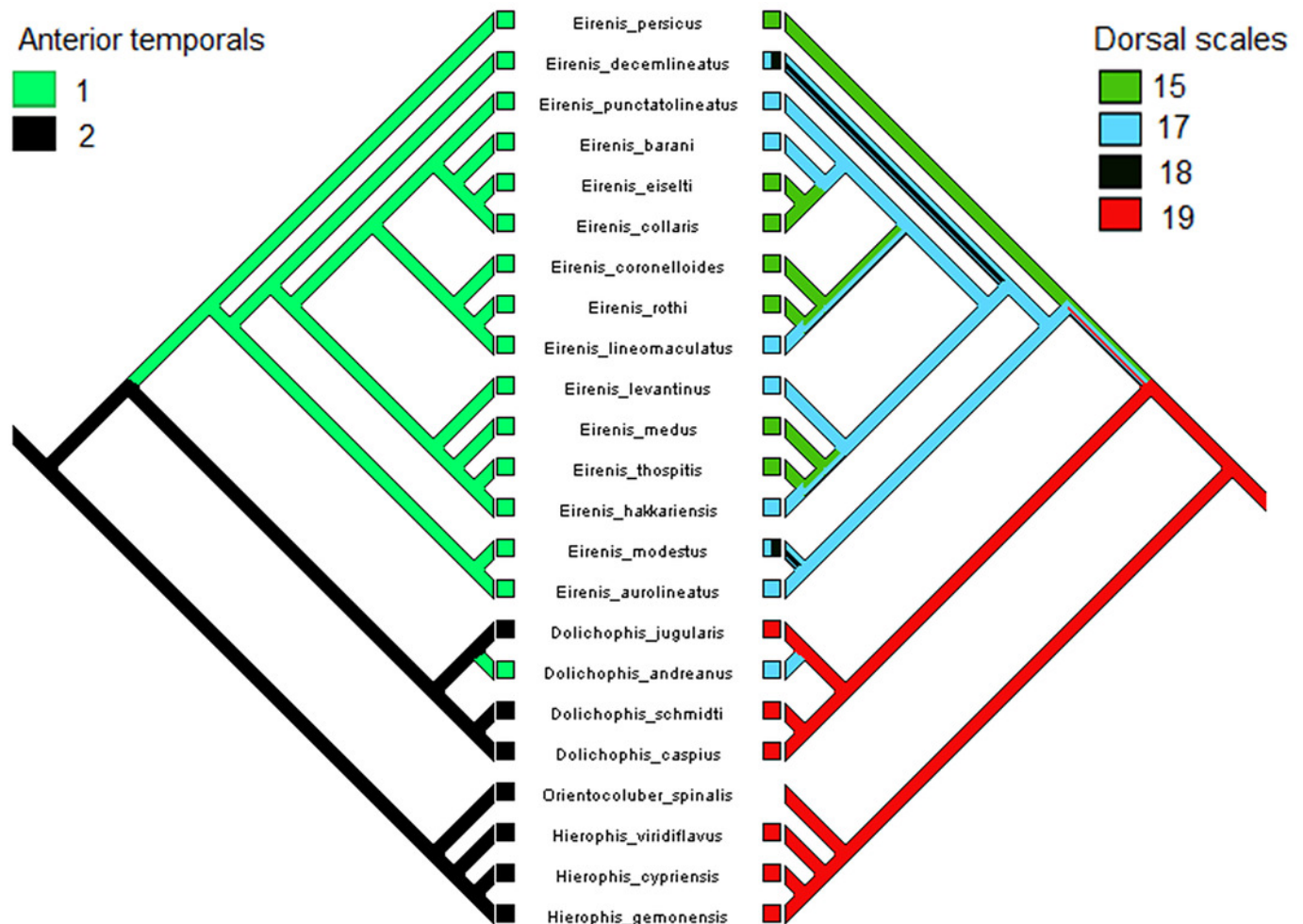


Figure 8

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

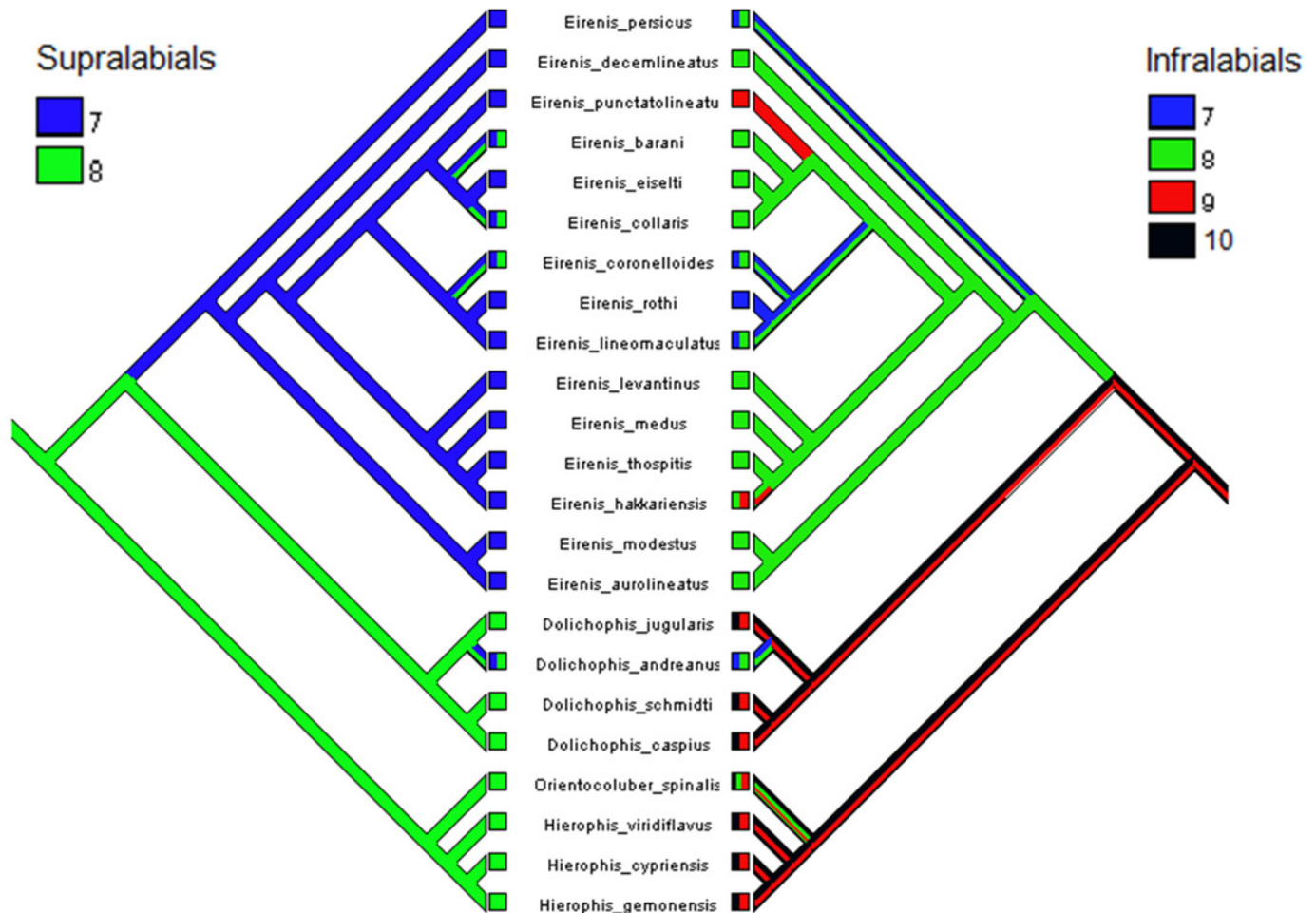


Figure 9

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

