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Mountain Vipers in Central-Eastern Turkey: Huge Range Extensions for Four Taxa Reshape Decades of Misleading Perspectives

Konrad Mebert[1,11], Bayram Göçmen[2], Naşit İğci[3,4], Mert Karış[2,5], Mehmet Anil Oğuz[2], Mehmet Zülfü Yildiz[6], Alexandre Teynié[7], Nikolaus Stümpel[8], and Sylvain Ursenbacher[9,10]

[1]Institute of Development, Ecology, Conservation and Cooperation, Via G. Tomasi di Lampedusa 33, 00144 Rome, Italy
[2]Department of Biology, Zoology Section, Ege University, Faculty of Science, TR 35100 Bornova-Izmir, Turkey
[3]Department of Molecular Biology and Genetics, Faculty of Arts and Sciences, Nevşehir Haci Bektaş Veli University, 50300 Nevşehir, Turkey
[4]Science and Technology Application and Research Center, Nevşehir Haci Bektaş Veli University, 50300 Nevşehir, Turkey
[5]Program of Laboratory Technology, Department of Chemistry and Chemical Process Technologies, Acigöl Vocational School of Technical Sciences, Nevşehir Haci Bektaş Veli University, Nevşehir, Turkey
[6]Zoology Section, Department of Biology, Faculty of Arts and Sciences, Adiyaman University, 02040 Merkez, Adiyaman, Turkey
[7]UMR Epidémiologie des Maladies Animales et Zoonotiques, INRA - VetAgro Sup, Centre INRA Auvergne-Rhône-Alpes, 63122 Saint Genès Champanelle, France
[8]Staatliches Naturhistorisches Museum Braunschweig, Gausstrasse 22, Braunschweig, D-38106, Germany
[9]Department of Environmental Sciences, Section of Conservation Biology, University of Basel, St. Johanns-Vorstadt 10, 4056 Basel, Switzerland
[10]Info fauna - CSCF and karch, Avenue de Bellevaux 51, 2000 Neuchâtel, Switzerland
[11]Corresponding author, e-mail: konradmebert@gmail.com

Abstract.—**Turkey harbors a high diversity of viperid snakes, many with a high threat level on the International Union for Conservation of Nature (IUCN) Red List, yet perception about even basic topics, such as distributions and conservation statuses, remain poor. We initiated a multi-year project 7 y ago to compensate these shortcomings and present herein dramatically improved information on the status of mountain vipers of central-eastern Anatolia (Asian Turkey): Bolkar Viper (*Montivipera b. bulgardaghica*), Albizona Viper (*M. b. albizona*), Wagner's Viper (*M. wagneri*), and partly Ottoman Viper (*M. xanthina*). The data originate from our fieldwork and a comprehensive search of all records available, including information from literature, online resources, locals, and herpetological experts. This resulted in 51 new localities, complemented by 36 published records, which were refined with new information, including four corrected/removed records and two records that were combined with new records due to their proximity. We summarized all records with precise information in a supplemented list of 85 localities, which is compared to current literature and the range maps available on the IUCN Red List of Threatened Species, the global standard reference for consultation on range maps and conservation status of species. Consequently, we report on large range extension of > 100 km in all four mountain viper taxa, increase the extent of occurrence for each viper taxon 4–8 times, reduce the distribution gaps between all pairs of parapatric, related, and ecologically similar mountain vipers, and discuss taxa delimitation, putative contact zones and conservation aspects.**

Key Words.—Albizona Viper; Anatolia; Bolkar Viper; conservation; IUCN Red List; *Montivipera b. albizona*; *Montivipera b. bulgardaghica*; *Montivipera wagneri*; *Montivipera xanthina*; Ottoman Viper; taxa delimitation; Wagner's Viper

Introduction

Turkey has a high viper diversity with at least 11 currently recognized species belonging to the genera *Macrovipera*, *Montivipera, Daboia,* and *Vipera* (e.g., Joger 1984; Mallow et al. 2003; Budak and Göçmen 2008; Mebert et al. 2015a; Göçmen et al. 2018; Freitas et al. 2020). This unusually high viper diversity for a Palearctic country likely is the result of its complex biogeographic history and habitat diversity (Stümpel et al. 2016); however, taxonomy and phylogeography of Anatolian vipers is still a controversial issue (Stümpel and Joger 2009; Mebert et al. 2016). Most of these vipers received a threat status from the International Union for Conservation of Nature (IUCN) higher than Vulnerable, including three of the eight viper species listed globally as Critically Endangered (IUCN 2020). Unfortunately, references about distribution and ecology of Anatolian

vipers are very limited (e.g., Göçmen et al. 2014, 2017; Mebert et al. 2016), and often portray an unrealistic situation, as explained herein. This also applies to the genus *Montivipera* (mountain or rock vipers), which has experienced a tumultuous history and was taxonomically separated from other Palearctic vipers by Nilson et al. (1999). A few taxa have been described in the last 150 y (Ottoman Viper, *M. xanthina*, Radde's Viper, *M. raddei*, Lebanon Viper, *M. bornmuelleri*, and Latifi's Viper, *M. latifii*), whereas more recent taxonomic research resulted in the description of a number of new taxa (Wagner's Viper, *M. wagneri*, Bolkar Viper, *M. bulgardaghica*, Albizona Viper, *M. albizona*; and Kuhrang Viper, *M. kuhrangica*). Species delimitation among these taxa has remained controversial (e.g., Nilson and Andren 1986, 1992; Schätti et al. 1991; Sindaco et al. 2013), but some recent studies provided more clarity on relationships among mountain vipers (Stümpel and Joger 2009; Stümpel 2012; Stümpel et al. 2016).

Some of the mountain vipers are rather colorful (*raddei*, *wagneri*, *albizona*) or show a highly variable and contrasting color pattern (*bulgardaghica, xanthina*) that, combined with their putative rarity, led to a temporary illegal collection frenzy for the pet trade in the 1980s–90s. Frequent commercial trading, privately and at reptile expositions, combined with the fear that the few known populations could be irreversibly negatively affected, led to the categorization of several species with a high threat status by the IUCN in the 1990s. A new round of IUCN reassessments in 2008 mainly implemented a higher threat level of mountain viper species compared to the ones published 15 y earlier in 1996, yet without any new supporting information about population aspects and taxonomic clarifications. Unfortunately, concerns about putative illegal over-collecting of many vipers have persisted, even though there is a complete lack of corroborating data over the last decade aside from anecdotes about illegal export of a few individuals that would have only a very limited impact at the population or species threat level. On the other hand, substantial threats caused by habitat destruction, e.g., mining activities, valley flooding for electric power generation, massive livestock grazing, or plantation sprawl, was strongly underestimated (Mebert et al. 2016; Zinenko et al. 2016).

Furthermore, competitive interactions among interested people (professionals and amateurs) have continued after the last IUCN Red List assessment in 2008 and produced a generally tense climate of distrust, misinformation, defamations, false assessments and unrealistic administrative perceptions in relation to Anatolian vipers. At the same time, a lack of basic biological studies about distribution, habitat, and population aspects of Turkish mountain vipers have prevented a realistic assessment of the extent of occurrence, population size/densities, and threat levels of most taxa to this day. To counter the widespread misunderstanding about these vipers, we initiated a project 7 y ago to better understand the phylogeny and biogeography of Anatolian vipers and have published results on a regular basis (e.g., Mebert et al. 2014, 2017a; Göçmen et al. 2015a,b; Nalbantsoy et al. 2016; Stümpel et al. 2019). This study, as well as the previous ones, represent additional information for a work in progress, which should culminate in a much more realistic assessment about the systematic allocation and true distribution of mountain vipers in Turkey than is currently presented in publications and unpublished governmental monitoring reports. Such documents are often based on the IUCN Red List files (IUCN 2020), which are regarded as the most influential source of information for species conservation in the world (AGENDA 21. 2010. Understanding NGOs' [non-government organizations] vision for the 21st Century. Available from https://agendatwentyone.wordpress.com/2010/06/28/understanding-ngos-non-government-organizations/ [Accessed 11 July 2019]; wiseGEEK. 2014. What is IUCN? by Ellis and Brownyn. Available from https://www.wisegeek.com/what-is-iucn [Accessed 10 July 2019]; and Saha et al. 2018). Our collection of new and refined information on the distribution of Anatolian mountain vipers will inform and guide key national and international policy and conservation activities and/or regulations. This information will also be useful for the scientific community and serve as an important education and information resource for the public, improve species identifications, help potential funding, and will be crucial in our goal to overhaul the respective IUCN Red List files (IUCN 2020).

We restrict our work here to four mountain viper taxa from south-central to north-eastern Turkey; hence, excluding *Montivipera raddei* and most of the core and western range of *M. xanthina*. Each species has a conservation status and current population assessment according to the IUCN Red List of Threatened Species (IUCN 2020). *Montivipera b. albizona* (Albizona Viper or Central Turkish Mountain Viper) is listed as an Endangered Turkish endemic, its Extent of Occurrence is fewer than 5,000 km^2, it is known from fewer than five locations, and has a continuing population decline inferred in the number of mature individuals due to the likely collection for the pet trade and intentional killing. *Montivipera b. bulgardaghica* (Bolkar Viper) is listed as Least Concern because it occurs in an area of extensive and suitable habitat that appears not under threat, has a presumed large overall population, and is unlikely to be declining fast enough to qualify for listing in a more threatened category. *Montivipera wagneri* (Wagner's Viper) is listed as Critically Endangered, is endemic to Turkey, has experienced a population decline of more than 80% from exploitation and collection for the

international pet trade over the past three generations (18 y), and is predicted to have a continued population decline from over-collection and planned dam construction in the Aras River Valley, which would cause a loss of over 80% of suitable habitat for this species. *Montivipera xanthina* (Ottoman Viper) is listed as Least Concern in view of its wide distribution, large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category.

Our primary objective is to initiate a process to counter the general lack of knowledge about Turkish mountain vipers, from simple distribution to population biology and ecology, which is preventing any reliable assessment of species recognition and conservation statuses. It is therefore urgent to rapidly improve our knowledge of the true range limits, population sizes, species delineation, and relevant environmental factors that may affect population dynamics. This can be achieved quickest with a multi-faceted approach by compiling geographic data on population extent and habitat occupancy in general and molecular and morphological data from contact zones or contiguous (parapatric) populations of two or more viper species (Mebert et al. 2015b, 2017b). Finally, it is our overriding objective to provide tools for appropriate future conservation assessments (Extent of Occurrence, Population Size/Trend) and actions/management by publishing herein the massively enlarged distribution size of Turkish mountain vipers than is officially known.

Material and Methods

Taxonomic and morphological considerations.— Beginning in 2013, we started to compile a database on *Montivipera*, focusing on Turkey. We engaged in a holistic approach and compiled data from all available sources, including annual field excursions and sampling of representative genetic tissues for species delineation, searching all literature references, contacting authors of online photos and reports, questioning locals as well as herpetologists that have been active in Turkey. We here largely follow the taxonomic concept of Stümpel et al. (2016) but expect changes in the future (Freitas et al. 2020).

The Albizona Viper was originally described as *Vipera albizona* by Nilson et al. (1990), placed into the genus *Montivipera* by Nilson et al. (1999), and subsequently confirmed by Garrigues et al. (2005). Recently, *M. albizona* was suggested as a subspecies of the Bolkar Viper (*M. bulgardaghica*) due to molecular evidence (Stümpel and Joger 2009; Stümpel et al. 2016). Because the distinction between the two subspecies has become blurrier with new, often photographic, material, we apply the subspecies epithet of such specimens listed herein based on its proximity to the historically known distribution, and/or topographically linked habitats. Potential contact (or transition) zones between them are purely speculative due to lack of data but are suggested and briefly discussed based on geographic proximity of new material.

The similar and somewhat overlapping color pattern between *M. wagneri* and *M. b. albizona* and the missing information of a putative contact zone (or most proximate populations) between them, may render the taxon allocation of some individual vipers solely based on photographic and geographic data difficult. Taxon allocation of such data, however, was decided based on its proximity to the nearest known mountain viper location, reflecting that no two *Montivipera* taxa are known to overlap (Mebert et al. 2016; Stümpel et al. 2016), and a combination of following features: (1) Morphology: To be viewed only tentatively because there seems to be a large overlap of external characters based on published and our own information. Furthermore, diagnosis by previous authors (see Table 1) was retrieved from very small samples, usually representing two to three populations from the northern range limit of each taxon, thus missing a more widespread geographic variation inherent in each taxon. (2) Habitat: Is the habitat linked to other conspecific populations? We visually evaluated potential connecting corridor to other known sites of *Montivipera* populations at < 5 km distance for suitable rocky habitat on plateaus or along valleys < 2,200 m elevation using satellite images from Google Earth Pro. (3) Molecular: We screened haplotype association for a few sampled specimens and compared them with published data. We investigated mitochondrial DNA following Stümpel et al. (2016) and compared the obtained sequences to the current published ones in GenBank using BLAST online. All the evaluation and

Table 1. Differences in morphology between Albizona Viper (*Montivipera bulgardaghica albizona*) and Wagner's Viper (*M. wagneri*) both from northern populations, based on Joger et al. (1988), Nilson et al. (1990), and Mulder (1994).

Morphological Character	*M. b. albizona*	*M. wagneri*
Lateral blotches	Blackish spots	Dark vertical stripes
Inner circumoculars	≤ 13	≥ 12
Ventral scales	≤ 155	≥ 161
Size mid-dorsal blotches incl. black borders	≥ 9 scales wide	< 9 scales wide
Contact occipital spots to first dorsal blotch	Disconnected	Connected up to 50%
Contact occipital spots to postorbital stripe or first lateral blotch	Connected up to 50%	Disconnected

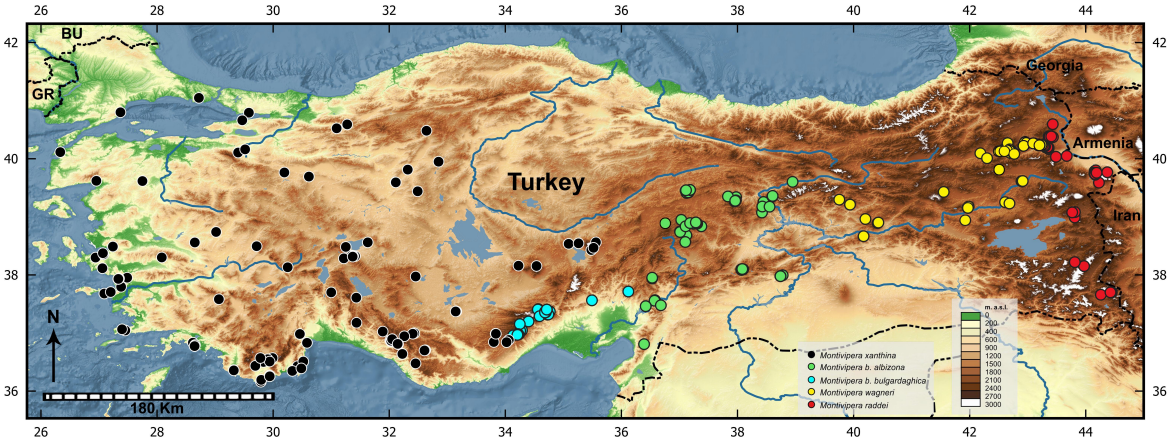

Figure 1. Updated distribution of mountain vipers in Turkey. Points represent locality records (see Locality List in Supplemental Information) for Ottoman Viper, *Montivipera xanthina* (black), Albizona Viper, *M. b. albizona* (green), Bolkar Viper, *M. b. bulgardaghica* (light blue), Wagner's Viper, *M. wagneri* (yellow), and Radde's Viper, *M. raddei* (red). Locality marks for western and inland Ottoman Viper (*M. xanthina*) are not complete, but sufficiently representative, as they are not the focus in this study. Black interrupted lines represent country borders. A larger version of this map is accessible in Supplemental Information.

taxon allocations, in particular those that originate from photos only, should be seen as provisional until finer analysis (i.e., a more complete genetic and morphological analysis) is available. We summarized and listed most relevant and available locality data of *Montivipera wagneri, M. b. bulgardaghica,* and *M. b. albizona,* but also the south-eastern range segment of *M. xanthina* which is most proximate to other mountain viper taxa (see Locality List in Supplemental Information).

Results

The updated range of the four mountain viper taxa (Fig. 1) generally shows a rather continuous range of *Montivipera* taxa from west to east, much different from the general perception of isolated populations or as presented in IUCN Red List files. Listed numbers in the distribution maps (Fig. 2 and subsequent maps presented for each taxon below) correspond to locality numbers in the specimen/habitat photographs and Locality List in the Supplemental Information.

***Wagner's Viper* (Montivipera wagneri).**—We provisionally assign all *Montivipera* specimens, including those based on photographs, that originate from south of the Munzur Mountains in the provinces Tunceli and Erzincan, and from east of the Euphrates River Valley in provinces farther south, to *M. wagneri*.

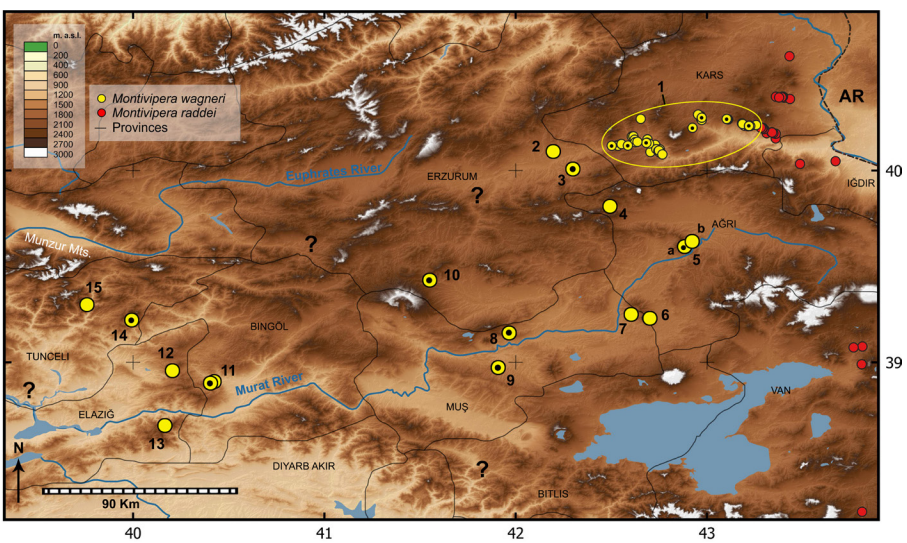

Figure 2. Updated distribution of Wagner's Viper (*Montivipera wagneri*) and adjacent locations of Radde's Viper (*M. raddei*) in Turkey. Numbers refer to the Locality List in the Supplemental Information, but only for *M. wagneri,* as *M. raddei* is not the focus of this study. Several samples used for genetic analysis originate from Aras Valley (circled locality-1) and other single locations that are indicated with a black center. Question marks indicate areas where further *Montivipera* populations are expected but require confirmation. A larger version of this map is accessible in Supplemental Information.

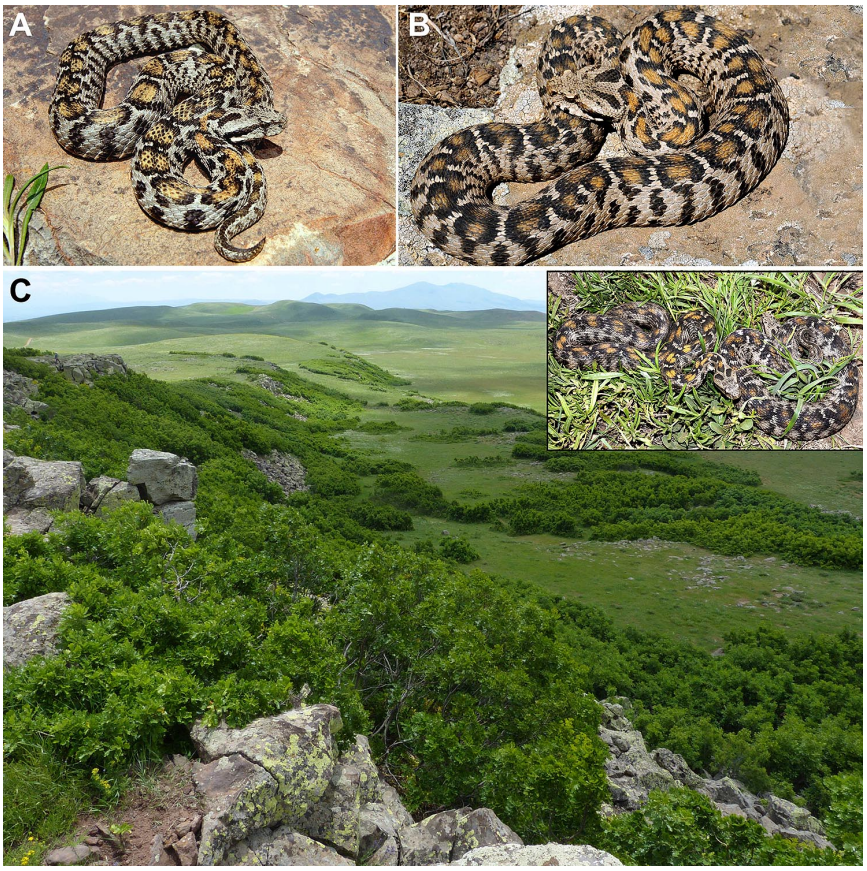

Figure 3. Range extensions of Wagner's Viper *(Montivipera wagneri)* in Turkey. (A) Individual from Günindi, district Kağizman/Kars, near eastern end of encircled locality-1, respectively contact zone with *M. raddei* (Mebert et al. 2016); (B) Individual from locality-4a, Dereköy, district Tutak/Agri; (C) locality-8, habitat and two Wagner's Viper from the area between Bostancilar and Akçakaynak, district Bulanik/Muş. (A, C, and insert photographed by Konrad Mebert and B by Naşit İğci).

The range extends about 250 km west of the previously known western limit near Horasan (locality-2 in Fig. 2; Kumlutas et al. 2015) and includes also recently discovered published (Göçmen et al. 2014; Yildiz et al. 2018) and unpublished sites in the provinces Kars, Ağri, Muş, Erzurum, Bingöl, Elazığ, and Tunceli (Figs. 3 and 4, plus Supplemental Information Figs. S1–S7). Complementary to these allocations, all *Montivipera* records from northwest of the Munzur Mountains and west of Euphrates River are assigned to *M. b. albizona*.

***Albizona Viper or Central Turkish Mountain Viper* (Montivipera bulgardaghica albizona).—**Correction of Terra Typica: the terra typica of *albizona* was originally given as Kulmac Daglari (Nilson et al. 1990), a mountain chain that begins in the west just north of the villages Harmandali and Kürkçüyurt, district Altinyayla/Sivas, and ends in the east at Yilanli Mountain, district Kangal/Sivas. The entire 70 km mountain chain appears to provide some suitable habitat for *Montivipera* vipers, but not as extensive as the Tecer Mountains parallel to the north, a well-known site for *M. b. albizona* (localities 25-28 in Fig. 5 and Supplemental Information Figs. S7E, S9). Recent discussions with the senior author of the description and provision of coordinates, however, revealed that the terra typica lies 100 km farther east near the Karaşar Geçidi (= K. pass), district Divriği/Sivas (see locality-23 below). We also present new and refined localities in the provinces Erzincan, Malatya, Kayseri, Sivas, Kahramanmaraş, and Hatay (Supplemental Information Figs. S7–S12), as well as a large southeastern extension into province Adiyaman (locality-45 in Fig. 5, photographs in Fig. 6, and more specimens depicted in Supplemental Information Fig. S13) about 145 km south and 195 km east of previously known sites (Göçmen et al. 2014). The distribution map in Fig. 5 also replaces the one presented in Çiçek et al. (2017), which is based on previous literature and photographic records, all presented herein with more precision and corrections, where appropriate. No vouchers could be located for the presence of *M. b. albizona* in Sivas-province districts Gemerek, Yildizeli and Zara (Çiçek et al. 2018; Kerim Cicek, pers. comm.), but see discussion appended to locality-34 in Supplemental Information.

Figure 4. First confirmed presence of Wagner's Viper *(Montivipera wagneri)* in Tunceli Province, Turkey. Habitat and a Wagner's Viper from locality-14, Tahkini Yaylasi-Pohoz Mevki, northeast of Turnayolu, district Nazimiye/Tunceli. (Photographed by Konrad Mebert).

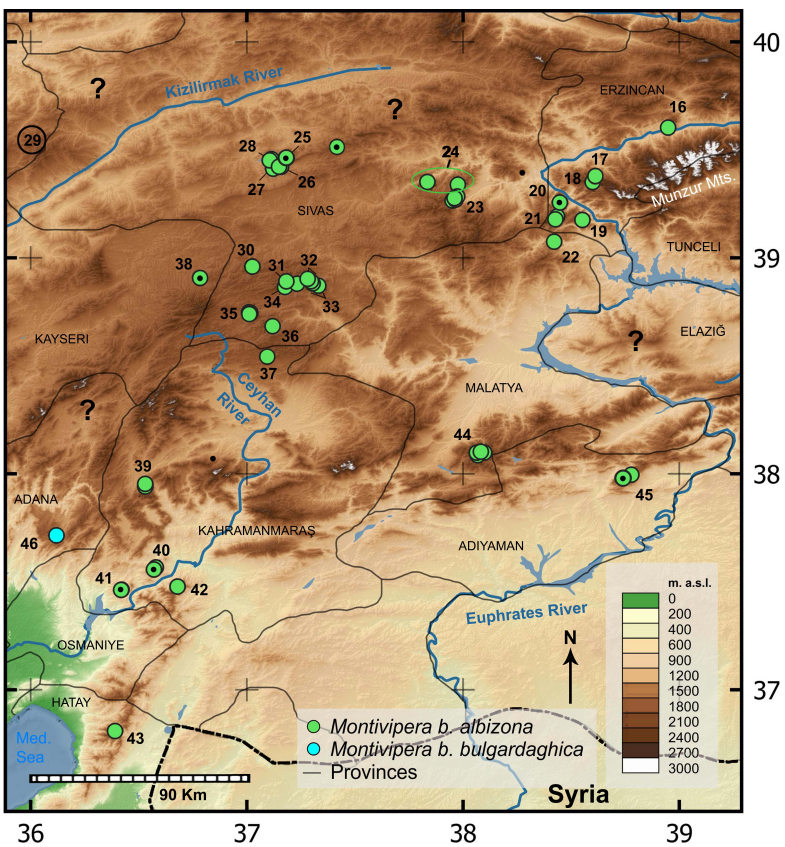

Figure 5. Updated distribution of Albizona Viper *(Montivipera bulgardaghica albizona)* and nearest record of the Bolkar Viper *(Montivipera b. bulgardaghica)* in Turkey. Numbers refer to the Locality List in the Supplemental Information. Samples used for genetic analysis are indicated with a black center, except for locality-40 from Başkonuş, Merkez/Kahramanmaraş, which refers to an albumin analysis by Göçmen et al. (2009). Question marks indicate regions where further *Montivipera* populations are expected but require confirmation. An enlarged version of this map is in Supplemental Information.

Figure 6. The new, currently most southeastern, locality of Albizona Viper *(Montivipera bulgardaghica albizona)* in Turkey at the Nemrut Archaeological site, district Kahta/Adiyaman, locality-45. Depicted is one of the treeless areas near the peak and one of the Albizona Vipers found there (see more examples in Supplemental Information Fig. S13). (Photograhed by Mehmet Zülfü Yildiz).

***Bolkar Viper* (Montivipera b. bulgardaghica).—** We extend the range about 13 km west within province Mersin and 130 km east in province Adana (Fig. 7). We include photographic vouchers (Fig. 8 and Supplemental Information Figs. S14–S16) of this species. Information about the records is given in the Locality List in the Supplemental Information.

***Ottoman Viper* (Montivipera xanthina).—**Only south-eastern records are mapped herein (Fig. 9; but see wider view in Fig. 1). In the Locality List (see Supplemental Information), we summarize new and refined (from previously published, mainly primary sources) records of the Ottoman Viper from its southeastern-most range, adjacent and as close as 11 km from *Montivipera bulgardaghica* ssp. We include photographic vouchers (Fig. 10 and Supplemental Information Figs. S17 and S18), including the first documentation of *M. xanthina* from the province of Mersin.

Discussion

***Distribution and conservation aspects.*—**Among snakes, vipers are perceived as disproportionately threatened with extinction, and thus, acquiring information on their distribution, ecological niche, and natural history is fundamental to better understand their biology and assess their conservation status (Maritz et al. 2016; Alencar et al. 2018; Saha et al. 2018). This has also become evident to us since the start of this project in 2013, because the biology of vipers in Turkey has remained poorly studied to this day, including studies on their distributions and population statuses with only fragmentary or misleading information. This lack of good data is reflected in the IUCN Red List files in three of four *Montivipera* taxa treated herein (*M. wagneri, M. b. bulgardaghica, M. [b.] albizona*) and in most recent scientific publications (Kumlutaş et al. 2015; Tok et al. 2015; Gül et al. 2016; Tuniyev 2016; Kurnaz et al. 2018; Ahmadi et al. 2019), Turkish provincial governmental reports (e.g., Çiçek et al. 2017; Avci et al. 2018), and in virtually all books that include chapters on vipers from Anatolia (e.g., Phelps 2010; Sindaco et al. 2013; Geniez 2015).

By using a combination of published results, satellite images from Google Earth Pro, as well as the increasing provision of open online landscape photos, we conclude that suitable habitat for most viper species appears relatively extensive across much of Anatolia. When combining key factors, such as southern aspect, elevation, and coarse-rocky surface structure (no fine sediments) to provide shelter for night, hibernation, and prey, potential new locations can often be pinpointed on satellite images. We have also extended the habitats of *Montivipera* spp. from rocky mountain slopes with bushes (e.g., Aras Valley in Kars, locality-1, Supplemental Information Fig. S1) and light forests

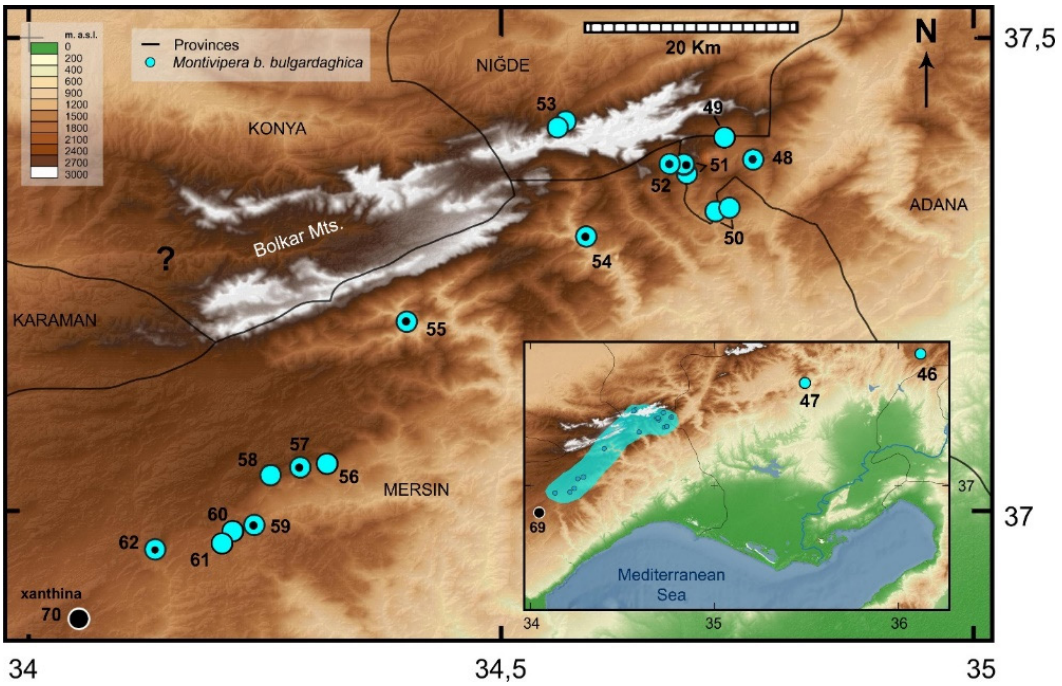

Figure 7. Updated distribution of Bolkar Viper (*Montivipera b. bulgardaghica*) in Turkey. Inset map repeats the same sites overlaid by a light blue shading but enlarged to show the two eastern-most sites (localities-46 and -47, see vouchers in Fig. 8). Numbers refer to the Locality List in the Supplemental Information. Samples used for genetic analysis are indicated with a black center. Question marks indicate areas where further *Montivipera* populations are expected but require confirmation. A newly discovered Ottoman Viper (*M. xanthina* (black dot-70) near *bulgardaghica*-locality-62 indicates a potential contact zone between them. An enlarged version of this map is in Supplemental Information.

(e.g., Kar Boğaz Valley in Fig. 8, from localities-50–52, and Göller in Adana, locality-46), to wet riparian habitats (e.g., Ovacik/Sivas locality-25, Supplemental Information Fig. S9), dry steppe-like stony hills (e.g., Otluca/Ağri locality-5 and Dolabaş/Muş locality-7 and Supplemental Information Figs. S2 and S3), treeless rocky mountain summits (e.g., Bozdağ Tepesi/Hatay locality-43 and Mt. Nemrut/Adiyaman locality-45, Fig. 6), agricultural fields at about 1,000 m elevation (Bostanli/Kahramanmaraş locality-41, Supplemental Information Fig. S11), and hilly-rocky high elevation plateaus around 1,800–2,200 m elevation (e.g., Karakuyu/Sivas locality-36, Yilanhöyük locality-31, Masman Basi/Erzincan locality-21, Hisarlik Plateau/Konya locality-78, Mağara-Kirobasi/Mersin locality-72, Supplemental Information Fig. S17). In particular, the extensive bush and grassland on flat, rocky plateaus are rarely listed as habitat for *Montivipera* spp. in surveys and the general literature (see example in Supplemental Information Fig. S4). Yet, these plateaus are common and extensive in eastern Anatolia and likely constitute a largely neglected habitat for mountain viper surveys with the potential for many overlooked populations. Hence, lack of finding vipers results from insufficient field exploration and coordination with good weather conditions for surface activities of these generally secretive snakes, particularly those living in semi-arid climates across most of inner Anatolia. In only seven years, we tried to compensate for those insufficiencies by systematically optimizing field and desk work, including networking, with a pioneering focus on new regions and addressing all available sources of recent locality data on vipers. This resulted in a rapid accumulation of distribution knowledge for some mountain vipers (other Turkish viper taxa show a similar trend and are currently being analyzed as well). Compared to the range maps published on the IUCN Red List of Threatened Species (IUCN 2019), the Extent of Occurrence for *Montivipera b. bulgardaghica* was enlarged by more than four times (from 1,300 to 6,000 km^2), with extensions of about 13 km in western (locality-62, Fig. 7) and 130 km in northeastern (locality-46, Fig. 7) directions from the corresponding IUCN range (see Fig. 11). The distribution area for *Montivipera b. albizona* was enlarged by about eight times (from < 5,000 km^2 to 38,500 km^2; see Fig. 11), with extensions of about 145 km to the south (locality-43, Fig. 5) and 160 km to the east (locality-45, Fig. 5); similarly the extent of occurrence for *M. wagneri* was enlarged about eight times (from 2,500 to 21,000 km^2; see Fig. 11), with extensions of about 226 km in southwestern (locality-15, Fig. 2), and 30 km in eastern directions to Günindi, Kars (locality-1, the eastern-most of the *wagneri*-localities shown in Fig. 2), whereas the range of *M. xanthina* was extended by 150 km east (locality-70, Fig. 9) across the vast highland plateau from its nearest previously published record in

Kumlutaş et al. (2004). We can safely assume that these large range extensions will concomitantly increase the total population size of each taxon, even though the many mountain valleys with suitable habitat between the listed localities have not been explored thus far. Yet, with the core of *Montivipera* diversity contained in Anatolia, it remains with the Turkish government to safeguard existing populations and implement any necessary conservation measures against threats from habitat destruction and climate warming (Mebert et al. 2016; Ahmadi et al. 2019).

We anticipate that many viper species of Anatolia will follow a similar path of revelations as was experienced with Orsini's Viper *Vipera ursinii* in France, which once was estimated to consist of six to nine populations with a total of 200–300 animals by the late 1980s (Corbett 1989; Stumpel et al. 1992), but surveys up to 2008 corrected those numbers to 21 populations with a potential carrying capacity of 168,000 vipers (Lyet et al. 2013). Similarly, there has been rapidly increasing distribution knowledge for Karst Viper *Vipera u. macrops* (Jelić et al. 2013) and Greek Meadow Viper, *V. graeca* (Mizsei et al. 2016, 2018). Not unexpectedly, the biogeographic situation of vipers in Anatolia is increasingly resembling other Palearctic vipers occurring in southern Europe, where every mountain/valley has (or had, if the habitat has since become too degraded or lost) its population of vipers, a situation already quite well predicted by Schätti et al. (1991).

The often-cited major threat through illegal collection by Baran and Atatür (1998) or IUCN (2020) appears outdated for Turkey, except for very small and isolated populations that could be quickly overexploited. Yet such specific cases are not known for Turkey. Indeed, neither reports by the Turkish authority, nor recent workshops with our attendance as viper experts at the Viper Specialist Group-IUCN meetings in Greece (2014) and Morocco (2017) revealed any large-scale sampling or smuggling of vipers out of Turkey. Similarly, no illegal snake smuggling aside from single specimens, which itself is biologically irrelevant for the survival of a population and much less that of a species, have been found by a governmental compilation of smuggling cases from 2007–2017 (General Directorate of Nature Conservation and National Parks, Turkey. 2018. Official statistics on the number of biosmuggling cases in Turkey from 2007–2017. Available from http://www.milliparklar.gov.tr/resmiistatistikleryeni [Accessed 5 March 2019]), or by a new summary study on bio-smuggling in Turkey (Birben and Gençay 2019), inquiries from NGOs, commercial markets, breeders or other scientists, as well as our own experience (Mebert et al. 2016). According to the Convention on Biological Diversity (https://www.cbd.int), however, in which Turkey participates, countries have the right to their biological diversity and should control the access

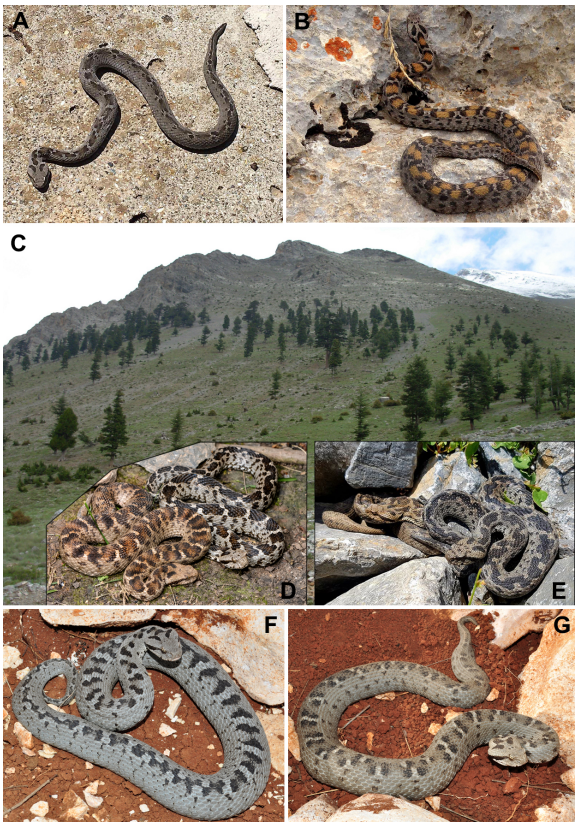

Figure 8. Distribution updates of the Bolkar Viper (*Montivipera b. bulgardaghica*) in Turkey. (A) locality-46, Göller Yaylasi, district Kozan/Adana (Photographed by Şensu Küçükateş); (B) locality-47, Kizildam, district Aladağ/Adana, specimen with a color pattern more typical for *albizona* (Photographed by Karim Amri); (C) locality-51, Kar Boğaz Valley, district Pozanti/Adana (Photographed by Mehmet Zülfü Yildiz); (D) male and female vipers (Photographed by Bayram Göçmen); (E) male and female vipers from nearby locality-50 (Photographed by Fabien Bettex; (F) male and (G) female vipers from western-most locality-62, Ünlük Tepesi, Gavuruçtuğu, district Erdemli/Mersin (Photographed by Mert Kariş).

to their biological resources to secure sustainable use. Precautions against bio-smuggling is important in this context even for single specimens. Although a variety of viper species were exported from Turkey in the past without permission, and illegal collection has been cited as a threat issue for all four *Montivipera* taxa treated herein (see respective files in IUCN 2020), this activity has significantly reduced in the past 20 y. This has been due to regulations and governmental projects on this subject and the increasing risk of illegally exporting bio-goods out of Turkey, and also due to the saturation of the pet market with captive-bred specimens. Fortunately, today, anyone from Turkey or abroad can conduct studies after receiving appropriate and collaborative permits from the governmental bodies.

Another aspect that grew out of the non-representative fear about illegal collecting relates to non-academic herpetologists and naturalists that post their new viper

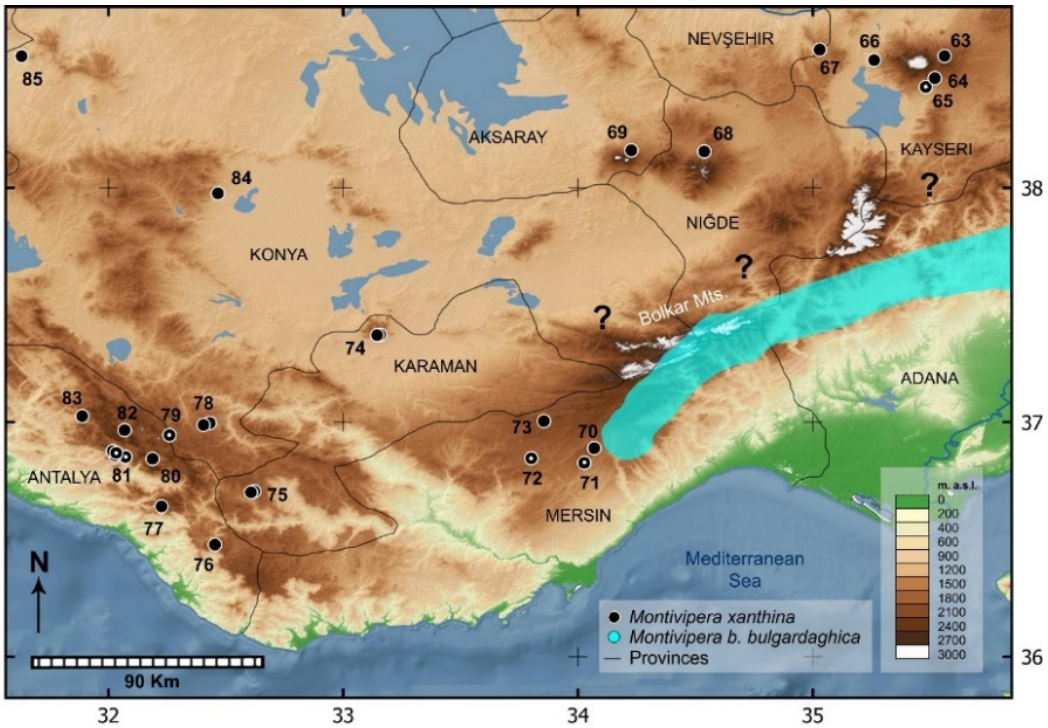

Figure 9. Southeastern distribution of Ottoman Vipers (*Montivipera xanthina*) in Turkey. Numbers refer to the Locality List in the Supplemental Information. The corresponding International Union for Conservation of Nature (IUCN) map also includes an area for *M. xanthina* near where Adana, Niğde and Kayseri provinces meet. Because none of the literature in the IUCN assessment (IUCN 2020) includes such a reference, we presume that area may represent district Ulukişla/Niğde and relates to the listing of *M. xanthina* for Bolkar Dağı Ulukişla in Başoğlu and Baran (1980), which later was described as *M. bulgardaghica* (Nilson and Andren 1985). Samples used for genetic analysis are indicated with a white center dot and are either listed in Table S1 (Supplemental Information), except for locality-65 from south Ercyies Mt., Develi/Konya, which refers to an albumin analysis by Göçmen et al. (2009). Question marks indicate areas where further *Montivipera* populations are expected but require confirmation of taxon allocation. An enlarged version of this map is in Supplemental Information

findings on social media. We have contacted most authors of such posts, yet a few were still unwilling to share their locality information to prevent population-damaging sampling. Such fear, however, is not realistic based on the extensive habitat and distribution that vipers occupy in Turkey today, as we demonstrate in this paper. On the contrary, locality data could be more usefully applied to conservation needs by assessing the extent of occurrence, habitat constituents, population sizes and immediate local threats to certain species that otherwise may risk extinctions of entire populations with 100s to several 1,000s of specimens. It was recently concluded that the most prevalent threats facing more than 8,000 threatened or near-threatened species on the IUCN Red List of Threatened Species (IUCN 2020) are agriculture and overexploitation (Maxwell et al. 2016; Grooten and Almond 2018). Habitat degradation through agriculture, but also through overgrazing, urban sprawl, and plantations poses massive structural landscape changes with often severe negative effects on susceptible terrestrial species such as vipers. Substantive information on the conservation status of a threatened species, such as range, population size, and its ecological context, will depend on comprehensive local data to better promote its survival in the future.

Concerning conservation aspects, we strongly argue that there are stronger and more realistic threats to viper populations than illegal collection for the international pet trade. The principal threats for Anatolian mountain vipers are likely posed by wide-scale habitat degradation and destruction, mainly through overgrazing by domestic livestock (goats, sheep, cattle), agriculture and plantations, suburban sprawl, and valley flooding through dam construction (Ettling et al. 2015; Maxwell et al. 2016; Mizsei et al. 2016; Çiçek et al. 2018; Grooten and Almond 2018). In particular, Palaearctic steppes have become one of the most endangered terrestrial biomes of the world through high rates of conversion and widespread degradation (Török et al. 2016). In Turkey alone, more than 44% of the natural steppe and steppe forest area has been lost due to conversion to cropland, afforestation, and overgrazing, putting Anatolian mountain vipers that depend on rocky montane grassland under increased conservation risk (Ambarli et al. 2016; Wesche et al. 2016; Mebert et al. 2016). Because livestock changes

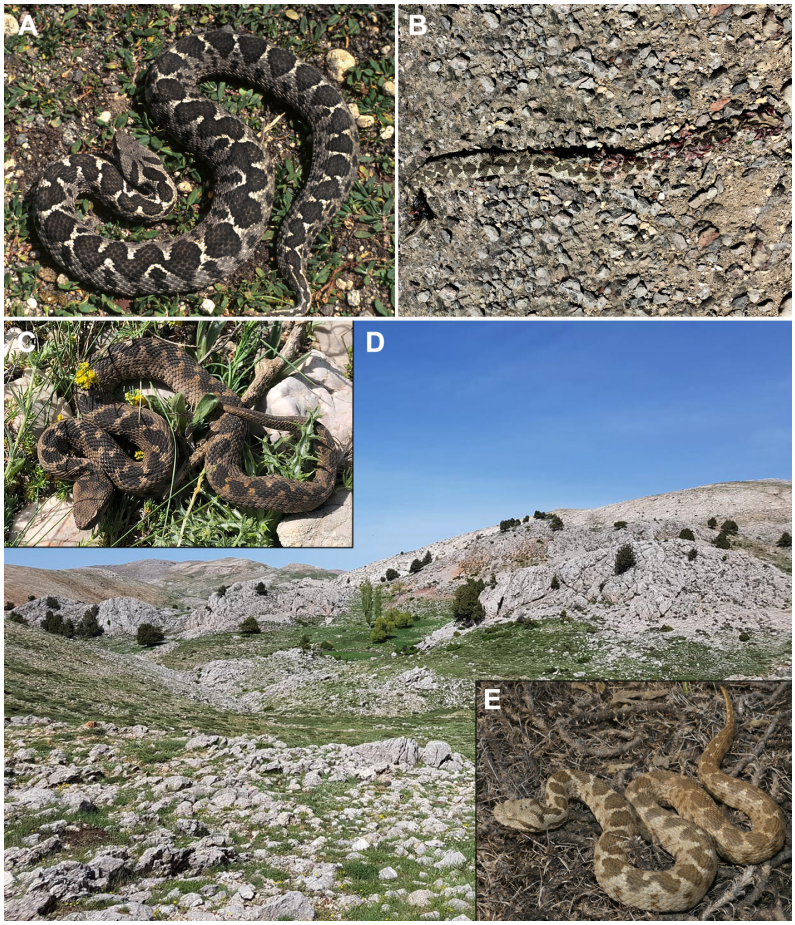

Figure 10. Updated distribution of Ottoman Vipers *(Montivipera xanthina*) from its southeastern range borders in Turkey. (A) Individual from locality-66, west of Erciyes Mt., Subaşi, district Incesu/Kayseri (Photographed by Johan Nylander); (B) Viper from locality-68, Azatli Dam, Çiftlik/Niğde (Photographed by Mert Kariş); (C) and (D) locality-70, *M. xanthina* and habitat, northwest Kuşluca (Toros), district Erdemli/Mersin (Photographed by Fabien Bettex); (E) Viper from locality-71, northwest Akpinar, district Erdemli/Mersin (Photographed by Konrad Mebert).

vegetation structure and cover in ways important to small mammals, community-level total abundance of small mammals typically declines with grazing (Schieltz and Rubenstein 2016), which in turn negatively affects the food base of snakes. Similarly, Rotem et al. (2016) found that reptile diversity decreased with grazing at arid sites. To maintain viper diversity in Turkey, as well as most other fauna and flora, it is necessary to consider those threats and publicly address them in the future.

Taxa delimitation.—Because the IUCN Red List assesses threat levels primarily at the species level (IUCN 2020), delimitation of species becomes relevant; however, insufficient geographic data often hampers the biologically meaningful categorization of taxa into species, subspecies, or local populations. This partly applies also to *Montivipera* species for which traditional species classification has been the standard in the IUCN Red List. This standard is increasingly challenged by means of expanding geographic sampling and delimiting species using molecular methods. In the most recent study, Stümpel et al. (2016) assessed roughly a low 2–3% sequence divergence of three mt-genes (CYTB, COX1, ND5) among *Montivipera wagneri, M. b. bulgardaghica*, and *M. b. albizona*, a situation asking for systematic re-evaluations in the future (Freitas et al. 2020). Comparativley, a new study on the Transcaucasian Ratsnake, *Zamenis hohenackeri*, largely sympatric with our *Montivipera* spp. herein, showed a broad intergradation zone (gene flow) between subspecies that diverged at around 5% cyt *b* (Hofmann et al. 2018), higher than in aformentioned *Montivipera* taxa. Bradley and Baker (2001) suggested that cyt *b* divergence by < 2% between small mammal taxa is indicative of subspecies level, whereas divergence from 2%–11% requires more methodological evaluation (morphological, genetic, ecological, etc.), and divergence of > 11% can be considered a species. Even though one may expect that snake genera delimit by different levels of cyt *b* divergence and might not be comparable to small mammals, various studies that include closely related snake species in sympatry, where species integrity is

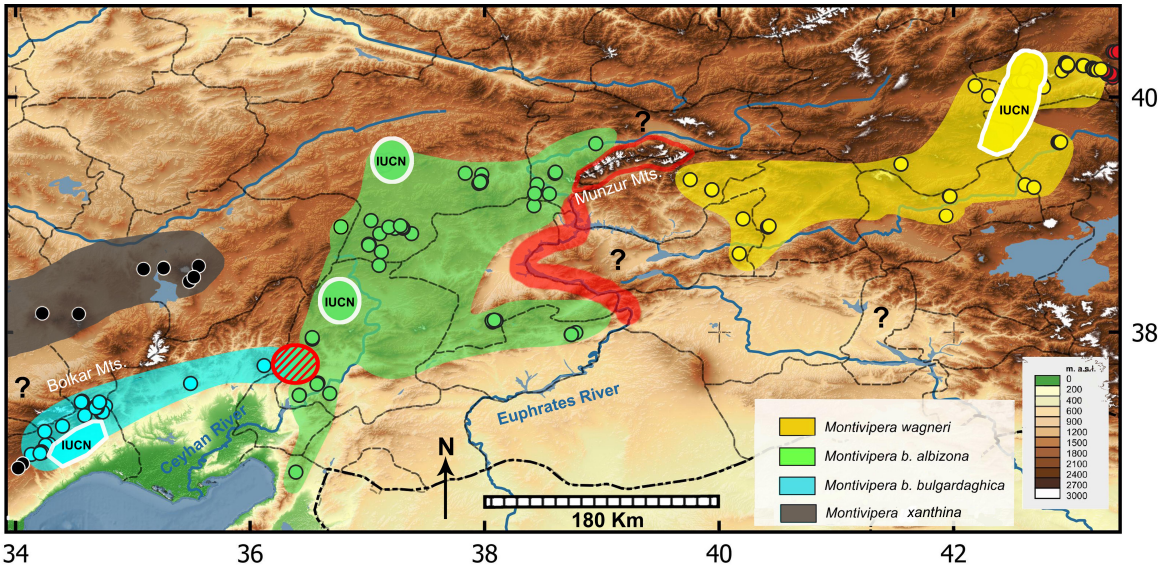

Figure 11. Updated distribution of mountain vipers in south-central to north-eastern Anatolia, Turkey, with known localities as colored circles on top of same color shaded areas representing their interpolated ranges: dark grey Ottoman Viper (*Montivipera xanthina*), light blue Bolkar Viper (*M. b. bulgardaghica*), green Albizona Viper (*M. b. albizona*), yellow Wagner's Viper (*M. wagneri*). For the latter three taxa, the smaller, white-bordered, and color-saturated polygons represent the approximate and much smaller distribution maps as depicted in the respective files of the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2020). The red transparent band over the Euphrates River leading north to a red-bordered area encircling the Munzur-Mercan Mountains indicates the prominent landscape feature separating most proximate populations between *M. b. albizona* and *M. wagneri* or may represent their potential contact zone. Similarly, the red-hatched circle near the Ceyhan River reflects a potential contact or transition zone between the subspecies of *M. b. bulgardaghica* and *M. b. albizona*. Question marks indicate areas where additional *Montivipera* populations are expected but require confirmation. An enlarged version of the map is placed in Supplemental Information.

naturally tested (Harrison 1993), show cyt *b* divergence at an equivalent magnitude and range. For example, the Southern and Northern watersnakes (*Nerodia fasciata* and *N. sipedon*, respectively), diverge by 9% cyt *b*, but produce very wide hybrid zones (20–100 km) that align (are constrained) along environmental factors (Mebert 2008, 2010); Western and Eastern grass snakes (*Natrix helvetica* and *N. natrix*, respectively), differ by 6.9% with limited unidirectional nuclear gene flow across a narrow contact zone between taxa (Kindler et al. 2017); a divergence of 5.2% exists between partly sympatric Mexican and Checkered gartersnakes (*Thamnophis eques* and *T. marcianus*, respectively), or 5.5% between Western Aquatic and Coast gartersnakes (*T. couchii* and *T. elegans*, respectively; de Queiroz and Lawson 1994); and sympatric North American brown snakes (*Storeria* spp.) differ by 8% (Alfaro and Arnold 2001). Within the Anatolian mountain vipers, a 9% difference separates *Montivipera wagneri* and *M. raddei* with no sign of introgression along a sharp parapatry line, consisting of a 5–10 m wide shallow stream separating them north of Kağızman, Turkey (Mebert et al. 2016; Stümpel et al. 2016).

In contrast, taxa with incomplete speciation and/or hybridization tend to show levels of cyt *b* divergence < 5%, such as indicated by the complete fusion of ratsnake lineages in southern Canada, classified as species by Burbrink et al. (2000) that differ by 3.5% and are regarded as conspecific (Gibbs et al. 2006), or the Plains and Butler's gartersnakes (*Thamnophis radix* and *T. butleri*, respectively), that differ in Wisconsin by < 1% (de Queiroz and Lawson 1994; Alfaro and Arnold 2001) or < 2% in the more variable ND4 (Placyk et al. 2012), likely as a result of ancient and long-standing mtDNA-introgression reflecting incomplete speciation (Placyk et al. 2012; McVay et al. 2015).

In Palearctic vipers, there are currently several recognized species with < 5% cyt *b* divergence, yet they all relate to allopatric populations or taxa for which no natural test (i.e., integrity in sympatry) is available, thus, they may as well represent temporarily isolated and locally variable subspecies, e.g., Armenian Steppe Viper *Vipera eriwanensis*, Iranian Steppe Viper (*V. ebneri*), Baran's Viper (*V. barani*), Dinnik's Viper (*V. dinniki*), Lotiev's Viper (*V. lotievi*), or some of the *Montivipera* indicated in the text (Freitas et al. 2020). Hence, one needs to compile more data from different lines of evidence (integrative approach) to show that there is a coherent pattern of distinct morphology, genetics, and geographic structure. Adequate sampling is the basis to compensate for the lack of required information with proximate populations or even contact zones between two taxa investigated for free gene flow today or in the past by molecular means (Mebert 2008, 2010;

Hillis 2019). We strive to improve our knowledge in locating these contact zones or proximate populations by molecular means, and if otherwise not possible, by consensus of color pattern variation.

Because some frequent color pattern variations between *Montivipera b. albizona* and *M. wagneri* are quite similar, taxon-allocation based on photographs of specimens from proximate populations between them presents some challenges. This convergence in color pattern might be the result of similar environmental pressure or gene flow in the past (Rajabizadeh et al. 2015), but with the knowledge that there is generally no large sympatry between two *Montivipera* taxa (Stümpel et al. 2016) save some narrow contact zones (Mebert et al. 2016), we can at least approach the delimitations or current separation between these *Montivipera* taxa based on consensus in color pattern. Indeed, there are two prominent topographic features producing a large (up to 100 km) longitudinal gap with vast stretches of unsuitable or qualitatively reduced habitat, potentially separating the ranges of the two mountain viper taxa: the huge Munzur-Mercan mountain ranges with a nearly 100 km stretch of > 2,700 m elevation along the border between the provinces Erzincan and Tunceli and the mighty Euphrates River with a hot-dry landscape of flat terrain or fine-sedimented hills and mountains < 1,000 m elevation reaching far inland from the river along the border of Malatya and Elazığ provinces. This unsuitable area is bordered in the south by the Malatya Mountain range west of the Euphrates and includes locality-45 (*Montivipera b. albizona*) in Adiyaman Province. From the eastern side of the Euphrates in southern Elazığ (Hazar Mountains) and Diyarbakir (Maden Mountains) provinces, we received credible, local reports of mountain vipers with yellow dorsal blochtes resembling Wagner's Viper. These mountain ranges on both sides of the Euphrates likely constitute the southern border for regional mountain vipers, as a flatter and lower arid landscape continues from there southwards towards Syria.

In respect to the Munzur Mountains, our current information assigns all specimens without genetic data from the western end of these mountains, Erzincan Province, to *M. b. albizona*, and predict their presence in the northwestern corner of Tunceli Province, with only 25 km continuous habitat from nearby *albizona* populations in Kabataş/Erzincan (localities-17 and -18), but additional *albizona* vouchers have been confirmed with genetic samples from nearby Erzincan and Sivas localities (e.g., localities-20 and -23, Supplemental Information Table S1). Regarding the occurrence of *M. b. albizona* north of the Munzur Mountains, however, only one shed skin of *M. b. albizona* has been reported (locality-16; Mulder 1995). The nearest populations of *M. wagneri* are found in the eastern part of Tunceli Province (photo voucher of Hengirvan, locality-15, and new specimen/molecular vouchers from 18 km distant Tahkini Yaylasi, locality-14, Fig. 4, Supplemental Information Table S1). These *M. wagneri* show virtually no cyt *b* genetic divergence (0–2 mutations over 700bp) to *M. wagneri* from 250 km farther east in Aras Valley, Kars Province, whereas there are 13–15 mutations to the currently nearest *M. b. albizona* 128 km farther west at Sandik, locality-20. The distance would be reduced to 78 km taking untested records between Hengirvan and Ziyaret Tepesi, respectively, localities-15–16. It becomes evident that the southern slopes and valleys of the Munzur Mountains need to be evaluated for a potential contact and/or transition zone between these two *Montivipera* taxa.

Whereas the Munzur Mountains might act as a potential topographic obstacle for exchange between northern populations of *Montivipera b. albizona* and *M. wagneri*, the Euphrates River is a potential barrier between these vipers farther south. The Euphrates River already flows through the Munzur Mountains in Erzincan Province where it is remarkably narrow and flanked by a steep valley, though only the Blunt-nosed Viper (*Macrovipera lebetina*) is known from its hot and dry riparian area < 1,500 m elevation (unpubl. data). Similarly, large portions of semi-arid southern and central Tunceli Province including mountains up to 2,000 m elevation appear void of *Montivipera* spp., but are inhabited by *Macrovipera lebetina* according to an experienced national park ranger with more than 30 y of province-wide service (Murat Özel, pers. comm.).

Farther south in Elazığ and Malatya provinces, the Euphrates River system widens substantially. Beginning at the northern end of the massive Keban Reservoir Lake (flooded Euphrates Valley and tributaries), the Euphrates River is flanked by alluvial plains with fine sediments on plateaus and gentle hills mostly < 1,100 m elevation, and leaving some rocky habitats in lower, drier, and warmer climate (Barry 2008), a semi-arid landscape that is less suitable for *M. wagneri* and *M. b. albizona*, but rather preferred by the larger *Macrovipera lebetina*, a potential competitor (Schätti et al. 1991). This remains speculative, however, without further field investigations and local data, and as the recently discovered contact zone between *M. wagneri* and *M. raddei* exemplified, such taxon divisions do not need to be accompanied by major landscape features (Mebert et al. 2015a, 2016). Nonetheless, there are two regions alongside the southern Euphrates River that potentially provide conditions suitable for *Montivipera* populations: between Keban and the Karakaya Reservoir Lake (40 km river course), and the outflow of this reservoir lake and the northern end of the huge Bayat-Atatürk Reservoir Lake, where the Euphrates River meanders through the eastern portion of the Malatya and Adiyaman Mountain

ranges flanked by steeper slopes and mountains > 1,000 m elevation, (e.g., see photographic vouchers from localities-22 and -45 in Fig. 8 and Supplemental Information Figs. S8, 13). These regions along the Euphrates River and the adjacent southern versant of the Munzur Mountains possibly constitute a non-continuous, first contact zone between *Montivipera* taxa. Indeed, preliminary cyt *b* analysis (750bp) shows that northern *M. b. albizona* from Sivas and Erzincan provinces show less genetic distance to populations 150–250 km farther south than to *M. wagneri* 130 km east across Euphrates (Supplemental Information Table S1).

A second contact may exist between *M. b. bulgardaghica* and *M. b. albizona* in Adana Province, previously thought to be separated by ca. 160 km between locality-48 at Elmali Bogazi (*bulgardaghica*) and locality-40 at Başkonuş Plateau (*albizona*). The contact zone is provisionally placed between the *bulgardaghica*-like specimen from Göller/Adana (locality-46 and Fig. 8A) and the more *albizona*-like specimens from about 38 km farther east at Başkonuş Plateau and Bostanli, Kahramanmaraş Province (localities-40 and -41, Supplemental Information Figs. S7G, S10, S11). This contact region has a low elevation, and thus less suitable habitat leading to reduced gene flow, of mostly < 1,000 m (red-hatched circle in Fig. 11), and begins at the city of Osmaniye in the south, forming a western border along Keşiş River north to Kadirli-Kesiksuyu Reservoir-Çağlayan Deresi-Çiçeklidere-Bağdaş Yaylasi (Y. = plateau) and Savrun Çayi (Ç. = river), and shows an eastern border with a line following Osmaniye-Aslantaş Reservoir Lake-Andirin-Köprüağzi Deresi. A high mountain, Ağaca Dağ at about 2,200 m elevation, borders this relatively lower region near the junction of the provinces Kayseri, Adana, Kahramanmaraş, and Osmaniye. The color pattern in south-eastern *Montivipera* populations from Kahramanmaraş and Adiyaman provinces show extreme variation, however, with large- to small-blotched specimens, with spotted to vertical-lined flanks, with round to rectangular blotches, often losing the light colored center posteriorly and with irregularly-formed borders reminiscent of *bulgardaghica* (Fig. 6 and Supplemental Information Figs. S10–S13). This large color pattern variation in the potential contact zone possibly reflect an intergradation between *M. b. bulgardaghica* and *M. b. albizona*, as it can be expected between these two conspecific clades (Stümpel et al. 2016); thus, the geographic transition might be much larger and gradual between these taxa. This is supported by an increasing genetic divergence by distance. For example, beginning with typical *M. b. bulgardaghica* at Kar Boğaz/Adana (locality-48), there are five mutations across 150 km east to *M. b. albizona* at Bostanli/Kahramanmaras (locality-41), but eight mutations across 360 km east to *M. b. albizona* at Adiyaman (locality-45). Yet, many more samples from the entire region are required to elucidate the genetic character of any contact or transition zone.

New information points to a third contact zone that exists between *Montivipera xanthina* and *M. bulgardaghica* in Erdemli district, Mersin Province. Previously published data showed a shortest distance of 150 km between these mountain vipers species, i.e. between type locality-53 of *bulgardaghica* (Nilson and Andren 1985) at Bolkar Dağı, border Niğde-Mersin provinces, to the *xanthina*-locality-63 at Erciyes Mountain, Kayseri Province (Nilson et al. 1988). A consensus of cyt *b* data (Supplemental Information Table S1) and/or color pattern reduces the distance between the western-most *M. b. bulgardaghica* at Gavuruçtuğu (locality-62) to *M. xanthina* near Akpinar to 16 km (locality-71, Fig. 10E) and 11 km near Kuşluca (only *xanthina* color pattern, locality-70, Fig. 10C, D). The habitat between these localities consists of continuous rock formation along high-elevation plateaus and southern versants of the Bolkar Mountains with two north-south valleys passing through Toros and Sungur at primarily > 1,400 m elevation, that may represent the contact zone.

In summary, the distances between the distribution areas of the different *Montivipera* taxa discussed herein have been reduced dramatically: between *Montivipera wagneri* and *M. b. albizona* from 280 km down to 78 km; between *M. b. albizona* and *M. b. bulgardaghica* from 160 km down to 38 km and for *M. b. bulgardaghica* and *M. xanthina* from about 150 km down to 11 km. Yet, for all the suggested contact zones or region of proximate populations, vouchers are missing to pinpoint precise areas of species delimitation or contact zones between these clades. Hence, much sampling, in particular for molecular data, is still needed for a fine-scaled phylogeographic analysis of these mountain vipers.

Conclusion.—This study revealed dramatic changes in the distribution of central-eastern Anatolian mountain vipers compared to what was officially perceived for decades by published and governmental information. With many new localities, but also refined-published (improved precision) ones, and increased habitat variation shown in figures and/or described for some localities in Supplemental Information, it becomes obvious that all four *Montivipera* taxa treated herein have not only much greater ranges but also larger population sizes. This updated information will have effects on the conservation statuses and facilitate new and more realistic assessments for the IUCN Red List of Threatened Species (IUCN 2020), including the shift of perceived threats from overcollection to overgrazing.

The results from this paper will help to locate proximate or parapatric populations or even find contact

zones between two *Montivpera* taxa. Consequently, we hope to stimulate new studies to investigate gene flow across species ranges and test for species integrity and relevant environmental correlates that could be incorporated into effective conservation measurements and specific action plans. Finally, we urge the conservation and scientific community to seek collaborative work with Turkish authorities and researchers, raise public awareness and understanding, and thus improve tools for the conservation of these valuable species and their habitat as national treasures.

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Konrad Mebert is an independent researcher and International Project Coordinator based in Switzerland, conducting studies globally on amphibians and reptiles with an emphasis on vipers. After completing a Master's degree at the University of Zürich, Switzerland, on geographic variation and the effects of inbreeding on the Dice Snake (*Natrix tessellata*), and a doctoral degree on hybrid zones in North American watersnakes (*Nerodia fasciata* and *N. sipedon*) at Old Dominion University, Norfolk, Virginia, he currently is associated with the State University of Santa Cruz, Ilhéus, Bahia, Brazil, and the Institute of Development, Ecology, Conservation and Cooperation (IDECC) in Rome, Italy. His work volume produced more than 130 professional and popular publications/reports and two books on water snakes including topics on evolution, ecology, biodiversity and conservation. Many expeditions and a passion for photography has led him to all relevant continents. Current (2020) principal study sites are located in Turkey, Panama, Ecuador, Brazil, Slovenia, Italy, Georgia, and China. (Photographed by Marco Sassoe).

Naşit İğci obtained his B.Sc. degree in zoology from Ege University Department of Biology, Izmir, Turkey, in 2008. He received his M.Sc. and Ph.D. from Ankara University Biotechnology Institute, Turkey, in 2009 and 2015, respectively, and is currently an Associate Professor in Nevşehir Haci Bektaş Veli University Department of Molecular Biology and Genetics, Nevşehir, Turkey, since 2016. His research includes biochemistry and pharmacology of snake venoms, and the ecology and systematics of amphibians and reptiles of Turkey. He worked as a reptile specialist in several projects related to biodiversity monitoring and conservation supported by the Government of Turkey. (Photographed by Konrad Mebert).

Mert Karış is a Lecturer at the Acigöl Vocational High School of Technical Sciences, Nevşehir Haci Bektaş Veli University, Cappadocia, Turkey. He received his Zoology B.Sc. degree from the Department of Biology, Faculty of Science, Ege University, Izmir, and M.Sc. and Ph.D. degrees in Biology/Zoology from the Institute of Natural and Applied Sciences, Ege University, Izmir, Turkey. His research focuses on systematics (taxonomy), ecology and diversity of amphibians and reptiles of Turkey. He also works on biochemical and pharmacological properties of snake venoms and amphibian skin secretions. (Photographed by Kürşat Bal).

Mehmet Zülfü Yildiz is an Associate Professor at the Department of Biology in Adiyaman University (Turkey) and has extensive experience of east and southeast Anatolia. He received his university education at Harran University in Şanliurfa (B.S. and M.S. degrees) and Ege University in İzmir, Turkey. His interests cover biodiversity, ecology, systematics, molecular phylogeny of reptile and amphibians, and venom studies of vipers. Mehmet contributes regularly to the Amphibians and Reptiles Monitoring & Photography Society in Turkey. He has authored or co-authored over 40 peer-reviewed papers on herpetology and is editor for Biharean Biologist, Commagene Journal of Biology, and Acta Biologica Turcica. (Photographed by Konrad Mebert).