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New cases of sympatry between vipers in southwestern Morocco

Gabriel Martínez del Marmol[1], Baudilio Rebollo Fernandez[2], Stéphane Clerc[3], Thor Håkonsen[4], Sonia Acierno[5], and Marco Sassoè-Pognetto[5,*]

Palearctic vipers frequently exhibit parapatric distributions. For example, European vipers belonging to the genus *Vipera* (Lenk et al., 2001) have spatially segregated distributions, although cases of sympatry have been reported at contact zones between two or even three distinct species (Saint-Girons, 1975; Monney, 1996; Martínez-Freiría et al., 2008, 2010; Scali et al., 2011; Mebert et al., 2015). In arid and semi-arid regions of north Africa, the eastern Mediterranean, the Arabian peninsula and the Iranian province (Sindaco et al., 2013), the geographical ranges of individual species show areas of potential overlap, although it is generally assumed that distinct habitat selection hampers sympatry at the local scale (for example see Brito et al., 2011). This assumption is concurrent with the view that vipers, contrary to other snakes, often partition habitat, rather than food resources, when they are found in the same habitat (Luiselli, 2006a,b).

Sporadic cases of sympatry between Palearctic vipers from arid environments have been described recently. For example, *Pseudocerastes urarachnoides* (Bostanchi et al., 2006), which is endemic to the western Iranian Zagros Mountain range, was observed in the same environment with congeneric *P. persicus* (Duméril et al., 1954) (Fathinia and Rastegar-Pouyani, 2010; Bok et al., 2017). In Morocco, an adult *Cerastes cerastes* (Linnaeus, 1758) and a subadult *Daboia mauritanica* (Gray, 1849) were found together in the sedimentation chamber of a water cistern, suggesting that the two vipers share the same habitat (Martínez-Freiría et al., 2016). This finding was reported as the first evidence of syntopy between vipers in Morocco, although in this case, syntopy was obviously caused by the trapping of the two snakes inside a man-made construction.

Southwestern Morocco is an environmental transition zone comprising suitable habitats for five species of vipers belonging to distinct biogeographical units (Bons and Geniez, 1996; Brito et al., 2011): the Afrotropical Puff adder, *Bitis arietans* (Merrem, 1820); the Saharan Horned viper, *C. cerastes*, and Sand viper, *C. vipera* (Linnaeus, 1758); the north African-Mediterranean Maghreb viper, *D. mauritanica*; and the Sahelian Carpet viper, *Echis leucogaster* (Roman, 1972). Ecological models have predicted sympatry of potentially all these vipers (Brito et al., 2011), but direct evidence supporting the coexistence of two or more species in the same habitat is scanty. Here we describe three novel cases of sympatry between vipers in southwestern Morocco, proposing that sympatry between Palearctic vipers occurs more commonly than it was generally thought.

Case 1: *Cerastes cerastes* and *C. vipera*.

These two Saharan vipers are widespread throughout North Africa, also extending through Sinai to the Negev desert in Israel (Schleich et al., 1996; Bar and Haimovitch, 2011; Sindaco et al., 2013). *C. cerastes* is present in a variety of arid habitats, including sandy and rocky deserts, but usually avoids extensive dune formations. In contrast, *C. vipera* is a psammophilous species mainly restricted to wind-blown dunes with sparse vegetation. Because of these distinct habitat affinities, it is generally supposed that the two species do not occur in syntopy (Spawls and Branch, 1995; Geniez et al., 2004).

On 19 August 2013, two adult specimens of *C. vipera* and one adult *C. cerastes* (Fig. 1A,B) were found by three of us (G. M., B. R. and M. S.-P.) inside a dry

[1] Cl. Pedro Antonio de Alarcon, 34, 18002 Granada, España.
[2] Urbanizacion Rio Gulf nº 38, La Rabida, Palos de La Frontera, CP 21819 Huelva, Spain.
[3] Batterie des Masses, Case Postale 176, 1987 Les Masses, Switzerland.
[4] Norsk Herpetologisk Forening, Tellusvegen 13f, 2165 Hvam, Norway.
[5] Department of Neuroscience "Rita Levi Montalcini", University of Torino, C.so Massimo d'Azeglio 52, 10126 Torino, Italy.
[*] Corresponding author. E-mail: marco.sassoe@unito.it

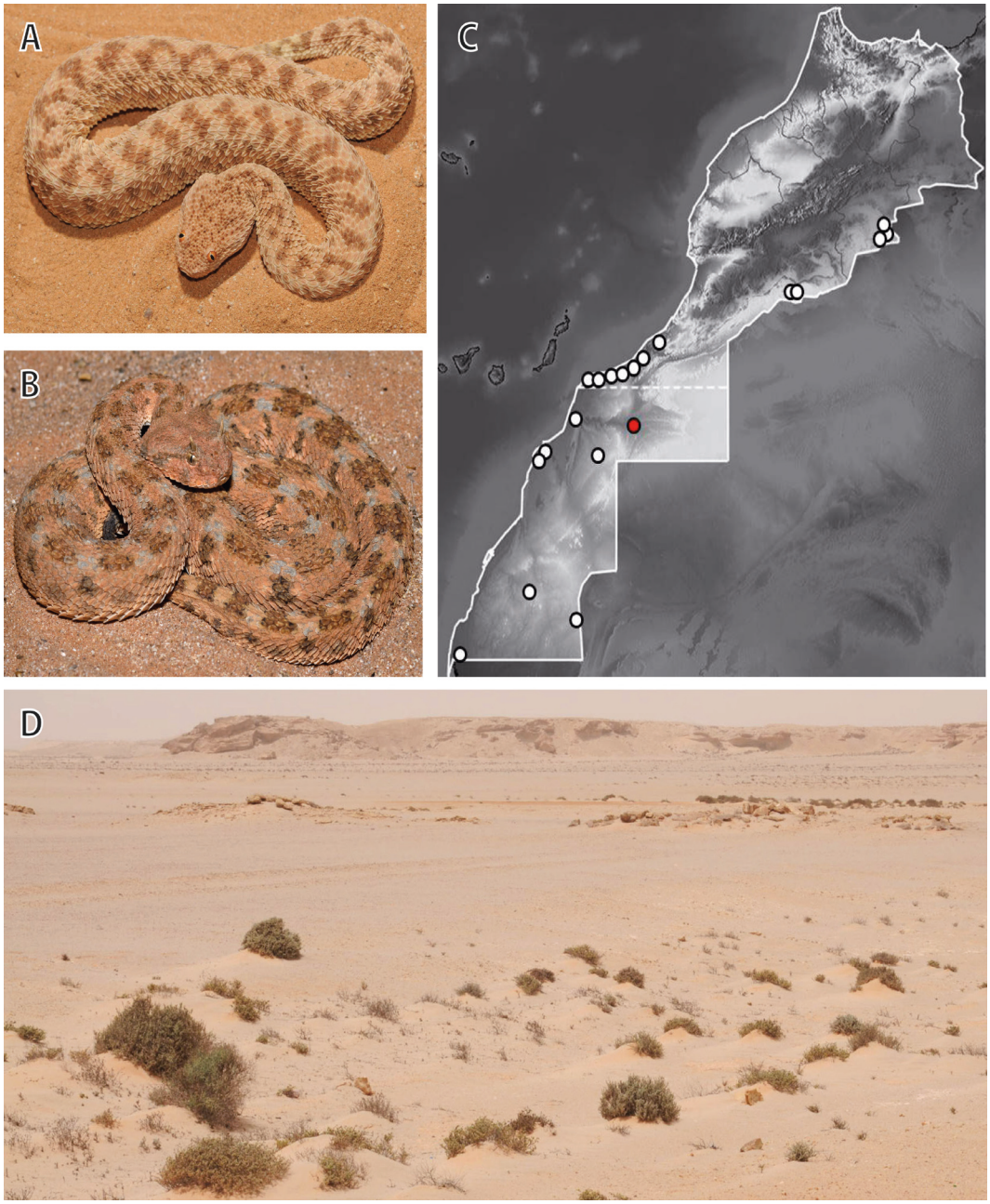

Figure 1. One of the two individuals of *Cerastes vipera* (A) found inside a water cistern with a *Cerastes cerastes* (B). (C) Known distribution (white dots) of *Cerastes vipera* in Morocco and site of the new observation (red dot). (D) Habitat in the vicinity of the water cistern.

water cistern located 50 Km north of Smara (27°13'36" -11°44'14"). The two conspecific vipers (i.e. *C. vipera*) were close to each other inside the tank, whereas *C. cerastes* was at a distance of about two metres away. The *C. vipera* individuals had a pale colouration (Fig. 1A), well distinct from the contrasted morph that is found

along the Atlantic coast in the Tarfaya-Laayune region (Bons and Geniez, 1996; Geniez, 2015). The water cistern is located in a flat desert (Fig. 1C,D) characterized by patches of accumulated sand with sparse rocky outcrops and scarce vegetation (mostly small bushes of *Hammada* sp.). To our knowledge, this is a new locality for *C. vipera*, a species known in Morocco from only a few sites (Fig. 1C), all characterized by extensive dune complexes (Bons and Geniez, 1996; Geniez et al., 2004). However, no major *erg* formations are present at this locality, suggesting that *C. vipera* can be found outside of dune habitats. This seems to be the case also in Egypt, where the species is sometimes found in areas of coarse sand and gravel (Baha El Din, 2006).

Sympatry of C. *cerastes* and *C. vipera* in approximately the same region north of Smara has been reported recently under similar circumstances, when individuals of the two species were found in the sedimentation chamber of a water cistern (García-Cardenete et al., 2017). Moreover, the authors also observed four individuals of *C. vipera* and a subadult *C. cerastes* run over by vehicles in a stretch of four kilometres of the R101 road connecting Tan-Tan to Smara. Altogether, these observations suggest that in suitable habitats (e.g. transition zones between sandy and rocky deserts) the two vipers can be found in the same environment. In Morocco, another location of potential coexistence of these two congeners is the M'Hamid El Ghizlane oasis, where both species are present (Bons and Geniez, 1996, and unpublished observations). Likewise, the two *Cerastes* are widespread in the western Negev desert in Israel (Bar and Haimovitch, 2011), where they have been observed in the same habitat (G. M. and B. R., pers. obs.). Additional fieldwork is required to gain a better understanding of how these congeneric vipers partition habitat resources through their extensive North-African range.

Case 2: *Cerastes cerastes* and *Echis leucogaster*.

The white-bellied carpet (or Roman's saw-scaled) viper *E. leucogaster* is known in Morocco from only a few localities, although recent findings have revealed that the species is more widespread than previously thought (Aymerich et al., 2004; Martinez del Marmol and Rebollo Fernandez, 2012; Koleska et al., 2018). In May 2017, during three consecutive nights S. A. and M. S.-P. found two specimens of *C. cerastes* and an individual *E. leucogaster* (Fig. 2A,B) in the vicinity of Aouinet Lahna (28°30'56" -9°51'44"). One of the *Cerastes* specimens was observed inside a local plantation, which is a well-known spot for *E. leucogaster*. Interestingly, other researchers have found both *C. cerastes* and *D. mauritanica* at a distance less than 10 kilometres from Aouinet Lahna (Martínez-Freiría et al., 2016). These observations suggest that the Aouinet Lahna region may be home to three species of vipers characterized by distinct biogeographical affinities. All the localities in which *E. leucogaster* has been observed in Morocco fall within the distribution range of *C. cerastes* (Bons and Geniez, 1996), suggesting that sympatry between the two species is common. The possibility that competition with *C. cerastes* is a factor limiting the distribution of *E. leucogaster* in Morocco has previously been recognized by Herrmann et al. (2000).

Case 3: *Bitis arietans* and *Daboia mauritanica*.

The distribution of these two large vipers overlaps extensively in the coastal region comprised between Agadir and Oued Draa, potentially extending along the Sous valley up to Taliouine (Bons and Geniez, 1996; Martínez-Freiría et al., 2017). This area of overlap corresponds to the northern and southern limits of the distribution range of the puff adder, *Bitis arietans*, and the Maghreb viper, *D. mauritanica*, respectively. Despite the extensive potential coexistence, there is scanty information about sympatry between these vipers (Brito et al., 2011). In April 2015, one of us (T. H.) found an adult *D. mauritanica* belonging to the "pale" morph (Fig. 2C) in the north of Oued Chbika (28°17'56" - 11°30'38"). This is allegedly a new locality for *D. mauritanica*, whereas *B. arietans* is regularly observed in the area, as communicated by a local Aissaoua snake catcher. In fact, a subadult puff adder, *Bitis arietans* (Fig. 2D) was observed a few hundred metres away from the *Daboia* spot on the same day. Evidence for the coexistence of the two vipers was also obtained along the Plage Blanche road west of Guelmin, where S. C. observed in May 16th-29th, 2017 a large female of Maghreb viper, *D. mauritanica* with total length of ~110 cm (Fig. 2E) as well as three other individuals (two males, one female) which had been run over by vehicles. These observations were made in a stretch of about 30 km of the Plage Blanche road spanning both sides of the Noun river (between 29°0'55" -10°22'44" and 29°0'24" -10°7'28"). This region falls within the known *Bitis* range in Morocco (Bons and Geniez, 1996; Brito et al., 2011) and not surprisingly six puff adders (three live adults and three death individuals) were also observed during the same period. These findings suggest that *B. arietans* shares its habitat with *D.*

Figure 2. (A,B) Photographs of *Echis leucogaster* (A) and *Cerastes cerastes* (B) from Aouinet Lahna. (C,D) *Daboia mauritanica* (C) and *Bitis arietans* (D) found north of Oued Chbika. The *Daboia* specimen belongs to the pale morph according to Bons and Geniez (1996). (E) The *Daboia mauritanica* with a contrasted pattern found on the Plage Blanche road West of Guelmin. (F) The habitat near Plage Blanche where both *Daboia* and *Bitis* have been observed.

mauritanica along much of the coastal topoclimatic unit of southwestern Morocco (Fig. 2F).

The observations reported here provide support to ecological models predicting potential sympatry between the five species of vipers that inhabit southwestern Morocco (Brito et al., 2011). It is notable

that sympatry involves not only species belonging to the same topoclimatic unit (i.e. the two Saharan *Cerastes*), but also species characterized by distinct bioclimatic affinities (*C. cerastes* and *E. leucogaster*, and *B. arietans* and *D. mauritanica*). The Maghreb viper, *D. mauritanica* appears to be the most generalist species in terms of habitat selection, as this snake is found both in the coastal environment, where it shares the habitat with *B. arietans*, and in more arid inland environments, where it may coexist with *C. cerastes* and possibly *E. leucogaster* (see Martínez-Freiría et al., 2016). While our data provide evidence for the co-occurrence of two species of vipers in the same habitat, it is likely that at least three species can be found in sympatry in suitable areas. These include the territory surrounding Aouinet Lahna, where *C. cerastes*, *D. mauritanica* and E. *leucogaster* have been observed, and the coastal region between Tiznit and Tarfaya, where *B. arietans*, *C. cerastes* and *D. mauritanica* may coexist (Brito et al., 2011). Notably, *C. vipera* is also present along the Atlantic coast, although this species seems to be strictly confined to the littoral dune habitat (Bons and Geniez, 1996). Since Morocco has become a popular destination for many professional and amateur herpetologists, it is likely that more cases of sympatry will be documented, together with a more detailed definition of the species local distribution ranges.

Obviously, the present observations are too limited to draw general conclusions about the extent of habitat overlap in Palearctic vipers, but they suggest that under favourable conditions vipers can coexist in the same environment. In this respect southwestern Morocco offers a particularly favourable situation, due to the fact that this region represents a transition zone between different topoclimatic units (Brito et al., 2011). Research in this area should be valuable to ascertain how vipers partition habitat resources to reduce niche overlap, thus restricting interspecific coexistence (Luiselli, 2006a). One factor that may favour the coexistence of vipers in southwestern Morocco is the apparent abundance of rodents (*Atlantoxerus getulus*, *Psammomys obesus*), especially in the coastal topoclimatic unit (Brito et al., 2011). Moreover, some of the sympatric vipers may be able to partition dietary resources. In this respect, a detailed investigation of preys consumed by *E. leucogaster* in Morocco would be valuable, given that some species of *Echis* feed on large arthropods, a trait considered atypical in vipers (see Barlow et al., 2009 and references therein).

In addition to southwestern Morocco, other potential diversity hotspots for Paleartic vipers are the Levantine region, the Arabian-Afrotropical transition zone in southwestern Arabia, the western Asian mountain transition zone and the Iranian province (Sindaco et al., 2013). Field studies are necessary to better investigate coexistence and syntopic relationships between vipers in these regions.

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