

Effects of ecological divergence in the westernmost Anatolian populations of *Montivipera xanthina* (Gray, 1849) (Serpentes Viperidae)

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ABSTRACT

The *Montivipera xanthina* (Gray, 1849) complex (Serpentes Viperidae) consists of two divergent species groups, the *xanthina* group with a western distribution (Western Turkey, Northeastern Greece), and the *bornmuelleri* group (*albizona*, *bornmuelleri*, *bulgardaghica*, *wagneri*) with a more eastern distribution (Central-eastern Turkey, Syria, Lebanon). New evidence suggests that the *xanthina* group's well-documented search for coastal habitats is dictated by intrinsic factors. Therefore, the author deems it appropriate to distinguish these western Anatolian populations of *Montivipera xanthina* with the subgeneric name *Planivipera* n. subgen., which would separate this group of vipers with their different ecology from the true mountain vipers of the Turkish inland (*bornmuelleri* group).

KEY WORDS

Montivipera xanthina; habitat; mountain end planitial environment; *Planivipera* n. subgen.

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INTRODUCTION

The genus *Montivipera* Nilson, Tuniyev, Andren, Orlov, Joger et Herrmann, 1999 (Serpentes Viperidae) includes all the species of the *xanthina* (Gray, 1849) and *raddei* Boettger, 1890 complexes. Nilson & Andr n (1997) assigned the name *Vipera* 2 to these complexes; subsequently Nilson et al. (1999) proposed to better define these entities by naming them *Montivipera*, as a subgenus of *Vipera* Laurenti, 1769, claiming that the European vipers diverge morphologically, genetically, serologically and ecologically from Anatolian mountain vipers. Later, the subgenus *Montivipera* was elevated to the rank of genus (Joger, 2005; Joger & Nilson, 2005).

The genus *Montivipera* inhabits a large area that includes Northeastern Greece, Asia Minor, Syria,

Lebanon, Armenia, Azerbaijan and Iran. The *raddei* complex has the most eastern distribution, the *xanthina* complex includes the Anatolian species.

Nilson et al. (1999) noticed how the easternmost species of the *xanthina* complex were distributed along a mountain range with peaks as high as 3000–4000 m a.s.l., arranged diagonally from northeast to southwest (the “Anatolian diagonal”) and hypothesized that the dispersion of a progenitor along this mountain range could have led to the speciation of isolated populations separated by large areas of unsuitable habitats and thus, with impeded gene flow.

The species distributed along the “Anatolian diagonal” represent the *bornmuelleri* group and along with the *raddei* complex form the true mountain vipers, adapted to live in extreme environmental

conditions. In contrast, the vipers that inhabit the Eastern Aegean Islands, Northeastern Greece and West Turkey (*xanthina* group), frequent lowlands, flat coastal regions or regions with low hills, so their constitution is suited to these new environmental conditions; as their relationships with the physical and biotic environment change, their morphology must adapt to new functions. Believing that ecology is the true driving force of evolution, it seems appropriate to propose that these western Anatolian populations be referred to as *Planivipera* n. subgenus, a term that would clearly indicate the different ecology of these populations.

MATERIAL AND METHODS

Twelve specimens from Southwestern Turkey, 102 specimens from Eastern Aegean Islands and 58 specimens from Northeastern Greece have been studied. Part of this material is kept in the author's private collection (Herpetological Collection Augusto Cattaneo, Rome, Italy).

ABBREVIATIONS: TL = total length; W = weight; D = number of dorsal scale rows at mid-trunk counted in a transverse line at the height of half the total number of ventral scales (counted with the classic method, see below); V = number of the ventral scales, counted with the classic method, which considers ventral the mid-ventral scales that are wider than they are long; SC = number of pairs of subcaudal scales, counted from the first postcloacal scale that is in contact with the contralateral along the caudal midline.

RESULTS

Considerations on the various populations of the xanthina complex

The genus *Montivipera* consists of two sister evolutionary lines, as follows.

The *xanthina* complex: eye in contact with the supraocular; a canthal between the supraocular and the supranasal.

The *raddei* complex: a series of small scales between the eye and the supraocular, two or more canthals between the supraocular and the supranasal (Armenia, Azerbaijan, Iran).

The *xanthina* complex consists of two groups of divergent species, the *xanthina* group with a western distribution (Northeastern Greece, West Turkey), and the *bornmuelleri* group (*albizona*, *bornmuelleri*, *bulgardaghica*, *wagneri*) with a more eastern distribution (Central-Eastern Turkey, Syria, Lebanon). To the *bornmuelleri* group belong the true mountain vipers distributed along the "Anatolian diagonal" (see Nilson et al., 1990); the *xanthina* group includes all the populations that have subsequently adapted to warm lowland environments except for some subpopulations with an inner continental distribution. The *xanthina* complex diversified during the Miocene, expanded during the warm phase of the Pliocene, and reached maximum population size in the early Pleistocene when the present evolutionary lineages formed. Avise et al. (1998) estimated that 57% of the recent herpetofauna dates back to Pleistocene speciation events (Stümpel et al., 2016).

The species belonging to the *raddei* complex (*raddei raddei*, *raddei kurdistanica*, *albicornuta*, *kuhrangica*, *latifii*) represent genetically homogeneous lineages with low genetic diversity. Their evolutionary path seems to have started in the Pliocene (Stümpel et al., 2016).

About xanthina complex: bornmuelleri group

Adaptation of the *Montivipera* group to mountainous conditions may have started during the Serravallian (about 13–12.2 Ma; Stümpel et al., 2016) in response to major environmental changes produced by the 1.5–2 km a.s.l. rise of the Turkish-Iranian plateau (Sapas & Boztepe-Güney, 2009; Codrea et al., 2017). With the increase in altitude came climatic changes (lower temperatures, increase of moisture, higher solar radiation, lower air pressure) as well as changes to spatial, biotic and evolutionary factors (Stümpel et al., 2016).

The *Montivipera* stem group thus arose in mountain biomes (plateaus and subalpine forests), adapting to a seasonal climate and diurnal life style dictated by extreme climatic conditions. Their type of reproduction also reflects their environmental situation; members of the *xanthina* group have a "berus" type of reproductive cycle, with sperm that do not fully develop until just before the start of spring mating, which, in turn, is triggered by the spring moult (Nilson, 1980; Nilson et al., 1999).

As stated above, according to Nilson et al. (1990) the *bornmuelleri* group was formed as a result of vicariance events that led to the speciation of isolated populations distributed along the “Anatolian diagonal” (mountain range with a Northeastern-Southwestern axis) and thus separated from the more western populations of the *xanthina* group.

The main interactions of this group with environmental factors are set out below (see Table 5).

Relationships with the geo-physical environment

Habitat: high mountains with long and very cold winters. The mountain environment involves temperature swings and high humidity, resulting in eurythermia and hygrophilia respectively for these vipers.

At high altitudes in heterothermic animals, there is a general reduction in the size and number of meristic characters (scales) due to the slowing of developmental and differentiation processes caused by low temperatures. This is especially evident in the species of the *bornmuelleri* group, which, compared to the species of the *raddei* complex, are more similar to the westerly populations of the *xanthina*

group (the latter adapted to the warm environments of the lowlands) and, as such, with less structural correspondence to the contingent functional requirements (high altitude life) (Tables 1–4). The species of the *raddei* complex constitute a distinct evolutionary lineage compared to the species of the *xanthina* complex since they are better adapted to high mountain life and are distributed further north-east than the species of the *bornmuelleri* group. According to Hubbs’ law or rule, in heterotherms of equal or related species, the number of meristic characters (in this case, scales) tends to increase as one goes up in latitude and altitude and, consequently, as temperatures decrease. In the context of true mountain vipers, this would justify the morphometric and pholidosis divergences between the *raddei* complex and the *bornmuelleri* group.

Exclusively daytime activity.

Relationships with the biotic environment

Low selective pressure exerted by ophiophagous snakes of the genus *Dolichophis* or *Malpolon*, which being thermophilic species, are increasingly rare with increasing altitude.

<i>Montivipera (Planivipera) xanthina</i>	80-85 cm; about 95 cm (Turkey); about 130 cm (Greek islands)
<i>Montivipera (Montivipera) albizona</i>	♂♂ about 75 cm
<i>Montivipera (Montivipera) bornmuelleri</i>	about 75 cm; ♀♀ Mt. Liban < 50 cm. ♂♂ about 55 cm
<i>Montivipera (Montivipera) bulgardaghica</i>	< 80 cm
<i>Montivipera (Montivipera) wagneri</i>	80-85 cm
<i>Montivipera (Montivipera) xanthina varoli</i>	about 55 cm (Afsar et al., 2019)
<i>Montivipera (Montivipera) raddei raddei</i>	♂♂ about 100 cm; ♀♀ about 80 cm
<i>Montivipera (Montivipera) raddei kurdistanica</i>	♂♂ about 90 cm; ♀♀ 70 cm
<i>Montivipera (Montivipera) albicornuta</i>	♂♂ about 65 cm
<i>Montivipera (Montivipera) kuhrangica</i>	♂♂ about 65 cm (Rajabizadeh et al., 2011)
<i>Montivipera (Montivipera) latifii</i>	♂♂ < 80 cm; ♀♀ 70 cm

Table 1. Maximum total lengths detected in the species of the genus *Montivipera* (from Mallow et al., 2003).

	D	V	SC
<i>Montivipera (Planivipera) xanthina</i>	21-23-25	147-169 (158)	27-38 (32.5)
<i>Montivipera (Montivipera) albizona</i>	23	149-155 (152)	23-30 (26.5)
<i>Montivipera (Montivipera) bornmuelleri</i>	21-23	142-153 (147.5)	23-31 (27)
<i>Montivipera (Montivipera) bulgardaghica</i>	23-25	145-156 (150.5)	24-33 (28.5)
<i>Montivipera (Montivipera) wagneri</i>	23	161-170 (165.5)	23-31 (27)
<i>Montivipera (Montivipera) xanthina varoli*</i>	23	157-160 (158.5)	26-28 (27)
<i>Montivipera (Montivipera) raddei raddei</i>	21-23-25	163-181 (172)	28-35 (31.5)
<i>Montivipera (Montivipera) raddei kurdistanica**</i>	23-25	165-178 (171.5)	28-33 (30.5)
<i>Montivipera (Montivipera) albicornuta</i>	22-23	165-171 (168)	♂♂ 35-38 (36.5)
<i>Montivipera (Montivipera) kuhrangica***</i>	23	163	37
<i>Montivipera (Montivipera) latifii</i>	21-23	161-169 (165)	26-39 (32.5)

Table 2. Pholidosis values detected in species of the genus *Montivipera* (the most diagnostic values in bold, the average values in brackets) (from Mallow et al., 2003; * from Afsar et al., 2019; ** from Nilson & Andrén, 1986, 1990; *** from Rajabizadeh et al., 2011).

	♂♂		♀♀	
	T L (CM)	W (G)	T L (CM)	W (G)
SAMOTHRAKI	93.4-109.1 (n = 2)	357-540 (n = 2)		
LESVOS	99-106.1 (n = 3)	450-526 (n = 3)		
CHIOS	108.9*-140 (n = 7)	635-1284 (n = 7)	79-116 (n = 6)	464-698 (n = 6)
SAMOS	102-110 (n = 3)	474-538 (n = 3)		
PATMOS	78.3-78.5* (n = 2)	240-275 (n = 2)		
LIPSI	83.5*	403	63-68 (n = 2)	199-225 (n = 2)
LEROS	94.3*-98* (n = 2)	489-560 (n = 2)	85	499
KALYMNOS	72	239	79.5*	407
SYMI	91.4-92.1 (n = 3)	319-345 (n = 3)	61.5-68.1 (n = 3)	187-194 (n = 3)
SW TURKEY	91-93.8 (n = 3)	320-370 (n = 3)	62	141
NE GREECE (EVROS)	91	375	73.7	241
NE GREECE (RHODOPE)	91-95 (n = 3)	400-460 (n = 3)	85	433

Table 3. *Montivipera (Planivipera) xanthina*: maximum size detected in the Eastern Aegean Islands, Southwestern Turkey and Northeastern Greece (* = incomplete tail).

	D	V	SC
SAMOTHRAKI	23	163-166 (164.5)	32-34 (33)
LESVOS	23	162-168 (165)	29-32 (30.5)
CHIOS	22- 23	157-166 (161.5)	29-36 (32.5)
SAMOS	23-25	166-175 (170.5)	30-34 (32)
PATMOS	23	158-163 (160.5)	33-35 (34)
LIPSI	23-25-27	148-168 (158)	28-33 (30.5)
LEROS	23-24- 25	152-165 (158.5)	27
KALYMNOS	23	162-166 (164)	31
KOS	23	168	31
SYMI	23	150-157 (153.5)	34-39 (36.5)
SW TURKEY	23	157-171 (164)	27-37 (32)
NE GREECE (EVROS)	23	158-163 (160.5)	29-34 (31.5)
NE GREECE (RHODOPES)	21-22-23	156-167 (161.5)	26-34 (30)

Table 4. *Montivipera (Planivipera) xanthina*: pholidosis detected in the Eastern Aegean Islands, Southwestern Turkey and Northeastern Greece (the most diagnostic values in bold, the average values in brackets).

About xanthina complex: xanthina group

The only species recognized so far: *Montivipera xanthina*.

The *xanthina* group includes almost all the populations that have adapted secondarily to warm lowland environments. The lowland populations are thus considerably younger. The ancestral ecological trait is mountainous and the adaptation to warmer lowland habitats occurred at a later stage (Stümpel et al., 2016).

There is a high genetic drift between *Montivipera xanthina* from western Anatolia and the *bornmuelleri* group (*bornmuelleri*, *albizona*, *bulgardaghica*, *wagneri*) (Freitas et al., 2020); this divergence reflects the disjointed geographic distribution (Stümpel & Joger, 2009).

Montivipera xanthina is an entity consisting of four divergent lineages: Greece, Aegean region, Lycia and Taurus (Stümpel et al., 2016).

Populations from the Taurus Mountains (Southern Turkey) represent the oldest evolutionary lineage, having separated from their sister group 5.2 Ma, but the Lycian populations (southern coast of Anatolia) are also of considerable age. Recently, Afsar et al. (2019) described *Montivipera xanthina varoli*, a typical subspecies of the Geyik Mountains (Taurus Mountains). Although the place of its occurrence would assign this taxon to the *xanthina* group (Stümpel et al., 2016), the ecological requirements, its morphometric features (TL max. about 55 cm) and low pholidosis values (23 D, 158.5 V on average, 27 SC on average) reveal its membership to the mountain vipers (*bornmuelleri* group) (as previously stated). Ultimately, the area inhabited by *M. xanthina varoli* Afsar, Yakin, Çiçek & Ayaz, 2019 represents the southwesternmost offshoot of the “Anatolian diagonal”. For this reason, I think it appropriate to confirm these populations in the subgenus *Montivipera* (see below).

The Evros River forms a geographical barrier between the populations of *M. xanthina* that inhabit NE Greece and those that inhabit the Turkish Thrace (Western Turkey). It appears that despite their spatial proximity, these populations originate from different dispersal events and do not share a common ancestor (Stümpel et al., 2016). With regards to Northeastern Greece, populations distributed west of the Evros river belong to a different clade than those that inhabit the Rhodope region (westward up to Xilagani village); the latter represent a pioneer entity undergoing active colonization whose morphometric and pholidosis features indicate rapid speciation that has earned the name *M. xanthina occidentalis* (Cattaneo, 2017).

The Turkish coastal mainland and the Eastern Aegean Islands host populations of *Montivipera xanthina* in active microevolution. So far, only two subspecies, both insular, have been described, *M. xanthina nilsoni* Cattaneo, 2014 (Chios Island) and *M. xanthina diana*e Cattaneo, 2014 (Leros Island and perhaps Lipsi) (Cattaneo, 2014, 2018), but considering that the lowland populations are ecologically more adaptable than those of the mountains and also that *Montivipera xanthina* from western Anatolia, while showing low comparative variability in the external morphology, has high levels of genetic diversity, new taxa could be described in this complex. The western populations could represent a complex of cryptic species (Stümpel & Joger, 2009; Stümpel et al., 2016). It is worth remembering that on the island of Chios, at Latomi, the fossil remains of a large Viperid dating back to the middle Pleistocene, comparable in size to *Macrovipera lebetinus* Linnaeus, 1758, were found (Schneider, 1975; Szyndlar, 1991; Georgalis et al., 2016; Georgalis & Delfino, 2022). The finding could be phylogenetically related to the current *Montivipera xanthina nilsoni*, a noted endemic to Chios, which differs from other conspecific populations precisely for its large size. Indeed, it is worth noting that the related complexes of *Montivipera* and *Macrovipera* inhabited the Middle East during the lower Miocene (Lenk et al., 2001). Their relationships are congruent with osteological findings (Szyndlar & Rage, 1999) and are biogeographically well-founded (Lenk et al., 2001; Garrigues et al., 2005). Based on phylogeographical and geotectonic data *Macrovipera* and *Montivipera* shared their last common ancestor on the Anatolian

subcontinent during the Langhian (15.3 Ma, Stümpel et al., 2016).

The main interactions of this group with environmental factors are set out below (see Table 5).

Relationship with the geophysical environment

Habitat: lowlands, flat coastal regions or those with low hills (“coastal viper”, Steward, 1971), high mountains too (up 2500 m a.s.l.), but only in the southern part of the species range (Joger & Nilson, 2005). Stojanov et al. (2011) claim that the spread of this viper took place exclusively along the Mediterranean coast and not inland, likely due to limiting climatic factors. Along the northeastern coast of Greece *M. xanthina* can in exceptional cases move up to 10–15 km inland. Herpetological surveys have ruled out the potential presence of this viper in the mountainous areas of the Eastern Rhodopes (Helmer & Scholte, 1985; Petrov, 2004). In the Evros region (Northeastern Greece) it is sympatric with *Vipera ammodytes* replacing it in flat coastal stretches (Cattaneo & Cattaneo, 2013). Thus, it seems plausible that intrinsic factors dictate the search for exclusively coastal habitats.

More mesophilic species adapted to a less wide thermal range.

Increase in the size and number of meristic characters (scales).

Potentially annual reproductive cycle (biennial or triennial in the *bornmuelleri* and *raddei* groups) with the completion of spermatogenesis in ♂♂ not necessarily in spring (as is the case in the *bornmuelleri* and *raddei* groups) (see closing paragraph).

Twilight and nocturnal activity in late spring and summer.

Relationship with the biotic environment

Strong selective pressure exerted by ophiophagous snakes of the *Dolichophis* Gistel, 1868 or *Malpolon* Fitzinger, 1826 genera (Cattaneo, 2011b, 2012).

In light of the aforementioned considerations and understanding the subgenus as a taxonomic category that splits the genus into groups of related species, all involved in the same micro-evolutionary process, I deem it appropriate to join the populations of the *xanthina* group in a new subgenus.

***Planivipera* n. subgenus**

<https://zoobank.org:act:DCAD3DB3-0345-4287-A486-90DBA4083BDD>

TYPICAL SPECIES. *Montivipera xanthina* (monospecific subgenus).

DIAGNOSIS. The snakes included in this taxon differ from other members of the genus *Montivipera* for their larger size (up to 130–140 cm in total length in the eastern Aegean Islands, Tables 1, 3), and for higher pholidosis (usually more than 160 ventral scales and more than 30 subcaudals) except for some microinsular Aegean populations (Tables 2, 4). It is worth noting that these morphological differences are more detectable than in the *bornmuelleri* group, and less detectable than in the *raddei* group, which appears to be genetically highly divergent from the *xanthina* complex (Freatas et al., 2020) (in this regard, see what previously stated).

They also differ in their ecology, inhabiting flat coastal regions or coastal regions with low hills rather than mountain biomes with extreme climatic conditions. As a result, instead of being purely diurnal with an active period during the day, they are also crepuscular and nocturnal during

late spring and summer. The members of this new subgenus are therefore adapted to a less wide thermal range and prove to be more mesophilic. The reproductive cycle is potentially annual (biennial or triennial in the *bornmuelleri* and *raddei* groups) with the completion of spermatogenesis in ♂♂ not necessarily in spring (as instead happens in the *bornmuelleri* and *raddei* groups) (see closing paragraph).

Furthermore, several biotic interactions result in greater selective pressure from ophiophagous snakes.

The differences between *Planivipera* subgen. nov. and *Macrovipera* A.F. Reuss, 1926 *Daboia* Gray, 1842 and *Vipera* genera, are similar to those that these genera have with the subgenus *Montivipera*. For completeness, they are reported below.

Planivipera differs from *Macrovipera* in being an ovoviviparous taxon (the species belonging to the *Macrovipera* genus lay eggs) and for having well-developed and unfractionated supraocular plates.

Compared to the genus *Daboia*, *Planivipera* is smaller in size, has less rows of dorsal scales at mid-trunk (21–25 instead of 27), gives birth to live young instead of laying eggs, and has a different color pattern.

	<i>bornmuelleri</i> group (subgen. <i>Montivipera</i>)	<i>xanthina</i> group (<i>Planivipera</i> subgen. nov.)
HABITAT	high mountain	lowlands, flat coastal regions or regions with low hills
TEMPERATURE/MOISTURE	hygrophilous and eurytherm species	species adapted to a less wide a thermal range and more mesophilic
MORPHOLOGY	overall decrease in size and number of meristic characters (scales)	increase in size and number of meristic characters (scales)
ACTIVITY	exclusively diurnal	crepuscular and nocturnal in late spring and summer
REPRODUCTIVE CYCLE	biennial or triennial	potentially annual
BIOTIC RELATIONSHIPS	low selective pressure exerted by ophiophagous snakes of the genus <i>Dolichophis</i> or <i>Malpolon</i>	high selective pressure exerted by ophiophagous snakes of the genus <i>Dolichophis</i> or <i>Malpolon</i>

Table 5. *Montivipera xanthina* complex: *bornmuelleri* group and *xanthina* group (*Planivipera* n. subgen.). Physical and biotic interactios in comparison.

Planivipera differs from the *Aspis* group of the genus *Vipera* in its larger size and its non-protruding snout. From the *berus* group of the genus *Vipera*, *Planivipera* differs by living in more temperate regions resulting in less restrictive and broader reproductive modalities (see closing paragraph), having well-fragmented cephalic scales (with the exception of the supraoculars) as well as other pholidosis features, and by its larger size (see the summary table).

DERIVATIO NOMINIS. The name originates from the habitat sought by these vipers “plains vipers”.

HISTORICAL-PALEONTOLOGICAL NOTES

The *Montivipera* genus is part of the “oriental vipers” (the large Afro-Oriental species) as are the genera *Macrovipera* and *Daboia* [the North African *Daboia* (*mauritanica*, *deserti*) are referred to by some authors as *Macrovipera*; others think that *Daboia* includes the species *russelii*, *siamensis*, *palaestinae*, *mauritanica*, *deserti*; and *Macrovipera* the species *lebetinus*, *schweizeri*, *razii*. The last distinction seems more plausible. Among other things, *Daboia* differs from *Macrovipera* in osteological features concerning the vertebrae (Szyndlar & Rage, 1991; Bailon et al., 2010; Codrea et al.,

2017), and in the high number of dorsal scale rows at mid-trunk (27 instead of 23–25 in the *Macrovipera* genus)]. The following is a brief overview of the paleontological history of these last two genera.

The earliest evidence of *Macrovipera* dates back to the middle Miocene (about 12 Ma), while modern species diverged relatively recently, in the late Miocene (7.2 Ma) (Smid & Tolley, 2019). It can be assumed that the center of the *Macrovipera* group spread was in the Middle East (Stümpel et al., 2016). In the late Miocene, *Macrovipera* probably extended its range of distribution northwards, and subsequently westwards along the northern margins of the central and eastern Paratethys reaching Ukraine, Moldavia, Romania, Hungary and Austria during the late Astaracian and Vallesian (Codrea et al., 2017). The appearance of large viperids in Europe (*Daboia*, *Macrovipera*) more or less coincides with the Miocene Climatic Optimum (Böhme, 2003; Georgalis et al., 2016). Indeed, an increase in global temperature occurred during the Middle Miocene (about 14–18 Ma). This increase in heat allowed these snakes to flourish, spread and diversify moving into regions that are currently less favourable to them, such as central and eastern Europe. The westward expansion of these snakes was facilitated by the resulting ongoing environmental changes, especially

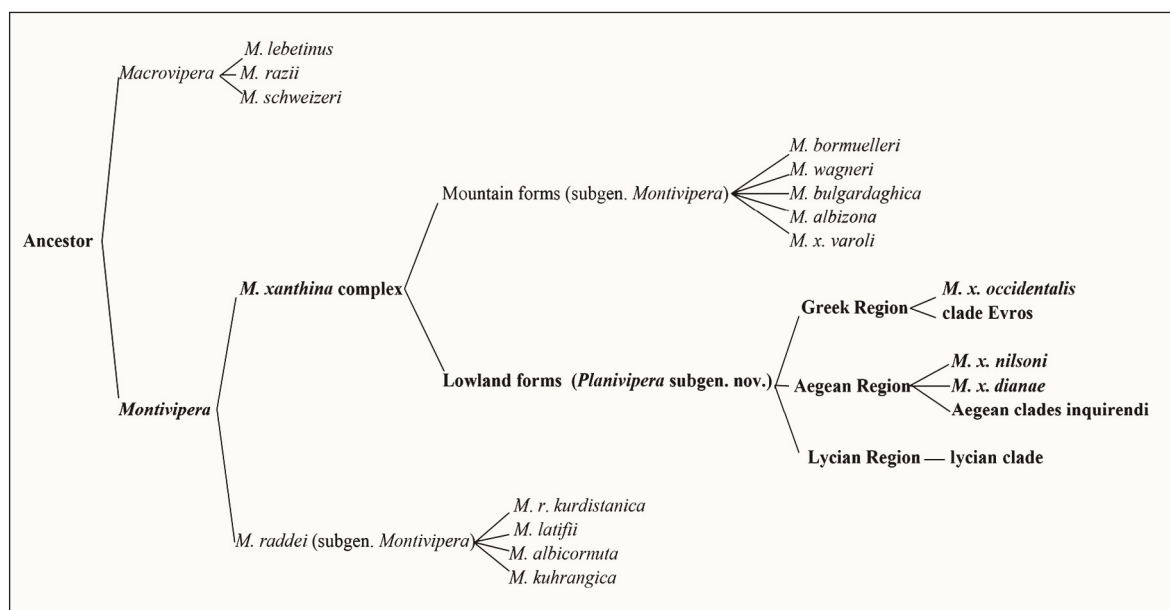


Figure 1. Summary table of the evolutionary events of the *Montivipera* (*Planivipera*) *xanthina*: group.

the expansion of steppe environments (Groombridge, 1986) where prey sought by these vipers was probably abundant (Iskenderov & Zavadov, 2016; Codrea et al., 2017). This warm phase was followed by a period of global cooling, which led to extinction, especially of the species distributed at high latitudes (e.g., *V. sarmatica*, *V. ukrainica*, *Macrovipera burgenlandica*) (Smid & Tolley, 2019).

The fossil-documented presence of Pliocenic large vipers, in Spain (Szyndlar, 1988, 1991), Greece (Georgalis et al., 2016), and on western Mediterranean islands is likely the result of a migratory event from Africa and possibly Asia Minor linked to the Messinian salinity crisis in the late Miocene (Codrea et al., 2017). In more detail, evidence of an earlier continuous distribution of *Daboia* across North Africa to Spain is provided, for example, by the discovery in Layna (Spain) of *Vipera maxima* from the Pliocene, a species very close to *D. russelii* (Szyndlar, 1988; Lenk et al., 2001).

A summary of the evolutionary events of the *Montivipera (Planivipera) xanthina* group is shown in Fig. 1

CONCLUSIONS

The environment of any species is made up of an extremely complex series of gradients of the various biotic or physical factors involved, gradients that interact with each other, affecting the distribution and the abundance of the species in question. Interdependent factors can exert far more decisive effects on the behaviour and physiology of a species than any single factor (Barry Cox et al., 1973).

The vipers of the *bornmuelleri* group live in the high mountains (between 1500 and 3000 m) where the prevailing environment is essentially made up of rocks and more or less bushy grasslands. The vipers seek shelter in crevices between the rocks and in piles of stones and pebbles, but the environment is generally bare and open. Under such conditions, sunlight, which is more intense at high altitudes, can heat the atmosphere and exposed surfaces, thus raising temperatures.

Vipers of the *xanthina* group live in environments characterized mostly by Mediterranean vegetation. The types of environments observed in the various locations investigated are reported below.

Southwestern Turkey - Hilly slopes overlooking large cultivated areas, ecotone stretches, hedge margins, path or dirt road edges, piles of stones, bushy waterway banks, and also marshy habitats (Cattaneo, 2011a: Fig. 9; Cattaneo, 2011b: Figs. 9, 10). Vipers were found between 15 and 70 m a.s.l.

Eastern Aegean Islands - Samothraki: low stretches and valley floors. Margins of hedges bordering wet grasses.

Lesbos, Chios: hilly slopes with southwest-facing olive groves. Ploughed lands bordered by dry stone walls and separated by narrow strips of vegetation.

Samos: flat areas and terraced slopes mostly cultivated with olive trees, with dry stone walls, abandoned or uninhabited buildings, abandoned greenhouses, not far from streams or water points (Cattaneo, 2019: Fig. 5).

Patmos: steep slopes covered by a phrygic vegetation furrowed by deep erosion channels, and also agricultural-pastoral areas.

Lipsi: agricultural-pastoral environments (Cattaneo, 2018: Figs. 12, 13, 14).

Leros: hillsides with bushy vegetation and dry-stone walls, but also valley orchards and plateaus, especially when cultivated with grasses. Areas with goat grazing (Fig. 2).

Kalymnos: fallow tracts near inhabited areas and terraced slopes (Cattaneo, 2005: Fig. 4).

Symi: agricultural-pastoral habitat with stone walls and fence nettings. Also, dry slopes, but bordering cultivated valleys (Cattaneo, 2007: Fig. 1).

Northeastern Greece - Evros: open and flat areas, sometimes steppe, sometimes low and marshy, not far from inhabited areas, also edges of ploughed lands (Fig. 3).

Rhodopes: extensive cereal crops alternating with large cotton-growing areas, all bordered and divided by dirt or asphalted roads. Field margins with hedges and piles of stones (Cattaneo, 2014: Fig. 7; Cattaneo, 2015: Figs. 6, 7).

The greater plant cover largely determines the habitat features described above and has a profound effect on their physical characteristics. Plants act as a buffer against extremes of heat and cold, their roots retain moisture in the soil, the water they transpire adds to air moisture, they provide shade and contribute to soil formation (Goin & Goin, 1971).



Figure 2. Leros Island (North Dodecanese): habitat of *Montivipera xanthina*.

It can be seen, however, that environmental conditions in Northeastern Greece are significantly different from those observed in other investigated locations. In both the Evros and Rhodope regions, *Montivipera xanthina* lives in open, flat areas where the predominant physical factor is therefore ventilation. Winds tend to make the environment less humid, and this condition may perhaps be tolerated by *M. xanthina* only because Northeastern Greece is notoriously rainy and rich in humid places. The above shows how interactions between the various factors that operate in an organism's environment can prove to be very complex and hard to understand, yet decisive in shaping the adaptation process.

Different habitats also result in different adaptations in these two groups of vipers. The vipers belonging to the *bornmuelleri* group have an active period that, for evident climatic reasons, should not exceed three-four months, whereas vipers of the *xanthina* group can lead active lives between

March and October. This leads to differences in various biological activities, especially reproductive cycles. High mountain vipers are expected to have biennial or triennial reproductive cycles, lowland vipers, when environmental conditions permit, are expected to reproduce annually (the presence of easy and abundant prey, conceivable in more complex ecosystems such as those of the immediate inland, would allow vipers to quickly replenish the energy reserves needed for reproduction, if necessary). The result is a higher rate of generational turnover, a greater increase in populations and fitness in the *xanthina* group, with production of continuous, new gene combinations that could explain the ecological plasticity and great genetic diversity found in these populations (Stümpel & Joger, 2009; Stümpel et al., 2016). The timing of ♂♂ spermatogenesis could also be affected by favourable environmental conditions. In true mountain vipers (*bornmuelleri* and *raddei* groups) spermatogenesis is completed in spring and an-



Figure 3. Eastern Evros (north-eastern Greece): habitat of *Montivipera xanthina*. Note the ploughed soil.

nounced by the ♂♂ moult, which precedes copulation (Nilson et al., 1999). During my herpetological research in the Eastern Aegean Islands, Western Turkey and Northeastern Greece, carried out in the month of May from 1998 to the present, I have come across 172 specimens of *Montivipera xanthina* and only four exuviae. Six of the specimens found were moulting, but only three adults (1.7%). This may mean either that the moulting occurred in March–April or that it was to take place in the following months. The latter case would argue in favour of spermatogenesis not necessarily being completed during the spring. Moreover, no copulating specimens were noted, only paired or close individuals of the opposite sex. Unfortunately, the specific literature lacks data from observation in nature concerning the reproductive biology of these lowland populations.

The perfect and complete adaptation to life in high mountains involves pregnancy by viviparous snakes that also includes the time necessary for the young's first moulting, which would ensure ex-

treme protection for the offspring at the highly vulnerable time that is moulting. In fact, in the better adapted species (i.e., *Vipera aspis*, *Vipera ammodytes*, *Daboia russelii*) the young moult immediately after birth, whereas, in vipers that live in warm and suitable environments and lay eggs (i.e., *Macrovipera* spp., *Daboia palaestinae*), the young moult 7–10 days after birth. *Montivipera xanthina* is ovoviviparous, but its young moult 7–10 days after birth, like large egg-laying vipers. This could confirm that adaptation to high mountain life occurred recently and subsequently to the ancestral stem group, which is composed of entities ecologically closer to the large Middle Eastern vipers. In short, it is as if *Montivipera xanthina* were “paleogenetically pre-adapted” to life in warm, low-altitude environments.

Summarizing and concluding, several physical and biotic environmental factors (or, better, their interaction) can be related to the different morphology, genetics and ethology of true mountain vipers (*bormuelleri* group and *raddei* complex) compared

to the same parameters found in lowland vipers (*xanthina* group). It is therefore logical to detach the latter with the name of *Planivipera* n. subgen. a term that would indicate their different ecology precisely.

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