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THE MORPHOTYPE OF *MONTIVIPERA XANTHINA* (GRAY, 1849)  
FROM THE AEGEAN ISLAND OF LIPSI  
(NORTHERN DODECANESE)  
(*Serpentes Viperidae*)

RIASSUNTO

*Il morfotipo di Montivipera xanthina* (Gray, 1849) dell'isola egea di Lipsi (nord Dodecanneso) (*Serpentes Viperidae*). La popolazione di *Montivipera xanthina* dell'isola di Lipsi presenta una sensibile riduzione delle squame ventrali, che corrisponde a una riduzione delle dimensioni lineari, ed è caratterizzata da un morfotipo con capo e ventre slargati, con un incremento del numero delle squame dorsali a metà tronco (sino a 27) generalmente riscontrabile nelle grandi vipere orientali e nordafricane del genere *Daboia*. Questa particolare morfologia potrebbe essere interpretata come adattamento alle condizioni di microinsularità, consentendo agli individui di questa popolazione il consumo di prede voluminose. Un adattamento simile, ma meno pronunciato, è stato riscontrato anche nella popolazione di *M. xanthina* della vicina isola di Leros, per cui si ipotizzano correlazioni filogenetiche e paleogeografiche fra le due popolazioni.

*Parole chiave:* *Montivipera xanthina*, Isola di Lipsi, Mar Egeo Orientale, morfotipo, microinsularità.

SUMMARY

The population of *Montivipera xanthina* from Lipsi Island shows a significant reduction in ventral scales, corresponding to a decrease in linear size, and is characterized by a morphotype with a slender head and belly, with an increase in the number of dorsal scales at mid-trunk (up to 27) that is generally known for large adders of the genus *Daboia* from southeast Asia and North Africa. This typical morphology could be interpreted as an adaptation to the microinsular conditions, allowing individuals from this population to consume bulky prey. A similar, but less pronounced adaptation in the *M. xanthina* population of the nearby island of Leros was also observed. Phylogenetic and paleogeographic correlations between the two populations are therefore hypothesized.

*Key words:* *Montivipera xanthina*, Lipsi Island, Eastern Aegean sea, morphotype, microinsularity.

## INTRODUCTION

Herpetological research was carried out on the Aegean island of Lipsi from 7-19 May 2022. These studies are added to those which took place in the last decade of May 2018 (CATTANEO, 2018). The main purpose of the research was to perform further studies on the morphology and eco-biology of *Montivipera xanthina*. The author began studying this species since 1998 with the population of the island of Samothraki in the Northern Aegean (CATTANEO, 2001). Information concerning Lipsi's herpetofauna can be gleaned from the writings of FOUFOPOULOS (1997), CLARK (2000) and BROGGI (2008).

## MATERIALS AND METHODS

Although difficult, scale counts, measurements and descriptions of phenotype were made on live snakes; none were sacrificed during the present study. Diet data were obtained from faecal and/or *ingesta* examination. All the collected individuals, once studied and photographed, were released at the capture site.

The characters studied, with relative definitions, methods and abbreviations, are reported below:

- 1) Sex.
- 2) Total length (OL).
- 3) Tail length (TL).
- 4) Weight, always measured when the animals were fasting (W).
- 5) Number of dorsal scales at mid-trunk (counted in a transverse line at the height of half the total number of ventral scales) (D).
- 6) Number of the ventral scales (counted with the classic method, which considers ventral the mid-ventral scales that are wider than they are long) (V).
- 7) Number of subcaudal scales (counted from the first postcloacal scale that is in contact with the contralateral along the caudal midline) (SC).
- 8) Colouration.
- 9) In vipers, number of mid-dorsal spots, obtained by counting the angularities formed by the zigzag pattern, i.e., the dark mid-dorsal sinuosity, unilaterally.

## GEO-BOTANICAL NOTES ON THE STUDY AREA

Lipsi is the largest island of an archipelago that lies between the islands of Leros and Patmos (12 km east of Patmos and 11 km north of Leros) (Fig. 1). It has an area of 17 km<sup>2</sup>. Geomorphologically speaking, Lipsi is made up of shale and crystalline and semi-crystalline limestone rocks. Topographically, it does not show particular environmental heterogeneity, as it is essentially hilly with gentle slopes (the highest altitude is 277 m a.s.l.). The western part of the island has a vegetation cover consisting of low scrub dominated by *Juniperus phoenicea* in association with *Pistacia lentiscus*, *Cistus creticus*, *Cistus salviifolius* and *Arbutus unedo*. In contrast, the landscape of the eastern part has been deeply modified by man and grazing. It can be defined as a substeppic environment mainly composed of grasses with occasional occurrences of shrubby phryganic formations.

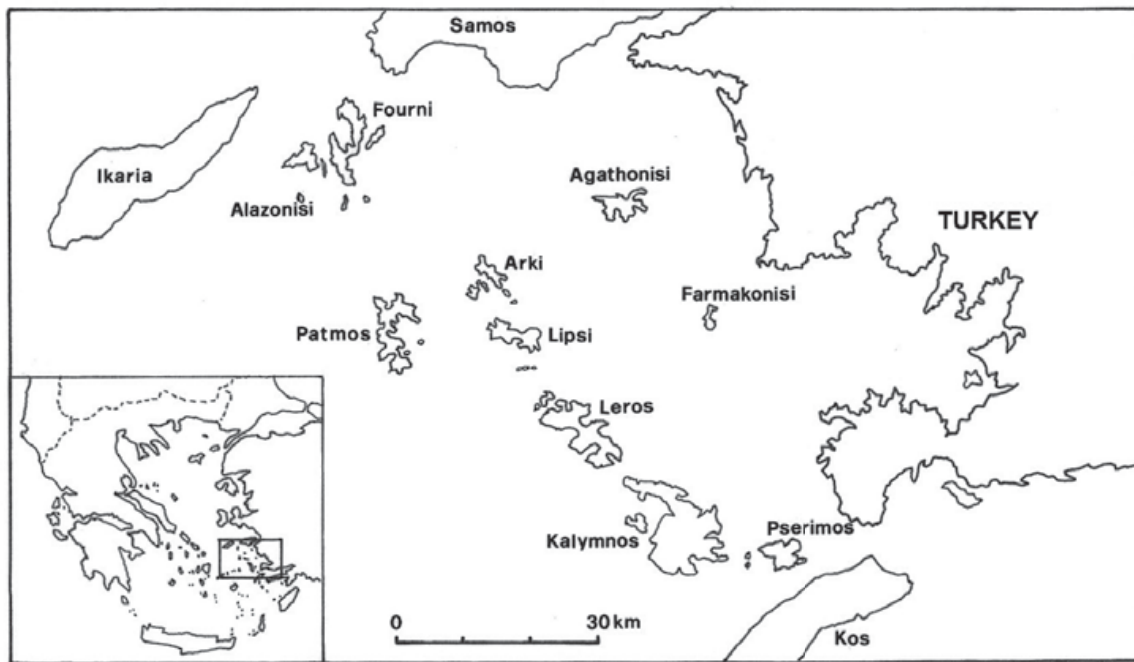


Fig. 1 — Northern Dodecanese with Lipsi Island.

## RESULTS

**Previous citations:** NILSON & ANDRÉN (1986), TIEDEMANN & GRILLITSCH (1986), FOUFOPOULOS (1997), HOS (1999), CLARK (2000), BROGGI (2008), CATTANEO (2018).

**Findings:** 1 exuvia, 4 carcasses and 19 specimens.

### Morphology

*Size* – This viper has a robust, stout morphology with a widened central part of the trunk which is especially evident in larger individuals. Large, relatively short head, well distinguished from the neck, with obtuse snout and a wide temporal-parietal region. Jaws more laterally protruding than usual (Fig. 2).



Fig. 2 — Male specimen of *Montivipera xanthina* from Lipsi Island (the animal was photographed on artificial substrate to better highlight its appearance).

For length and weight see Table 1.

*Pholidosis* - Table 1.

The number of rows of dorsal scales at mid-trunk ranges from 23 to 27, with an arithmetic average of 23.9.

23 dorsal scales found in 9 individuals (64.2%);

**Table 1**  
*Montivipera xanthina*, Lipsi Island: size, pholidosis and phases of the active cycle during the month of May. \* = incomplete tail.

		OL (CM)	TL (CM)	W (G)	D	V	SC (PAIRS)	DATA	NOTES
1	♀	56.5	6.5	84	23	152	31	10.05.2022	incipient moulting
2	♂	79*	4.5*	278	23	154	17*	13.05.2022	in moulting
3	juv.	27.5	3	20	23	156	29	15.05.2022	in moulting
4	♂	51	6.5	80	23	157	33	15.05.2022	in moulting
5	juv.	33.5	3.5	23	23	168	33	15.05.2022	-
6	♀	57*	4*	114	25	153	19*	17.05.2022	-
7	juv.	37	4	33	25	158	33	18.05.2022	-
8	juv.	36	3.5	34	23	164	31	18.05.2022	in moulting
9	♂	58.5	6.3	125	23	154	31	22.05.2018	with prey
10	♀	68	7	225	24	155	31	23.05.2018	with developing eggs
11	♀	63	7	199	23	155	30	25.05.2018	with developing eggs
12	♀	47	5.2	60	27	151	31	28.05.2018	-
13	♂	83.5*	3.5*	403	27	156	13*	30.05.2018	with prey
14	juv.	31.2	3.1	21	23	148	28	01.06.2018	with prey

24 dorsal scales found in 1 individual (7.1%);

25 dorsal scales found in 2 individuals (14.2%);

27 dorsal scales found in 2 individuals (14.2%).

Therefore, there are 5 specimens that exhibited more than 23 dorsal scales (35.7%).

The number of ventral scales ranges between 151 and 158, with an arithmetic average of 154.6 ( $n = 11$ ). Excluded from this count were one specimen with 148 ventral scales (*minus-variante*) and two specimens with 164 and 168 ventral scales (*plus-varianti*), as it was deemed that these values were less diagnostic (well beyond the normal range of variability detected in the population) and could have misled from the real trend of this parameter within the population.

The number of subcaudal scale pairs ranges from 28 to 33 with an arithmetic average of 31 ( $n = 11$ ).

*Colouration* - Strong sexual dichroism. Compared to the normal colouration of the species, the ♂♂ have greater development of the dorsal pattern; spots appear expanded so that the general and overall chromatic tone appears darker; light belly with dark speckles. In contrast, the ♀♀ seem brighter; on a gray-ocher background, the zigzag pattern appears less developed, narrower and clearer (Fig. 3); ventrally there is a dark speckling on a light background, sometimes suffused with tawny. In both sexes, the clear, luminous mid-dorsal band is always well represented (between the spots of the zigzag pattern).

The number of angularities of the zigzag pattern ranges from 25 to 30.



Fig. 3 — Female specimen of *Montivipera xanthina* from Lipsi Island.

**Summary diagnosis of the morphotype** - Widened central part of the trunk. Head larger than normal, disproportionate to the rest of the body, with a highly developed width-wise temporo-parietal region and jaws that protrude laterally more than usual.

23 rows of dorsal scales at mid-trunk, but high percentage of individuals (about 36%) with higher values (from 24 to 25, up to 27).

151-158 (154.6) ventral scales.

Strong sexual dichroism.

**Habitat** - In Lipsi the species seems to occupy mainly environments characterized by agricultural-pastoral use (Fig. 4), where, in fact, the viper can more easily find food and water on a very arid island that is poor in trophic resources. Unfortunately, this also leads to the systematic killing of the animal by man.



Fig. 4 — Habitat of *Montivipera xanthina* in Lipsi Island.

More in detail, *Montivipera xanthina* has been found along the edge of extensive mastic shrubs (*Pistacia lentiscus*) and of bean trefoil (*Anagyris foetida*), at the base (but also at the top) of dry stone walls (especially those surrounded by dense vegetation, which provide more shelter from the winds, Fig. 5), on piles of stones, on pebbles covered with mastic shrubs (*Pistacia lentiscus*) and along the densely grassy banks of ancient, now inactive, streams. The juveniles were mostly found under stones.

In one case, a viper in the moulting phase was found in an entangled mass of sun-exposed grasses. The physical conditions of such a microhabitat fit well with those required by the snake in that phase. Similar, sunny and safe microhabitats can be found on the island in heaps of cut grasses, hay bales and even dry seaweed litter near the sea (the vipers can be located in or under these formations).



Fig. 5 — Habitat of *Montivipera xanthina* in Lipsi Island (the shrub at the base of the stone wall is bean trefoil, *Anagyris foetida*).

**Prey found** - *Rattus rattus* in specimen no. 9 in Table 1; Rodentia sp. indet. in specimen no. 13 in Table 1; *Scolopendra cingulata* in specimen no. 14 in Table 1.

The latter data refers to a juvenile specimen; in this regard it is worth noting that all other juveniles encountered were found in a stretch of the valley that stood out both for its higher humidity and (consequently) for the conspicuous presence of scorpions and scolopendras, the latter being a highly sought food source of juveniles.

**Reproductive cycle** - A study on the reproductive biology of the species is being defined and will be proposed shortly.

**Predators** - The hooded crow (*Corvus cornix*) is very common on Lipsi, and this can adversely affect especially the young of *Montivipera xanthina*, as they are less experienced and therefore less elusive than adults. Furthermore, their high growth rate leads them to be more active in the search for food, and therefore more vulnerable. Moreover, the island is also inhabited by the hedgehog (*Erinaceus roumanicus*), which occasionally feeds on young vipers. Also, the black rat (*Rattus rattus*) is very common on



the island (FOUFOPOULOS, 1997; BROGGI, 2008) and can threaten the juveniles of the species.

The unusual presence of several *Montivipera xanthina* specimens with mutilated tails both on Lipsi and Leros and nowhere else (or at least not as often) suggests a specific predator among those listed above (Fig. 2). Severed tails are generally found in colubers, which come into direct bodily contact with their prey to overpower them, but not among the vipers, which limit themselves to biting their victims in order to return to them later and swallow them after death.

Man negatively affects this viper both directly (by killing it) and indirectly (through rodent control, with the diffusion of poisoned baits); rats killed by poisoning can subsequently be eaten by the vipers and might cause their death in turn (pers. obs.). Moreover, “snake repellent” products are sold in local supermarkets.

Finally, it should be kept in mind that the scarcity of saurians on Lipsi could lead to strong juvenile selection among snakes, including *Montivipera xanthina*. However, this viper is in fact still well represented on Lipsi, and could indeed be considered the dominant ophidic species (i.e., species that ecologically influence the others: ODUM, 1973). This is probably due to its better adaptation to borderline conditions during juvenile stages, following the exploitation of alternative trophic resources (for example, predation of scolopendras instead of lizards). At times, the other ophidic species appear so rarely that *Montivipera xanthina* seems to be the only snake on the island.

**Anti-predator behaviour** - On Lipsi, when frightened or threatened, *Montivipera xanthina* hissed loudly and quickly fled; during operations to study the meristic characters, it showed an impressive reactivity, similar to that of the *Montivipera xanthina dianae*, subspecies from the nearby island of Leros, not seen in the other studied populations of the species. During thermoregulatory phases, the diamond-shaped spots of its pattern, especially when the viper is coiled, created an extraordinary somatolytic effect. It emitted defensive excreta of similar smell to that produced by representatives of the genus *Elaphe (s.l.)*. During moulting phases, its greater vulnerability is compensated for by lower visibility; indeed, moulting snakes take on dull and opaque tones and colours, with increased camouflage effects.

**Poison** - Cases of poisoning by bites from this viper have been recorded in both humans and pets (4-5 incidents involving dogs were reported in spring 2018).

### Coexisting herpetological species - See Table 2.

The presence of *Pelophylax* sp. on Lipsi refers to the discovery of a dead individual, found pressed by vehicles, near the port in May 2022. Given the lack of suitable wet places on the island, it is very likely that the frog arrived by passive transport through commercial ships.

The presence of *Telescopus fallax* on Lipsi has been known for many years (about 45), but the recorded specimens are few. In May 2022, two specimens were found; the first was inside a metal container for electrical equipment, the second was found dead on a paved road in the immediate outskirts of the town near the port; based on the injuries detected, it is plausible that the latter animal was killed by a cat. Their size and pholidosis are reported below; typical coloration.

1) ♀; OL 57 cm, TL 9,5 cm, W 25 g; D 19, V 220 + 1/1, Sc 69/69 + 1.

2) juv.; OL 38,2 cm, TL 6,4 cm, W 10 g; D 19, V 220 + 1/1, Sc 74/72 + 1.

**Table 2**

*Herpetofaunal species of the Aegean island of Lipsi.*

	LITERATURE
<i>Bufo viridis</i>	HOS (1999), CLARK (2000)
<i>Pelophylax</i> sp.	the present study
<i>Hemidactylus turcicus</i>	FOUFOPOULOS (1997), BROGGI (2008), CATTANEO (2018)
<i>Mediodactylus kotschy</i>	BROGGI (2008)
<i>Ophisops elegans</i>	FOUFOPOULOS (1997), BROGGI (2008), CATTANEO (2018)
<i>Ablepharus kitaibelii</i>	HOS (1999), BROGGI (2008)
<i>Hemorrhois nummifer</i>	CHONDROPOULOS (1989), HOS (1999)
<i>Platyceps najadum</i>	FOUFOPOULOS (1997), HOS (1999), BROGGI (2008), CATTANEO (2018)
<i>Telescopus fallax</i>	GRILLITSCH & GRILLITSCH (1999), HOS (1999), CATTANEO (2018)

### MICRO-EVOLUTIONARY CONSIDERATIONS

The low number of ventral scales indicates that the Lipsi population of *Montivipera xanthina* tends to be shorter in length, plausibly paralling the reduced size of the island. However, this shorter length seems to be compensated for by the increase in cephalic and body volume especially at mid-

trunk, where there are as many as 27 rows of dorsal scales. This process may be interpreted as adaptive adjustment to microinsular conditions: size decreases, but the species continues to play its trophic role, still able to feed on voluminous prey (rats) due to the correspondence of its constitution to its functional needs. Moreover, it is known that these adaptive processes are more frequent and faster in low-density populations due to genetic drift phenomena.

In snakes, body volume may increase through an increase in the number of dorsal scales rows or through an increase in the size of the scales themselves. With an increase in scale number, the tissue that separates the scales, the truly elastic component of the skin, also increases (the scales themselves are not elastic). Due to their constitution, snakes must swallow their prey whole, even relatively voluminous prey as is the case for the Lipsi viper. Thus, an increase in scale number leads to increased fitness. As proof of this claim, sometimes a small decrease in neck caliber, due to not fully removed and hardened parts of the old exuvia, can constitute serious impediments to food intake (pers. obs.). In this regard, it is worth noting that in the insular populations of *Montivipera xanthina*, adapted to feed on larger prey than the homologous continental populations due to the decrease in the predatory pressure in the islands (less predators, slower and therefore more voluminous prey), the number of dorsal scale rows at the neck is certainly higher than in continental ones (from 23 to 26 and more).

Points of convergence between the Lipsi vipers and those of nearby Leros have been noted, including the increase in body volume with consequent increased number of dorsal scales at mid-trunk, and unprecedented and impressive behaviour and manner in defensive reactions. In fact, the proximity of the two islands not only allows us to hypothesize contact between the lands in earlier times, but also the possibility of wildlife exchanges between them; the depth of the sea between these islands does not exceed 100 m and it appears that they were connected to each other, the other Eastern Aegean Islands and Asia Minor about 20.000 years ago, i.e., during the late Pleistocene (PANITSA & TZANOUDAKIS, 2001; KOUGIOUMOUTZIS *et al.*, 2016; SFENTHOURAKIS & TRIANTIS, 2017).

In conclusion, assuming phylogenetic and paleogeographic correlations between the two populations, the evolutionary trend that led to growth in body volume with a consequent increase in the number of dorsal scales in the Leros population, has seen a further adaptive impulse in the Lipsi population, leading to a morphotype with widened head and belly, and up to 27 dorsal scales at mid-trunk a value found only in the large east-

ern and north African vipers of the genus *Daboia*. When the sudden appearance of aberrant characters occurs (27 dorsals, 168 ventrals), as is the case here, we are in the presence of very small, isolated populations exposed to continuous “bottle necks”. Here genetic drift plays a decisive role compared to selection. Inbreeding causes the appearance of “hidden” characters that are nevertheless part of the at least phyletic variability of the species.

#### THE MORPHOTYPE OF SYMI

This paragraph has been inserted due the similarities in ventral scales between the Lipsi and Symi *Montivipera xanthina* populations.

The *Montivipera xanthina* population of the Aegean Island of Symi (Southern Dodecanese) shows three very particular and distinctive features: low number of ventral scales, relatively high number of subcaudal scales and an agile and slender body line (silhouette).

The number of ventral scales ranges from 150 to 157, with an arithmetic mean of 153.5 ( $n = 6$ ). Among the various Aegean microinsular populations of the species, only the Lipsi population has such ventral scale values, which is why the Symi population is considered in this study.

Subcaudal scales range from 34 to 39 pairs, with an arithmetic mean of 36.3 ( $n = 6$ ). These values are the highest among those detected among the Aegean populations, both insular and coastal continental.

The low number of ventral scales and the relatively high number of subcaudal scales indicate a reduction in trunk length (compatible with the small size of the island: 58 km<sup>2</sup>) and respectively, an increase in tail length. The longer tail could biodynamically compensate for the shortening of the trunk. As seen, this particular morphometry could plausibly be put in correlation with microinsularity (in the geographical sense), but also, to some extent, with the dense network of interactions that a complex ecosystem such as that of Symi entails (the island is rich in animal and plant species). Among the snakes is the notoriously viperophagus *Dolichophis jugularis*. The slender silhouette and the greater tail length could be indicative of faster movements, useful and suitable for avoiding predation attempts from the coluber. Even the trophic spectrum could also correlate with the particular morphology of this viper, but, at present, there is insufficient data to establish this. Ultimately, the low number of ventral scales shared between the Lipsi and Symi populations of *Montivipera xanthina* could be due to phenomena of parallel evolution or homology, although the selective forces operating in the environment are apparently different.

PALEONTOLOGICAL-PHYLOGENETIC HYPOTHESES ON THE DISPERSION OF LARGE MIDDLE EASTERN VIPERS

The Anatolian Peninsula or, more generally, the Middle East represents the center of dispersal, the *hot spot* of the spread of the large Middle Eastern vipers belonging to the genera *Macrovipera*, *Daboia*, *Montivipera*. Let's try to reconstruct the evolutionary path of these taxa (Fig. 6).

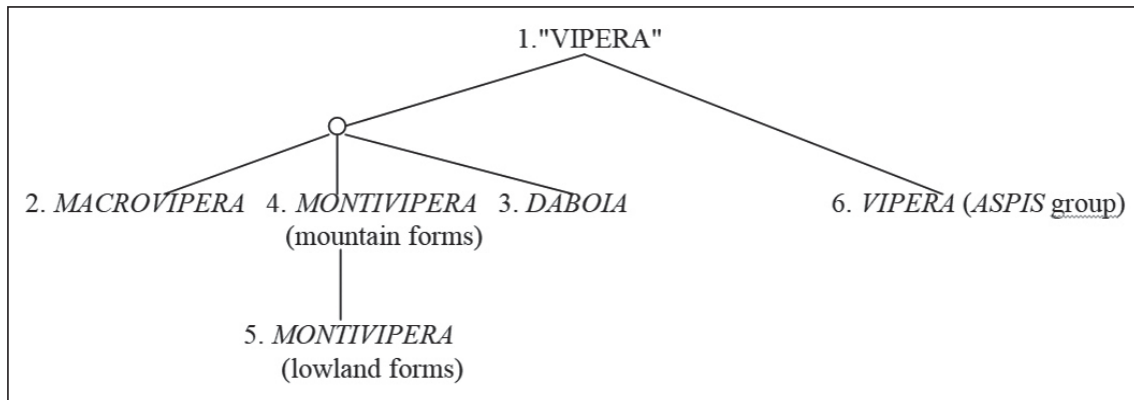


Fig. 6 — Hypothetical reconstruction of the evolutionary path of *Macrovipera*, *Daboia* and *Montivipera*.

1. “*Vipera*” - The genus “*Vipera*” appeared in the fossil record in the early Miocene (about 22.5 Mya), but diversification of the group dates back to the middle Miocene (13.4 Mya) (ŠMID & TOLLEY, 2019). Based on phylogeographical and geotectonic data, *Macrovipera* and *Montivipera* shared their last common ancestor during the Langhian (15.3 Mya; STÜMPEL *et al.*, 2016) in the long-isolated Anatolian subcontinent.

2. *Macrovipera* - The first evidence of *Macrovipera* dates back to the late middle Miocene (about 12 Mya), while the modern species (*M. lebetinus*, *M. schweizeri*, *M. razii*) relatively recently diverge, in the late Miocene (7.2 Mya) (ŠMID & TOLLEY, 2019). It is likely that the spreading center of the *Macrovipera* group was located in the Middle East (STÜMPEL *et al.*, 2016). During the middle Miocene (about 14-18 Mya) an increase in global temperatures took place (the Miocene Climatic Optimum). Warmer temperatures allowed *Macrovipera*-related species to thrive and spread to areas that currently are less favourable to them, such as Central and Eastern Europe. This warm phase was followed by a period of global cooling, during which some of the aforementioned species became extinct and others migrated to more suitable southern regions (ŠMID & TOLLEY, 2019).

3. *Daboia* - This genus, currently represented by the *russelii*, *siamensis*,

*palaestinae*, *mauritanica* and *deserti* species, differs from *Macrovipera*, among other things, for the higher number of dorsal scale rows at mid-trunk and osteological features concerning the vertebrae. In the lower Miocene, *Daboia* inhabited the southern areas of the Mediterranean basin. The fossil-documented presence of large Pliocene vipers in Spain (SZYNDLAR, 1988, 1991), Greece (GEORGALIS *et al.*, 2016) and in the western Mediterranean Islands (BAILON *et al.*, 2010) could be evidence of a migratory event from Africa and perhaps Asia Minor that could have involved *Daboia*, an event linked to the Messinian salinity crisis in the last 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* of Pliocene, a species very similar to *D. russelii* (SZYNDLAR, 1988; LENK *et al.*, 2001).

4. **Montivipera (mountain forms)** - Members of this group inhabit plateaus and subalpine forests of the Near and Middle East with extreme climatic conditions. Mountain forms of the genus *Montivipera* include the *raddei* (*Montivipera raddei*, *M. albicornuta*, *M. latifii*, *M. kuhrangica*) and the *bornmuelleri* (*Montivipera bornmuelleri*, *M. albizona*, *M. bulgardaghica*, *M. wagneri*) groups. The latter group also includes *Montivipera xanthina varoli*, typical of the Taurus Mountains, due to its morphological characteristics and ecological demands. The adaptation of these vipers to mountain conditions could have started during the Serravallian (about 13-12.2 Mya; STÜMPPEL *et al.*, 2016) in response to the 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). Indeed, with the elevation gain, came climatic changes (lower temperatures, increased moisture, more intense solar radiation, lower air pressure) as well as changes to spatial, biotic and evolutionary factors (STÜMPPEL *et al.*, 2016).

5. **Montivipera (lowland forms)** – All the lowland forms of the genus *Montivipera* belong to a single species: *Montivipera xanthina*. This viper inhabits the Eastern Aegean Islands, the western Turkish coastal regions and the north eastern Greek coastal regions with different clades and subspecies. The lowland populations are considerably younger and more ecologically adaptable than the mountain ones, being endowed with high genetic diversity. The ancestral ecological trait is mountainous and adaptation to warmer lowland habitats occurred secondarily (STÜMPPEL *et al.*, 2016).

6. **Vipera (aspis group)** - The *aspis* group is composed of the following species, from east to west: *Vipera transcaucasiana* (Caucasus), *V. ammodytes* (Balkan Peninsula), *V. aspis* (Italy and France), *V. latastei* (Iberian Peninsula), *V. monticola* (Morocco). The range of these species is complementary and parapatric, which indicates the development of the same evolutionary line on a geographical basis. These species are characterized by their upward-protruding

snouts, so much so that they were once all assembled in the subgenus *Rhinaspis* Reuss, 1933 (now recognized as a synonym of *Vipera* Laurenti, 1768).

Species of the *aspis* group have several similar features to the homologs of *Montivipera xanthina*, both in terms of colouring (for example, the dorsal pattern) and pholidosis (for example, the fragmentation of the dorsal cephalic scales, but not the supraocular, Fig. 7). These homologies could indicate a common parental line. Furthermore, the immunological distances of the



Fig. 7 — *Vipera aspis* (above) and *Montivipera xanthina* (below): comparison of pattern and dorsal cephalic pholidosis.

genus *Montivipera* from *Vipera* are smaller than those separating it from *Macrovipera* and *Daboia* (HERRMANN *et al.*, 1992; HERRMANN & JOGER, 1997). In this regard, I consider it relevant to report some considerations derived from field observation. On occasion, *Vipera ammodytes* has been reported without the nasal horn (Fig. 8). In these cases, the question is whether we are in the presence of a specimen of *Vipera aspis* or a specimen of *Montivipera xanthina*, which highlights the similarity between the two entities. Furthermore, often while doing research in areas where *V. ammodytes* and *M. xanthina* lived in sympatry, it was necessary to examine, once the viper was immobilized on the ground, the apex of the snout in order to be able to quickly establish the taxon.



Fig. 8 — Specimen of *Vipera ammodytes* lacking the horn at the apex of the snout (courtesy of J. Speybroeck).

In summary, starting from its center of dispersal and based on current biogeographical data, *Macrovipera* has expanded its range eastwards, into central Asia. The arrival of *Macrovipera schweizeri* on Sifnos and in the Milos Archipelago (south-western Cyclades) is thought to have occurred during the Messinian salinity crisis in the last Miocene (about 5 Mya).

*Daboia* first extended its presence along the Middle Eastern coasts (*D.*



*palaestinae*) and then along the North African coasts (*D. deserti*, *D. mauritanica*). The occurrence of *D. russelii* and *D. siamensis* in Southeast Asia shows that the genus *Daboia* once had a much wider distribution than today.

The mountainous environment, with the increased elevation of the Turkish-Iranian plateau, has allowed the evolution of the genus *Montivipera*. The emergence of new characters, especially physiological ones, in some populations of this taxon endowed with high genetic variability, along with the availability of new ecological opportunities such as the lowland environment, has led to the formation of new entities, adapted for living in Mediterranean habitats along the Aegean coasts from southeast Turkey to northeast Greece.

The *aspis* group of the genus *Vipera* could represent a collateral phyletic line compared to the lowland forms of the genus *Montivipera*. *Vipera ammodytes* continues westward, replacing the migratory path undertaken by these lowland forms, which was interrupted along the coasts of north eastern Greece. This path led the *Vipera* genus to colonize the Balkan Peninsula (*V. ammodytes*), Italy and France (*V. aspis*) as well as the Iberian Peninsula (*V. latastei*).

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