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Morphological Convergence or Recent Divergence in the Cryptic Species *Montivipera xanthina* (Gray, 1849)

Augusto Cattaneo

Via Cola di Rienzo, 162 – 00192 Rome, Italy.

***Corresponding Author:** Augusto Cattaneo, Via Cola di Rienzo, 162 – 00192 Rome, Italy.

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Abstract

In 2022, Cattaneo proposed the subgenus Planivipera *to encompass all the lowland populations of* Montivipera xanthina*. The author indicated* Montivipera xanthina *as the type species of the new taxon as it was the* only *taxonomically recognized species of the* xanthina *group at the time. Since Cattaneo's research on the species primarily focused on the eastern Aegean islands, it is plausible that the "type species" indicated by the author actually referred to the Aegean clade. Based on these considerations, the type species of the genus* Montivipera *remains* Montivipera xanthina*, Lycian clade. This is because, described* Montivipera xanthina *based on two specimens, at least one of which originated from Lycia (type locality: Xanthos). Since* M. xanthina *appears to represent a cryptic species complex containing three or four additional taxa, the entity corresponding to the proposed* subgenus *should be regarded as* Montivipera *sp. inquirenda, Aegean clade [1-3].*

The xanthina *group emerged in the early Pliocene (4.7 Ma), expanding during the warm phase of that same period and reaching its maximum population size at the beginning of the Pleistocene. The currently recognized* xanthina *lineages are all Pleistocene, except for those from Lycia and the Taurus Mountains, which are older (5.2 Ma). It is plausible that an evolutionary lineage from this stem group of the Lycian-Taurus mountainous region, favored by the high temperatures of the Pliocene, expanded westward, colonizing the Mediterranean coasts of western Turkey and northeastern Greece (*xanthina *group). Another evolutionary lineage likely spread eastward along the Anatolian Diagonal, fragmenting into separate vicariant entities adapted to low temperatures (the b*ornmuelleri *group).*

Since phenotype is the product of the interaction between genotype and environment, coevolutionary units in Montivipera xanthina *tend to produce distinct entities depending on their composition. On Samothraki,* M. xanthina *exhibits color characteristics consistent with an incipiently evolving entity. On the three large islands of the eastern Aegean (Lesvos, Chios, Samos),* M. xanthina *exhibits large body size and a well-developed dorsal pattern. Leros and Lipsi host the subspecies* M. xanthina dianae*, characterized by increased body diameter and a tendency toward a higher number of midbody dorsal scales. On Symi,* M. xanthina *is distinguished primarily by a high number of subcaudal scales.*

Key Words: *Montivipera xanthina*, Taxonomy, Evolutionary Chronology, Ecological Interactions, Eastern Aegean Islands.

Introduction

The present contribution represents a monographic study of the snake species *Montivipera xanthina*. This Viperid is examined from a taxonomic perspective (Part I), a chronological-evolutionary perspective (Part II), and in terms of its interactions across the eastern Aegean islands (Part III).

Materials and Methods

For details regarding the examined material and the adopted methodologies, reference should be made to the author's previous publications on the species, particularly [4-7].

Results

Part 1: Taxonomy

The genus *Montivipera*

The subgenus *Montivipera* (later elevated to genus rank) was proposed by Nilson et al. 1999. The type species of the new taxon was designated as *Montivipera xanthina* Gray (1849). Current knowledge indicates that *Montivipera xanthina* (*s.l.*) actually consists of a complex of cryptic species distributed along the Mediterranean coasts of northeastern Greece and western Turkey, as well as in the highlands of Lycia and the Taurus Mountains. More specifically, the genus *Montivipera* comprises two species complexes: the *raddei* complex and the *xanthina* complex [1-3].

The *raddei* complex

The *raddei* complex comprises the following species: *Montivipera raddei, M. albicornuta, M. kuhrangica, M. latifii* (Armenia, Azerbaijan, Iran). It constitutes the subgenus *Oculocircumcincta* with *Montivipera raddei* (Boettger, 1890) as the type species [8].

The *xanthina* complex

Regarding the *xanthina* complex, it is plausible that, from the stem group in the mountainous regions of the Lycia and the Taurus Mountains approximately 5 Ma, an evolutionary lineage, facilitated by the high temperatures of the Pliocene, expanded westward, colonizing the Mediterranean coasts of western Turkey and northeastern Greece (the *xanthina* group). The appearance of new traits, especially physiological ones, in some populations of this group, characterized by high genetic variability, together with the availability of new ecological opportunities such as lowland environments, would have led to the formation of new entities adapted to life in Mediterranean environments. Another evolutionary lineage likely spread eastward along the Anatolian Diagonal, fragmenting into separate vicariant entities adapted to lower temperatures, with daily activity largely restricted to late spring and summer (the *bornmuelleri* group) [9].

Thus, the *xanthina* complex includes both the *bornmuelleri* species group and the *xanthina* entities. The phenotypic uniformity observed in the *xanthina* group may be attributed to a form of "adaptive inertia" that developed during the Miocene Climatic Optimum (approximately 14-18 Ma) when steppe environments spread widely. The cryptic effects of such habitats on these vipers, promoted by natural selection, may have persisted despite underlying genetic changes (either morphological convergence or recent divergence). A similar phenomenon appears to occur in other snake species, for example in *Elaphe sauromates* (*s.l.*) [10]. The coloration of both the "Oriental Vipers" and European vipers (typically grayish or brownish with dark blotches) effectively matches the patterns of light and shadow patterns characteristic of these herbaceous ground-level habitats.

bornmuelleri Group

The *bornmuelleri* group comprises the following species: *Montivipera albizona, M. bornmuelleri, M. bulgardaghica, M. wagneri* (central-eastern Turkey, Syria, Lebanon). As this group occupies a more eastern geographic range than the *xanthina* group, it could be referred to as the "Levantine" group. The most representative species may be considered *Montivipera bornmuelleri*, as it most typically combines the characteristic features of the group.

xanthina Group

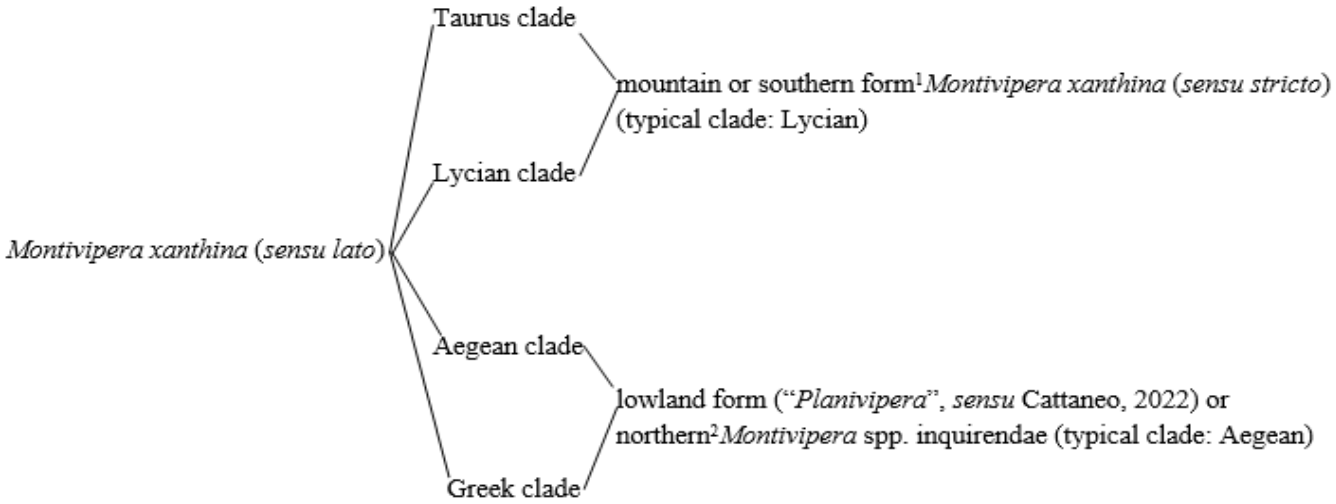
The *xanthina* group consists of cryptic entities distributed across four distinct evolutionary lineages: two montane lineages (the mountainous regions of Lycia and the Taurus Mountains) and two lowland lineages (along the coastal regions of western Turkey and northeastern Greece). The latter two lineages constitute the "*Planivipera*" group [2]. Some authors consider the Lycian clade to be a lowland clade, but in reality, Lycia includes some of the most mountainous and rugged landscapes found in Turkey. The region is surrounded by mountains (the highest peak is Mount Bey Dağları which reaches an elevation of 3,086 m and is still covered in snow at the start of summer). A series of mountain ranges along the coast renders many areas inaccessible by sea. These ranges form the western Taurus Mountains, extending in an arc from the Teke Peninsula (between the Gulf of Fethiye and the Gulf of Antalya) to the north of the city of Antalya. This territory corresponds to ancient Lycia and is therefore also known as the Lycian Taurus. Specimens found along the coasts of this region represent coastal offshoots of mountain populations.

The mountain lineages (Lycia and the Taurus Mountains) exhibit morphological characteristics similar to those of the *bornmuelleri* group (e.g., reduced size and fewer meristic characters) due to the specific physical conditions at high altitudes. In contrast, lowland populations differ from the montane ones, having adapted to environmental conditions more suitable to heterothermic animals. Nilson & Andrén noticed these differences, which led them to distinguish two forms of *Montivipera xanthina*: a northern form and a southern form [11].

The Two Forms of *Montivipera xanthina*

The southern form includes the Lycian and Taurus Mountains clades, while the northern form includes the Aegean and Greek clades (see summary). The southern form, as well as the microinsular populations, exhibits greater morphological variability than the northern form, likely due to the adaptive pressure induced by more variable and sometimes limiting environmental conditions. The characteristics of the southern form compared with those of the northern form can be summarized as follows: less intense coloration; fewer dorsal blotches, on average 26.2 vs. 31.4; oblique neck blotches connected to the dorsal band in 56% vs. <16% of cases (one or both blotches); on average, more interoculars, intercantals, intercantals + intersupraoculars, and fewer apicals; a more variable number of supralabials (9/9, 9/10, 10/10, 11/10, 11/11); fewer ventrals in females (mean 153.4 vs. 161.2) and in males (mean 155.5 vs. 163.5); fewer subcaudals in females (mean 29.8 vs. 31.2) and in males (mean 32.1 vs. 34.3); on average more anterior dorsals (23.7 vs. 23.0) and fewer posterior dorsals (17.0 vs. 17.4); less variable mid-body dorsals (stable at 23).

Summary of the Differing Distribution and Morphology of the Southern and Northern Forms of *Montivipera xanthina* (*s.l.*).



[1]Compared to the northern form, there are fewer ventricles (mean 154), and the coloration is lighter and brighter in both sexes, with a less-developed pattern (mean 26 mid-dorsal blotches) (Nilson & Andrén, 1986).
[2]Mean 162 ventrals; compared to the southern form, the coloration is more intense, with more pronounced sexual dichroism; mean 31 vertebral blotches (Nilson & Andrén, 1986).

Taxonomic conclusions

In 2022, Cattaneo proposed the subgenus *Planivipera* to encompass all lowland populations of *Montivipera xanthina*. He designated *Montivipera xanthina*, as the type species of the new taxon, being the *only* known species in the *xanthina* group (from a taxonomic perspective). In doing so, *Planivipera* became an objective junior synonym of *Montivipera*. Since Cattaneo's research on the species involved *only* the northeastern Greek coasts, the western Turkish coasts (thus excluding the Lycian region), and the eastern Aegean islands, it is reasonable to assume that the "type species" identified by the author referred to the Greek and/or Aegean clade (more likely the latter, given Cattaneo's extensive interest in the eastern Aegean islands).

In conclusion, the type species of the genus *Montivipera*, remains *Montivipera xanthina*, Lycian clade, since, in describing *Montivipera xanthina*, Gray referred to two specimens, at least one of which originated from Lycia (*locus typicus*: Xanthos). Given that *M. xanthina*, based on genetic data, appears to constitute a cryptic species complex with three or four new taxa, the entity of the proposed "subgenus *Planivipera*" , becomes *Montivipera* sp. inquirenda, Aegean clade [1-3, 12].

Dichotomous Key to the Species Groups of the Genus *Montivipera*

1. A series of small scales between the eye and the supraocular; two or more canthals between the supraocular and the supranasal.

- *raddei* complex (subgenus *Oculocircumcincta*): *Montivipera raddei, M.albicornuta, M. kuhrangica, M. latifii*. Armenia, Azerbaijan, Iran.

2. Eye in contact with the supraocular; a canthal between the supraocular and the supranasal.

- *xanthina* complex.

2a. Smaller size (maximum total length 50-85 cm); low pholidosis values (usually around 150 ventral and 27 subcaudal pairs). Higher ventral scale values can be found in *Montivipera wagneri**.

- *bornmuelleri* group (subgenus *Montivipera*): *Montivipera albizona, M. bornmuelleri, M. bulgardaghica, M. wagneri*. Central-Eastern Turkey, Syria, Lebanon.

- *xanthina* group, mountain forms (subgenus *Montivipera*): *Montivipera xanthina* (*s.str.*) (Lycian and Taurus clades). Inland regions of western Turkey up to the Konya province.

2b. Large size [up to 140 cm in total length and almost 1300 g in weight (corresponding values) in Chios population (eastern Aegean); usually 90-100 cm in total length and 300-500 g in weight; high pholidosis values: 156-175 (165.5) ventral scales and 26-37 (31.5) subcaudal pairs].

- "*xanthina*" group, lowland forms (group "*Planivipera*"): *Montivipera* spp. inquirendae (Aegean and Greek clades). Western coastal Turkey, Northeastern Greece, eastern Aegean islands.

*According to Hubbs' rule, in heterotherms of the same or similar species, the number of scales tends to increase with increases in latitude and altitude and the resulting decrease in temperatures. In the *bornmuelleri* group, *M. wagneri* is the species with the northeasternmost distributio.

Part II - Evolutionary History of the *xanthina* Group

The genus "*Vipera*" – The genus "*Vipera*" first appears in the fossil record at the beginning of the Miocene (around 22.5 Ma).

***Macrovipera/Montivipera* Ancestor**
Based on phylogeographic and geotectonic evidence, *Macrovipera* and *Montivipera* shared their most recent common ancestor (a large oviparous viper) during the Langhian (15.3 Ma; on the long-isolated Anatolian subcontinent [12].

Climatic-Ecological Conditions
The appearance of large viperids in Europe (*Daboia, Macrovipera*) broadly coincides with the Miocene Climatic Optimum. Indeed, during the middle Miocene (ca. 14-18 Ma) global temperatures increased markedly. This warm pulse allowed these snakes to thrive and spread, differentiating in regions that are currently less favorable to them, such as central and eastern Europe. Their westward expansion was further facilitated by ongoing environmental changes, particularly the expansion of steppe-dominated habitats, where prey sought by these vipers was likely abundant [13-17].

Separation of *Macrovipera/Montivipera*
Diversification of the group dates back to the middle Miocene (13.4 Ma) [18].

The genus *Montivipera*
Adaption of these vipers to montane conditions may have begun during the Serravallian (approximately 13-12.2 Ma; likely as a response to environmental changes associated with the uplift of the Turkish-Iranian plateau to about 1.5-2 km a.s.l. Increased elevation resulted in changes in climatic factors (lower temperatures, higher humidity, more intense solar radiation, and reduced air pressure) as well as spatial, biotic and evolutionary factors[12- 17].

However, in *Montivipera* adaptation to high altitudes is not complete, as the various species produce offspring that undergo their first shedding 7-10 days after birth, whereas complete adaptation would require the shedding process to take place entirely within the maternal body, with the shed skin removed immediately after birth. For viviparous snakes to be fully and completely adapted to life at high altitudes, their gestation period must also include the time needed for the young to complete their first shedding; this would provide the offspring with the maximum protection during the highly vulnerable shedding period. In fact, in the most well-adapted species (e.g., *Vipera aspis, Vipera ammodytes, Daboia russelii*) the young shed immediately after birth.

In contrast, in vipers that live in warm and favorable environments and lay eggs (e.g., *Macrovipera* spp., *Daboia palaestinae*) the young shed their skin 7-10 days after birth. *Montivipera xanthina* is ovoviviparous, but its young shed 7-10 days after birth, like large vipers that lay eggs. This may indicate that adaptation to high-mountain life occurred recently and secondarily with respect to the ancestral stem group, composed of taxa that are ecologically more similar to the large Middle Eastern vipers. In short, it is as if *Montivipera xanthina* were "paleogenetically pre-adapted" to life in warm, lowland environments.

The group *xanthina*
The *xanthina* group first appeared in the early Pliocene (4.7 Ma), expanded during the warm phase of that same period, and reached its maximum population size at the beginning of the Pleistocene. As the Earth's climate continued to cool, *xanthina* ancestors responded with a negative population growth rate. It was only at the end of the Pleistocene that *xanthina* showed evidence of population growth. However, all current *xanthina* lineages are Pleistocene, with the exception of those from Lycia and the Taurus Mountains, which are older (5.2 Ma).

Part III - Coevolutionary Units Associated with M*ontivipera xanthina* Across the Eastern Aegean Islands
Definition of "Coevolutionary Unit": Nuclei of Species That Maintain Tighter and More Systematic Interactions (Direct And/Or Indirect) With One another than with other Species in the Biocoenosis[21].

Brief Introduction
Each species plays a role complementary to that of the others, enabling their coexistence. When the interactive nucleus is incomplete, the species present, no longer subject to the selective pressures of the interacting species, may disperse ecologically, adapting to newly available resources. On this topic: "The spatial isolation of a functional system leads to the formation of a relatively original assemblage, characterized by a particular specific structure and a particular network of interactions."[20].

Composition of the Various Coevolutionary Units (*Zamenis situla* is Indicated with a Question Mark, as its Role in the Coevolutionary Nucleus is Uncertain)

Samothraki: *Lacerta viridis, Podarcis muralis, Dolichophis caspius, Hemorrhois nummifer, Zamenis situla?, Montivipera xanthina*.

Lesvos, Chios, Samos (species always present)
Lizards: *Laudakia stellio, Lacerta diplochondrodes, Ophisops elegans.*
Snakes: *Dolichophis caspius, Hemorrhois nummifer, Malpolon insignitus, Zamenis situla?, Montivipera xanthina.*

Fourni: *Laudakia stellio, Dolichophis caspius, Montivipera xanthina.*

Patmos, Leros, Kalymnos (species always present)
Lizards: *Laudakia stellio, Ophisops elegans.*
Snakes: *Dolichophis caspius* or *D. jugularis, Hemorrhois nummifer, Montivipera xanthina.*

LIPSI: *Ophisops elegans, Hemorrhois nummifer, Montivipera xanthina.*

SYMI, KOS (species always present)
Lizards: *Laudakia stellio, Ophisops elegans, Heremites aura-*

tus.

Snakes: *Dolichophis jugularis, Hemorrhois nummifer, Montivipera xanthina.*

On all these Islands, the Most Common Lizard species are:
Laudakia stellio (absent only on Samothraki and Lipsi)
Ophisops elegans (absent only on Samothraki and Fourni)

Apart from *Montivipera xanthina*, the Most Common Snake Species are:
Hemorrhois nummifer (absent only on Fourni)
Dolichophis caspius or jugularis (absent only on Lipsi)

As for *Hemorrhois nummifer,* its close syntopy with *Montivipera xanthina* could represent an example of mutualistic symbiosis: the remarkable resemblance between the two snakes could act as a deterrent to potential predators which may be uncertain whether to risk a venomous bite or expend considerable energy attempting to subdue a large colubrid snake (Fig. 1). The phenotypic uniformity observed in *Montivipera xanthina*, despite its high genetic variability, may also be reinforced by this extraordinary resemblance between the two species, selectively increasing the viper's fitness by hindering the expression of novel traits and allowing it to settle into a sort of "adaptive inertia" [12].

Figure 1: Specimen of *Hemorrhois nummifer*, mistaken for *Montivipera xanthina* and killed by locals on Kalymnos Island (central-eastern Aegean Sea). Note the morphology and tail length typical of a colubrid. (Photo kindly provided by Michael Karvounis).

Brief overview of the distribution of the various *Montivipera xanthina* entities on the eastern Aegean islands

Since phenotype results from the interaction between genotype and environment, in the case of *Montivipera xanthina,* coevolutionary units tend to produce different entities depending on their composition. On Samothraki, we find a population of *Montivipera xanthina* with characteristics that allow it to be considered an incipiently evolving entity: a dark gray dorsal ground color, well-developed and numerous black vertebral blotches (mean ~40) connected in a posterior zigzag pattern and interspersed with a few poorly defined light marks. (Fig. 2).

Figure 2:Male specimen of *Montivipera xanthina* ssp. from Samothraki Island (northern Aegean Sea).

On the three large islands of the eastern Aegean (Lesvos, Chios, Samos) *Montivipera xanthina* exhibits a large body size and a well-developed pattern, characteristics that are particularly pronounced in the subspecies *nilsoni*, which is native to the island of Chios (Fig. 3). The taxonomic position of the Fourni viper is undefinable, given its extreme elusiveness.

Figure 3: Female specimen of *Montivipera xanthina nilsoni* from Chios Island (northeastern Aegean Sea).

From a microevolutionary perspective, the islands of the central eastern Aegean (Patmos, Lipsi, Leros, Kalymnos) are likely the most interesting. Leros is home to the subspecies *dianae,* which is characterized by a larger body diameter and a tendency to have more dorsal scales at mid-body (23 to 25) (Fig. 4).

Figure 4: Female specimen of *Montivipera xanthina dianae* from Leros Island (central-eastern Aegean Sea).

Furthermore, Leros is the only island in the group that is home to *Dolichophis jugularis* (and also the northernmost Aegean distribution of this colubrid species). The subspecies *dianae* also inhabits the small island of Lipsi, located further north of Leros, where exceptionally, *Dolichophis caspius* and its potential natural prey, *Laudakia stellio*, are absent. The Lipsi viper has characteristics similar to those of the Leros viper, but more advanced: up to 27 dorsals at mid-body, a mean of ~155 ventrals, and a broadened, stocky trunk (Fig. 5).

Figure 5: Male specimen of *Montivipera xanthina dianae* from Lipsi Island (central-eastern Aegean Sea).

On Symi, the *Montivipera xanthina* population resembles the "southern form" of the species described in many key characteristics: a mean of ~154 ventrals (like on Lipsi), a reduced dorsal pattern, a light gray dorsal ground color in both sexes, and poorly developed or absent bright light color between the dorsal blotches [11]. This viper is distinguished above all by its high number of subcaudals (mean ~36), the highest value observed among Aegean populations, both insular and continental (Fig. 6).

Figure 6: Male specimen of *Montivipera xanthina* ssp. from Symi Island (southern Aegean Sea).

The meristic characters of these microinsular populations sometimes appear to overlap, as is normal in populations undergoing incipient evolution. In such cases, the modal value is the one to which reference should be made in order to establish the true microevolutionary position of the population; it expresses the degree of adaptation to the specific biophysical conditions of the environment, adaptation being the correspondence of the organization to the functional needs. Values differing from the modal one are part of the genetic repertoire available to the species.

Considerations

A cryptic species is one that is overall very similar to other closely related species, differing only in certain genetic or molecular traits. In this regard, Stümpel et al., 2016 write: "In the light of our genetic data, *M. xanthina* appears to constitute a cryptic species complex with three or four new taxa". This phenotypic uniformity could be the result of similar environmental conditions and, consequently, the absence of different selective pressures favoring other types of coloration, size, or proportions [what Fišer et al. call "morphological convergence"] [22].

It is also possible that the separation between the species occurred relatively recently and therefore, the effects of the new genetic composition have not yet fully manifested in the phenotype [the "recent divergence" described by Fišer et al.] [22]. It is as if the new species are reluctant to abandon their traditional habitus due to a kind of adaptive inertia induced by natural selection (see "Part III", regarding *Hemorrhois nummifer*). In other words, it may be safer to rely on a "tried-and-true" form than on something new whose effects are unknown. A similar phenomenon appears to occur in other snake species as well, for example in *Elaphe sauromates* (*s.l.*) [10].

References

1. Nilson, G., Tuniyev, B., Andrén, C., Orlov, N., Joger, U., Herrmann, H. W. (1999). Taxonomic position of the *Vipera xanthina* complex. Kaupia, 8, 99-102.
2. Cattaneo, A. (2022). Effects of ecological divergence in the westernmost Anatolian populations of *Montivipera xanthina* (Gray, 1849) (Serpentes: Viperidae). Biodiversity Journal, 13, 785-798.
3. Gray, J. E. (1849). Catalogue of the specimens of snakes in the collection of the British Museum. British Museum (Natural History).
4. Cattaneo, A. (2014). Variabilità e sottospecie di *Montivipera xanthina* (Gray, 1849) nelle isole egee orientali (Reptilia: Serpentes: Viperidae). Naturalista Siciliano, 38, 51-83.
5. Cattaneo, A. (2017). Note sull'erpetofauna dell'Evros sud-occidentale (Grecia NE) e nuovo contributo alla conoscenza di *Montivipera xanthina* (Gray, 1849) della Tracia greca centro-orientale, con descrizione di *Montivipera xanthina occidentalis* subsp. nova (Reptilia: Serpentes: Viperidae). Naturalista Siciliano, 41, 53-74.
6. Cattaneo, A. (2019). Nuovo contributo alla conoscenza dell'erpetofauna (Reptilia) dell'isola di Samos (Egeo orientale). Naturalista Siciliano, 43, 155-172.
7. Cattaneo, A. (2024b). La vipera dell'isola egea di Lipsi (Dodecaneso settentrionale): Un esempio di adeguamento adattativo alla microinsularità (Serpentes: Viperidae). Naturalista Siciliano, 48, 3-24.
8. Cattaneo, A. (2023). New considerations on the systematics of the genus *Montivipera* Nilson, Tuniyev, Andrén, Orlov, Joger et Herrmann, 1999 (Serpentes: Viperidae). Biodiversity Journal, 14, 325-327.
9. Nilson, G., Andrén, C., Flärdh, B. (1990). *Vipera albizona,*

a new mountain viper from central Turkey, with comments on isolating effects on the Anatolian "Diagonal." Amphibia-Reptilia, 11, 285-294.
10. Cattaneo, A. (2024a). Eco-morphological notes on the Sarmatian rat snake, *Elaphe sauromates* (Pallas, 1814) (Reptilia: Serpentes: Colubridae), from Greek Thrace. Biodiversity Journal, 15, 630-648.
11. Nilson, G., Andrén, C. (1986). The mountain vipers of the Middle East: The *Vipera xanthina* complex (Reptilia, Viperidae). Bonner Zoologische Monographien, 20, 1-90.
12. Stümpel, N., Rajabizadeh, M., Avci, A., Wüster, W., Joger, U. (2016). Phylogeny and diversification of mountain vipers (*Montivipera*, Nilson et al., 1999) triggered by multiple Plio-Pleistocene refugia and high-mountain topography in the Near and Middle East. Molecular Phylogenetics and Evolution, 101, 336-351.
13. Böhme, M. (2003). The Miocene climatic optimum: Evidence from the ectothermic vertebrates of Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology, 195, 389-401.
14. Georgalis, G. L., Szyndlar, Z., Kear, B. P., Delfino, M. (2016). New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences, 109, 103-116.
15. Groombridge, B. (1986). Phyletic relationships among viperine snakes. In Z. Roček (Ed.), Studies in herpetology (pp. 219-222). Charles University.
16. Iskenderov, T. M., Zavadov, S. A. (2016). Some aspects of thermobiology of the South Caucasian gyurza (*Macrovipera lebetina obtusa* Dwigubsky, 1832). Journal of Entomology and Zoology Studies, 4, 960-963.
17. Codrea, V., Venczel, M., Ursachi, L., Rățoi, B. (2017). A large viper from the early Vallesian (MN 9) of Moldova (Eastern Romania) with notes on the palaeobiogeography of late Miocene "Oriental vipers." Geobios, 50, 401-411.
18. Šmid, J., Tolley, K. A. (2019). Kalibrating the tree of vipers under the fossilized birth-death model. Scientific Reports, 9, Article 5510. https://doi.org/10.1038/s41598-019-41290-2.
19. Şapaş, A., & Boztepe-Güney, A. (2009). Shear wave splitting in the Isparta Angle, southwestern Turkey: Anisotropic complexity in the mantle. Journal of Earth System Science, 118, 71-80.
20. Lamotte, M. (1961). Les mécanismes génétiques à l'origine de la formation des races insulaires. In Le peuplement des îles méditerranéennes et les problèmes de l'insularité (pp. 299-311). Colloques Internationaux du CNRS.
21. Lamotte, M., Blandin, P. (1985). La transformation des écosystèmes: Cadre et moteur de l'évolution des espèces. In L. Bullini, M. Ferraguti, F. Mondella, & A. Oliverio (Eds.), La vita e la sua storia: Stato e prospettive degli studi di genetica (pp. 161-206). Scientia.
22. Fišer, C., Robinson, C. T., Malard, F. (2018). Cryptic species as a window into the paradigm shift of the species concept. Molecular Ecology, 27(3), 613-635. https://doi.org/10.1111/mec.14486 .

Summary Overview of the Evolutionary History of the Group *Montivipera xanthina* (*s.l.*)