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Augusto Cattaneo

MACROVIPERA SCHWEIZERI (WERNER, 1935): COMPARISON OF THE POPULATIONS OF MILOS AND SIFNOS ISLANDS (SW CYCLADES) *(Serpentes Viperidae)*

SUMMARY

New evidence and the re-elaboration of old data confirm that the viper of Sifnos is distinct from that of Milos, *Macrovipera schweizeri schweizeri* (Werner, 1935), based on its: consistently larger dimensions, greater number of ventral scales and diverse coloring, as well as differences in the structure and development of the egg shell (also larger) and the embryos at time of deposit. It therefore seems plausible to consider it a geographic subspecies in its own right, of the name *Macrovipera schweizeri siphnensis* (Wettstein, 1952). The presence of *Dolichophis caspius* on Sifnos must have played a key role in this speciation process. For the first time, the effects of the Milos viper's venomous bite on man are described as well as its relative treatment. Also noted is the importance of dry stone walls as an indispensable ecological element for the survival and conservation of the Cyclades viper.

Key words: *Macrovipera schweizeri*, Milos, Sifnos, morphology, eco-ethology, reproduction, poison, taxonomy

RIASSUNTO

Macrovipera schweizeri *(Werner, 1935): confronto delle popolazioni delle isole di Milos e Sifnos (Cicladi sud-occidentali) (Serpentes Viperidae)*. Nuove evidenze e la rielaborazione di vecchi dati consentono di affermare che la vipera di Sifnos si distacca da quella di Milos, *Macrovipera schweizeri schweizeri* (Werner, 1935), in base alle dimensioni di norma maggiori, al maggior numero di ventrali, alla diversa colorazione e alla diversa struttura e sviluppo rispettivamente del guscio delle uova (peraltro più voluminose) e degli embrioni alla deposizione. Appare quindi plausibile considerarla una sottospecie geografica a sé stante, alla quale spetta il nome di *Macrovipera schweizeri siphnensis* (Wettstein, 1952). La presenza a Sifnos di *Dolichophis caspius* deve aver giocato un ruolo chiave in questo processo di speciazione. Per la prima volta vengono descritti gli effetti del veleno provocati

all'uomo dal morso di una vipera di Milos e le relative terapie di controllo. Viene rilevata altresì l'importanza dei muretti a secco quale elemento ecologico indispensabile per la sopravvivenza e la conservazione della vipera delle Cicladi.

Parole chiave: *Macrovipera schweizeri*, Milos, Sifnos, morfologia, eco-etologia, riproduzione, veleno, tassonomia

INTRODUCTION

Macrovipera schweizeri inhabits the south-western Cyclades Islands (Aegean Sea, Greece); more precisely in the Milos archipelago (Milos, Kimolos, Poliegos) occurs the nominal subspecies, while on the island of Sifnos is instead present the controversial subspecies *siphnensis*. For Milos, this viper was first reported by BEDRIAGA (1882: 316, as *Vipera euphratica*) and for Sifnos, the first report is due to WERNER (1935). It should be observed that also BIRD (1935), ignoring the presence of *Macrovipera schweizeri* on Sifnos, have reported the presence of vipers on the island, referring them to *Vipera ammodytes*.

A debate involved MERTENS (1951, 1955) and BUCHHOLZ (1955) about the typus assignment and the type locality of the *Macrovipera schweizeri* (at the time *Vipera lebetina schweizeri*), due to the fact that WERNER (1933, 1935) in his first descriptions of the *taxon* (related to a ♀ of Milos and two ♀♀ of Sifnos) didn't establish a typus. MERTENS, trying to interpret WERNER's intentions (1933, 1935), has chosen the ♀ of Milos as lectotype and, consequently, Milos as type locality. BUCHHOLZ (1955), not in agreement with MERTENS (1951, 1955), has indicated as lectotype one of the two specimens from Sifnos and this island as type locality. According to the international rules of zoological nomenclature, the "*intentio autoris*" and continuity in the nomenclature [WERNER (1935) called the Milos viper *schweizeri*, whereas BUCHHOLZ (1955) (even without validating it) took into consideration the name *siphnensis*] are the discriminating elements to invoke in these cases, and for this reason, I agree with the opinion of MERTENS (1951, 1955), that acted as "first revisor". WERNER (1938), in his summarizing work on the Amphibians and Reptiles of Greece, includes inexplicably the Cyclades viper in its nominal form (*Vipera lebetina* subsp. *lebetina*).

With regards to the Sifnos viper, it is important to explain a bit of history. In 1951, through an exchange of letters, Schweizer communicated to Mertens about two vipers from Sifnos with 25 dorsal scales (the species normally has 23). MERTENS (1951) published this information as part of a general study on the Cyclades viper. WETTSTEIN (1952, 1953), based on data from the literature and therefore considering only the four known specimens from

Sifnos – all with 25 dorsal scales, [two from WERNER (1935) and the two from Schweizer] – distinguished the population of Sifnos with the name *siphnensis* (name taken from a label of a specimen from WERNER's collection regarding one of the two vipers of Sifnos above mentioned) and compiled a short diagnosis of the subspecies, in which the main diagnostic feature was the presence of 25 scales halfway up the trunk. SCHWEIZER (1957) later pointed out that his two aforementioned specimens from Sifnos had 23 scales, not 25.

In a previous article (CATTANEO, 1989) I had the opportunity to back up the validity of the subspecies *siphnensis*; new evidences and the re-elaboration of previous data allow to present here new considerations, with the aim of proving the differences between the nominal subspecies of Milos and the population of Sifnos. In this perspective, various parameters concerning the morpho-ecology of the two populations will be compared and their distinctive characteristics will be highlighted.

For details about the locations and research periods, see CATTANEO (1989).

MATERIALS AND METHODS

Specimens studied - MILOS: 105 specimens (56 collected in nature, 24 found dead, 7 observed, 18 born in captivity). SIFNOS: 25 specimens (16 collected in nature, 3 found dead, 2 observed, 4 born in captivity).

Some vipers, among those collected and those born in captivity, were kept (with authorization from the Prefecture of Rome) just long enough to draw useful information regarding feeding, molting times, reproductive cycle, growth rates, etc. Their scales were counted on the exuviae. Other vipers were studied and left on site. The specimen measurements collected (keeping in mind that the measurements *in vivo* can be slightly larger) refer to the time of capture or, if born in captivity, the time of birth. In nature, diet information was deduced from examinations of fecal matter and/or gastric contents. Some of the eggs found in water were opened to verify the developmental stage of the embryos (generally eggs laid in water result in the death of the embryos).

Abbreviations used: TL = total length; TR = tail ratio (overall length/tail length); W = weight.

MACROVIPERA SCHWEIZERI SCHWEIZERI (WERNER, 1935)

ETYMOLOGY - *Macrovipera:* from the Greek "makrós" = big and the latin "vipera" = viper (long snake); *schweizeri*: name created by WERNER (1935) in

honor of Hans Schweizer, a Swiss herpetologist who in the early 1930s alone undertook and gave impetus to the study of the herpetofauna of the island of Milos.

COMMON NAME – Blunt-nosed viper, Cyclades Viper

LOCAL NAME - Ochiá.

MAIN SYNONYMS - *Vipera lebetina schweizeri* Werner, 1935; *Daboia lebetina schweizeri* Obst, 1983; *Vipera schweizeri* Nilson & Andrén, 1988.

TYPUS – The typus is kept in the Herpetology Department of the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts, USA under the number MCZ 37008 (WALLACH *et al.*, 2014) (it was from this museum that Werner obtained subsidies for his travels: WERNER, 1933: 105). It is a female, 48 cm long (tail 6 cm), collected by H. Schweizer in July 1932. MERTENS (1951: 208) designated it as lectotype. The specimen has 148 ventral scales and 39 pairs of subcaudal scales.

DESIGNATED TYPE LOCALITY (MERTENS, 1951) – "Milos" = Island of Milos, Southwest Cyclades, Greece.

MACROVIPERA SCHWEIZERI SIPHNENSIS (WETTSTEIN, 1952)

ETYMOLOGY – See *Macrovipera s. schweizeri*; *siphnensis* = proper, inhabitant of the island of Sifnos.

LOCAL NAME - Ochiá.

MAIN SYNONYMS - *Vipera lebetina siphnensis* Wettstein, 1952, 1953.

HOLOTYPE – The holotype is part of the herpetological collection of the Natural History Museum of Vienna (Austria) with the number CLXVII/1952-53. It is an adult female, 68 cm long (tail 8.8 cm) collected in May 1934 and belongs to the Werner Collection (according to the display label). The specimen has 156 ventral scales and 41 pairs of subcaudals (WERNER, 1935: 114; Fig. 7, Abb. 18).

TYPE LOCALITY – "Siphnos" – Island of Sifnos, Southwest Cyclades, Greece.

SYSTEMATICS

GENUS *MACROVIPERA* REUSS, 1927

The genus *Macrovipera* was designated and distinguished from the genus *Vipera* by HERRMANN *et al.* (1992) in order to include the large

Eurasian and North African vipers. Currently, it includes five species: *lebetinus*, *razii*, *schweizeri*, *mauritanica* and *deserti*; *schweizeri*, *mauritanica* and *deserti* are often considered subspecies of *lebetinus*, and LENK *et al.* (2001) assigned *mauritanica* and *deserti* to the distinct genus *Daboia*. These vipers are all characterized by their large size, oviparity and adaptation to hot and dry habitats (MALLOW *et al.*, 2003). The species type of the genus is *Coluber Lebetinus* Linnaeus, 1758; *Lebetinus* is a masculine proper noun (and for this reason the first letter of the name was capitalized) non declinable, used by LINNAEUS (1758) as an apposition (FRÉTEY, 2019) (the name derives from the Greek "λεβης" = lebetes, a kind of drum that was played by women in Sparta during funerals). *Vipera lebetinus schweizeri* WERNER, 1935 was raised to a specific rank by NILSON & ANDRÉN (1988), although some authors currently prefer to maintain as subspecies this *taxon*.

Various subspecies of *Macrovipera lebetinus* have been described, though some are still being defined. They are shown below.

– *M. l. lebetinus* (Linnaeus, 1758), the nominal form, present in Cyprus.

_ *M. l. transmediterranea* (Nilson & Andrén, 1988), typical of the coastal mountain area of Algeria and Tunisia.

_ *M. l. obtusa* (Dwigubskij, 1832), spread from eastern Turkey east all the way to Afghanistan.

_ *M. l. peilei* (Murray, 1892), uncertain subspecies, reported in southern Afghanistan, western Pakistan and Kashmir.

– *M. l. euphratica* (Martin, 1838), another uncertain subspecies, reported in the Euphrates river basin of Turkey, Syria and Iraq (typical location: Birecik, southern Turkey). It seems to be characterized by a darker coloration and larger size.

– *M. l. cernovi* (Chikin & Ščerbak, 1992), distributed in northeastern Iran, southern Turkmenistan and northern Afghanistan.

– *M. l. turanica* (Černov in Terent'ev & Černov, 1940), present in eastern Turkmenistan and southern Uzbekistan. It is a valid subspecies which is distinguished by its orange-colored dorsal design that contrasts with its light background.

Macrovipera razii Oraie, Rastegar-Pouyani, Khosrovani, Moradi, Akbari, Sehhatisabet, Shafiei, Stümpel & Joger, 2018 is a recently described species belonging to the *lebetinus* group. It has been reported in south-central Iran. It is distinguished from *M. l. cernovi* and *M. l. obtusa* (to which it is more similar) by its peculiar pholidosis.

Macrovipera mauritanica (Gray, 1849) lives in Morocco and the coastal region of Algeria and Tunisia.

Macrovipera deserti (Anderson, 1892) is found in Tunisia, northwestern Libya and in the foothills of the Atlas Range in Algeria. These two species of

north African vipers are distinguished by their dorsal ornamentation which is more pronounced in *M. mauritanica* and less in *M. deserti.* They also are distinguished from the subspecies of the group *lebetinus* and from *M. razii*, among other features, by the usual presence of 27, instead of 25, longitudinal rows of dorsal scales halfway up the trunk.

Macrovipera schweizeri (Werner, 1935) lives in the southwestern Cyclades (Aegean Sea, Greece) and more precisely on the islands of Milos, Kimolos, Poliegos (where it is represented by the nominal subspecies) and Sifnos (where it is instead represented by the subspecies *siphnensis*).

IDENTIFICATION

Macrovipera schweizeri schweizeri

MORPHOLOGY - A relatively large, robust, and well-shaped viper. The head is distinct from the neck, with a blunt, rounded snout and outwardly protruding jaw edges. The eye, with its vertically elliptical pupil, is relatively small (its vertical diameter is less than its distance from the mouth slit). The nostril is large and its opening is positioned diagonally up and back. The tail length almost always corresponds to1/7-1/8 of its total length. Keeled scales.

DIMENSIONS - Juveniles: 18 juveniles born in captivity were 18.7-21.1 cm long (arithmetic mean 20.1).
♂♂ adults: 21 specimens had total lengths between 64.5 and 83.2 cm, with an arithmetic mean of 70.9 cm.
♀♀ adults: 17 individuals ♀♀ measured between 50 and 68.4 cm, with an arithmetic mean of 62.5 cm.

The aforementioned male specimens were collected and measured in the field and then released. Five specimens of larger size which were kept (for their dimensions before and after captivity, see Tab. 1). It is worth noting that of the 57 adult specimens found, only these five (that is 8.7%) had dimensions exceeding the norm.

The specimens with an incomplete tail were not considered for the morphometric evaluation.

PHOLIDOSIS – Head: the head is covered with small scales (including small supraoculars which clearly differentiates *Macrovipera* from *Montivipera*) and are distributed as follows: 33-39 intersupraoculars, 13-19 intercanthals, between the eyes there are 7-12 longitudinal series of scales, 2 canthals per side, 2 apicals, 2-3 supraoculars per side, 10-11 supralabials per side (usually the 4th and 5th under the eye), 12-14 sublabials per side, 14-16 circumoculars (both internal and external) per side, eye separated from the supralabials by 2-3 suboculars (NILSON, 2005).

Trunk and tail - *Number of longitudinal rows of dorsal scales at mid-trunk*: 19-25 (22.7), *n* = 48 (30 adult specimens and 18 juveniles).

The different measurements were distributed as follows: 19 in one specimen, 21 in five specimens, 22 in six specimens, 23 in thirty specimens, 24 in two specimens and 25 in four specimens.

Number of ventral scales: ♂♂ adults, 144-158 (152.6), *n* = 22; ♀♀ adults, 151-155 (152.5), *n* = 8; juveniles, 140-154 (148.3), *n* = 18.

Number of subcaudal scales (pairs): ♂♂ adults, 41-45 (42.5), *n* = 12; ♀♀ adults, 40-43 (41.5), *n* = 6; juveniles, 31-41 (37.6), *n* = 18. Incubation of eggs in captivity, especially when not provided with adequate temperatures, can slow down blood circulation in the fetuses of the snakes and cause ischemic effects on the most peripheral structures. This explains the low number of subcaudal scales found in the juveniles. I have also observed this phenomenon in young of oviparous species (for example *Elaphe quatuorlineata*: CATTANEO, 1999), born from eggs kept at unsuitable incubation temperatures.

COLORATION - During the research period (May), the population resulted essentially monochrome: all the individuals encountered had a general and overall brownish gray intonation (Fig. 1). The ♂♂ appeared however darker than the ♀♀ and, sometimes, with reddish tones, especially ventrally. The ornamentation was generally not very marked. It consisted of large dark spots or subrectangular bars, sometimes asymmetrical (divided into two staggered halves), arranged transversely on the back and vertically on the sides, alternating with each other and often separated by a clear longitudinal line; the belly exhibited thick dark speckling on an isabella colored background, often suffused with reddish hues. The tail becomes more and more yellow towards the apex. On the sides of the head a dark line goes from the eye

Fig. 1 — Macrovipera schweizeri schweizeri: pair of specimens found on Milos Island (left ♂, right ♀) (Photo F. Paysant).

to the labial commissure, sometimes curving and reaching the sub-labials. A dark spot from the eye to the mouth slit has also often been observed. Of the specimens in captivity, the brown gray tones disappeared with the first detachment of the exuviae (July 1983) and lighter shades, ash gray (grayish phenotype) took over, which made the design more evident. Of the juveniles born in captivity, a gray tone with a very evident dark brown pattern appeared immediately after the postnatal molting.

A reddish ♂ specimen, belonging to a different phenotype than the one described above, was also found on Milos. In this regard SCHWEIZER (1957) writes: "In the mountain aquifers, where there are also red rocks, we find, although not frequently, on Milos, the splendid brick red variety, whose magnificent dress is completely devoid of design, except for rare pale-yellow spots". This *reddish morph* seems to be exclusive, or at least, more present in the male sex (SCHWEIZER, 1935, 1938). It is worth reporting what KLEMMER (1982) claims about the occurrence of these showy-colored phenotypes in nature: "In snakes, the showy colors (often associated with a fading or complete lack of pattern) are transmitted by a recessive gene. Obviously, the transmitted recessive traits are manifested only in populations in which the genetic exchange is limited or prevented, as is the case in isolated populations who inhabit the margins of the species' distribution area or island populations. The brightly colored specimens can only be found where this genetically fixed anomaly is not so disadvantageous as to immediately eliminate its carrier, therefore, where the interactions are not very dense (e.g. lack or scarcity of predators). Typical examples are the red vipers of Milos and the red specimens of *Gloydius halys caraganus* (the westernmost subspecies of that specific *taxon*)".

SEXUAL DIMORPHISM - The ♀♀ have relatively shorter tails than those of the ♂♂: TR ♂♂, 6.7-8.1 (7.4), $n = 16$; TR ♀♀, 7.5-9.8 (8.2), $n = 10$. This characteristic seems to reflect little on the number of subcaudal scales (see "Pholidosis"). The ♂♂ are larger and have a more intense coloring than the ♀♀.

Macrovipera schweizeri siphnensis

MORPHOLOGY- See *Macrovipera s. schweizeri.*

DIMENSIONS - 16 adult specimens were encountered; 11 of these (68.7%) had considerable size. The dimensions of these large specimens before and after time in captivity are shown in Tab. 1. In addition, two ♂♂ (72.2 cm and 76.5 cm) and one ♀ (66.4 cm) were measured in nature. The other two specimens, having incomplete tails, were not considered for the

Table 1
Total length and weight of some specimens of Macrovipera schweizeri *from the Islands of Milos and Sifnos (western Cyclades) at time of capture and after being in captivity.*

		At capture (at birth for n°. 12, 13, 14)			After captivity (maximum dimensions recorded)		
		Date	TL (cm)	W (g)	Date	TL (cm)	W (g)
MILOS (5/57 adult specimens collected)							
1	♂	08/05/1983	95	493	–	–	–
2	♂	08/05/1983	92*	555	11/01/1990	112*	1070
3	♀	10/05/1983	73	252	18/01/1990	89	502
4	♂	11/05/1983	97*	684	15/01/1989	106.7*	1080
5	♂	19/05/1983	93*	530	12/01/1989	127.8*	1485
SIFNOS (11/16 adult specimens collected + 3 born in captivity)							
1	♂	20/04/1981	82	410	08/01/1989	119.2	1110
2	♂	22/04/1981	107*	660	10/01/1988	113.5*	1140
3	♂	28/04/1981	92	604	09/01/1986	118	1115
4	♂	01/05/1981	88	590	15/01/1987	130	1351
5	♂	04/05/1981	98*	663	03/01/1985	118.1*	1044
6	♂	06/05/1981	97*	570	09/01/1986	112.8*	1031
7	♀	24/05/1985	88*	720	03/01/1988	102.1*	1031
8	♂	24/05/1985	93*	683	05/01/1992	119.8*	1130
9	♀	25/05/1985	77	454	07/01/1990	112.4	995
10	♀	27/05/1985	82	649	24/01/1988	103	770
11	♂	27/05/1985	102	735	04/01/1995	145.3	1820
12	♂	30/08/1985	22.5	7	08/01/1995	127.3	1446
13	♂	30/08/1985	22	7	15/01/1995	135.7	1622
14	♀	30/08/1985	21	7	17/01/1991	110	947

* Incomplete tail

morphometric evaluation.

In addition to the three specimens shown in Tab. 1, a fourth individual was born in captivity and died shortly after hatching; it was much shorter and lighter than its siblings (17.2 cm and 2.5 g respectively).

PHOLIDOSIS - Head: see *Macrovipera s. schweizeri.*

Trunk and tail - *Number of longitudinal rows of dorsal scales at mid-trunk*: 22-25 (23.2), $n = 20$.

The different values were distributed as follows: 22 in one specimen, 23 in sixteen specimens, 24 in one specimen and 25 in two specimens.

Number of ventral scales: ♂♂, 154-163 (157), $n = 14$; ♀♀, 155-158 (156.2), $n = 5$; 155 in a juvenile.

Number of subcaudal scales (pairs): ♂♂, 37-44 (41.3), *n* = 8; ♀♀, 37-42 (40.2), *n* = 4; 31 in a juvenile.

COLORATION - All the coloring variations (seasonal, sexual, individual, age-related) can be traced back to two fundamental phenotypes, definable almost from birth, greyish (Fig. 2) and ocher (Fig. 3), in appar-

Fig. 2 — Macrovipera schweizeri siphnensis: specimen ♂ of the greyish phenotype in spring habitus (Photo F. Paysant).

ent selective balance, given that the ratio found in both observation periods (1981 and 1985) was 1:1 (in fact the two phenotypes have been found to be cryptically adapted to different substrates in the same habitat. It is true that the spring season in Sifnos is much shorter than the summer, but it is equally dangerous for the vipers in terms of exposure. This means the grayish morph could be more favored in spring due to the general and relative agreement of its coloring with the seasonal tones whereas the ocher coloration would be favored in summer for the same reasons). Among the chromatic variations mentioned above, the seasonal ones are noteworthy; in fact, in spring, the ♂♂ adults (especially the larger ones) reach the peak of a darkening process that starts in autumn (according to observations in captivity) perhaps in relation to the seasonal thermal drop (low temperatures tend to darken reptiles). In ♂♂ born in captivity, the first autumn

Fig. 3 — Macrovipera schweizeri siphnensis: ♀ specimen of the ocher phenotype in spring habitus (Photo F. Paysant).

darkening occurred five years after birth, which points to a hormonal component in the process. The dorsal side of these reproductive ♂♂ is usually a dark reddish brown, such that the two phenotypes are not always easily distinguishable (the grayish one however appears darker and sometimes without the reddish tones that make up the pattern and/or are part of the belly coloration that extends out to the sides. This would allow them to thermoregulate more quickly and therefore dedicate more time to the search for reproductive ♀♀, who, by contrast, appear lighter in spring (the increased brightness could make it easier for them to be recognized by the ♂♂); during this search, which may require crossing large open spaces, the dark pigmentation would also oppose the harmful effects of solar radiation. The darkening ceases with the detachment of the exuviae in July, when the two phases are clearly distinguishable (observation in captivity).

The dorsal ornamentation of the Sifnos viper generally appears more faded and blurry than that of the Milos viper, so much so that the dark bars on the back and sides tend to turn often into shaded spots with indefinable outlines; the fading of the pattern reaches its maximum expression in the ocher phenotype (specimens belonging to this morph have been found almost completely devoid of ornamentation: Fig. 4). Occasionally, speci-

Fig. 4 — Macrovipera schweizeri siphnensis: ♀ specimen of the ocher phenotype with almost absent dorsal ornamentation (Photo F. Paysant).

mens were found with scattered and fragmented patterns, including circular dorsal spots and dark, horizontal, unconnected lines along the sides. As for the belly coloration and coloration of the young, the information regarding *Macrovipera schweizeri* of Milos Island applies.

SEXUAL DIMORPHISM - The information given on *Macrovipera schweizeri* of Milos Island applies here. The difference in tail length between the two sexes seems less pronounced, but the examined material is scarcer: TR ♂♂, 7.6-9.2 (8.5), *n* = 8; TR ♀♀, 8.4-9.3 (8.8), *n* = 4.

ECO-ETHOLOGY

Macrovipera schweizeri schweizeri

HABITAT - The survival of this viper on these islands depends on the presence and conservation of dry stone walls; these anthropogenic structures guarantee protection, shelter and isolation from external factors as well as constitute visual topographical references useful for encounters between the sexes. More specifically, their use seemed congruent with three types of factors: 1) psychological; 2) trophic; 3) physical.

1) Psychological factors - Related to relations with man and any com-

petitor species. *Macrovipera schweizeri* was almost always found far from residential areas and often, in Sifnos, along low walls located at a certain distance from the valley floor (never more than 300-400 m a.s.l., NILSON, 2005), where partially active waterways flowed (locally called "potamos"). This habitat was generally avoided by *Dolichophis caspius*, which remained at lower altitudes (Tab. 2). These two species can compete on a trophic level (see "Feeding Notes" */M. schweizeri siphnensis*).

2) Trophic factors - In general, the walls frequented by *Macrovipera schweizeri* were never far from cultivated fields and humid sites, that is environments that could widely satisfy its demand for micro-mammals. Note that, probably for the psychological reasons mentioned above (human presence), the walls that directly surrounded the crops seemed to have been avoided.

3) Physical factors - Above all, *Macrovipera schweizeri* seemed to seek dry walls that were rather high and parallel to the rivers. Both characteristics that helped provide greater shelter from the very strong winds that blow on these islands, especially in the river valleys, where the winds get channeled and acquire strength and speed (i.e., in the Kamares valley in Sifnos: Fig. 5). In fact, many vipers were found at wall junctions, where wind flow is even more reduced. Other elements sought are permeable soils with proximity to water or humid sites with good sun exposure; these conditions make the inhabited walls suitably humid and hot.

Other components, almost always present in these habitats, are the dense mastic shrubs *Pistacia lentiscus* that flank the walls, the abandoned fields of grasses that surround them and the bushy or grassy vegetation that extends to

Table 2

*Relationship between the geomorphological characteristics of Sifnos localities studied and the ophidic presence (*Dolichophis caspius*,* Macrovipera schweizeri*) (at Kamares the flat expanses prevail over raised terrain; in Faros the opposite is found; intermediate features were observed in Plati Yalos).*

	KAMARES Valley (very wide, extensive and shallow)	PLATI YALOS Valley (wide and shallow)	FAROS Valley (narrow and deep)
Dolichophis caspius (n. spec. collected)	14	2	5 (3 captured at bottom of valley)
Macrovipera schweizeri (n. spec. collected)	2	8	6

Fig. 5 — Flowering of oleander (*Nerium oleander*) in the stream ("potamos") that runs through the Kamares valley on the island of Sifnos: habitat of *Macrovipera schweizeri siphnensis* and *Dolichophis caspius* (May 1985).

their base. Sometimes in the vicinity of these walls, there are dilapidated abandoned houses, which *Macrovipera schweizeri* could enter for trophic purposes (they attract rodents) or use as a visual reference for encounters of the sexes (Fig. 6). Additionally, a typical habitat found in Milos is the stone agglomerations that mark off the white roads (habitat also found in *Montivipera xanthina*); vipers have been observed on the stones along these roads.

Vipers were found at the base of the walls, on the walls (half hidden by dry twigs) or just before the top of the walls (below the first stone, especially if flat, as it is more suitable for thermoregulation). They were found on the sunny side of the wall, but sometimes also on the opposite side. Juveniles and others have often been found under stones.

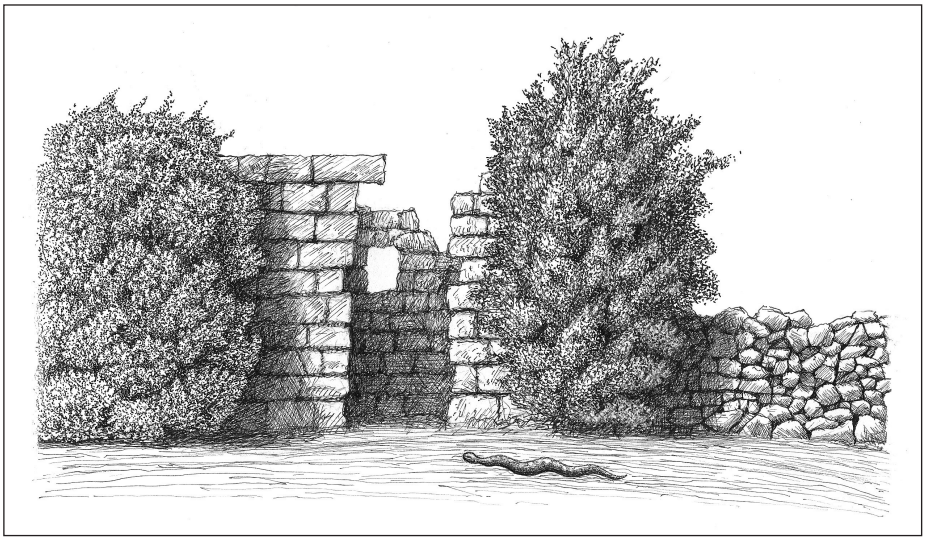

Fig. 6 — Habitat of *Macrovipera schweizeri siphnensis* of the island of Sifnos with its typical components: stone wall, impressive mastic shrubs (*Pistacia lentiscus*) and ruined buildings (Drawing N. Falchi).

MAN/VIPER RELATIONSHIP - Human activity is the main enemy of *Macrovipera schweizeri* on the study islands. The numerous vipers that I found dead, both in Milos and in Sifnos, had either been killed by shepherds or farmers, or above all hit by cars on mostly dirt roads. In the past, fear and distrust of this viper led the local administration of Sifnos to offer a prize of 25 drachmas for each specimen killed and delivered (WERNER, 1935, 1938). Direct human intervention on the environment, such as cutting, burning, the use of herbicides and pesticides, overgrazing, and the extraction of minerals (with its consequences) have also contributed to reducing this viper's fitness. Until the early 1980s, traders, collectors and scholars took large numbers of specimens. In 1981 a presidential decree (Presidential Decree 67/1981) forbade the killing and collection of most Greek reptiles, including *Macrovipera schweizeri* which was considered a "species of high priority", but the abusive collection of this animal has continued until now (NILSON, 2005). In any case, the indispensable condition for this viper's survival on these islands is the presence and conservation of the dry stone walls (see "Habitat").

As endemic microinsular entity, it is protected by the Berne Convention (Annex II and Annex I of Resolution 6 of 1998, revised in 2011) and by the EU Habitats Directive (Annex II and Annex IV); it is also listed as "Endangered" in the IUCN Red List.

ACTIVE TIMES - In both islands considered, *Macrovipera schweizeri* was

found in thermoregulation between 9^h and 12^h, mostly around 10^h. It is very active on Milos. Under the reproductive impulse, it was seen crossing roads (especially dirt roads) and reaching as far as coastal stretches. It was also active in the early hours of the night (20^h-22^h), probably taking advantage of the terrestrial thermal radiation and the fact that the Etesian winds stopped or decreased in intensity during the night. Strictly diurnal in the early spring and late autumn, this viper conducts nocturnal activity in the summer; at the end of autumn it goes into hibernation (NILSON, 2005).

PHENOLOGY - For both physical and biological reasons, large snakes (like the species in question), compared to small and medium-sized snakes, are forced to greater external activity: heating, feeding and reproducing a larger body requires more sun exposure and more searching.

Sun Exposure (thermoregulation) - Vipers lay out in the sun and flatten themselves dorso-ventrally, stretching out their ribs to the maximum, a position that can also be assumed with a partially rolled up body. This posture ensures a greater surface area for heat absorption on the back, as well as heat conduction from the substrate on the ventral surface. It is adopted in times of severe thermal *deficit* and allows thermoregulation times to be shortened (which are generally longer and therefore more dangerous in large snakes); it also strengthens crypsis and increases the probability of survival in the case of attack by predatory species (a flattened reptile becomes practically two-dimensional, including the head, and thus hinders being grasped by enemies that attack from above, such as birds of prey). The dorso-ventral flattening prohibits an immediate defense reaction (enough to simulate thanatosis) and, for obvious mechanical reasons, should not be practiced routinely or, at least completely, by pregnant females or females with well-developed eggs, nor by specimens with massive prey in the stomach.

The hormonal conditions during the sexual phase lower the sense of alertness; in fact, this thermoregulatory flattening has been found mostly in animals that were presumably in their sexual phase. They displayed signs of mental obfuscation and were situated out in the open, both on Sifnos and Milos. As their sexual instinct yields, they start to display more and more alertness and reactivity.

COEXISTING HERPETOLOGICAL TAXA - *Pelophylax kurtmuelleri*, *Testudo marginata*, *Mediodactylus kotschyi concolor*, *Hemidactylus turcicus*, *Lacerta trilineata hansschweizeri*, *Podarcis milensis*, *Ablepharus kitaibelii*, *Zamenis situla*, *Natrix natrix schweizeri*, *Telescopus fallax*.

FEEDING NOTES – The genus *Macrovipera* is predominantly theriophagous. According to research carried out by NILSON *et al.* (1999) from 1993

to 1998, the density of micro-mammals on the island of Milos is low. Indeed populations of indigenous rodents are absent from the western Cyclades (NIETHAMMER, 1974; NIETHAMMER & KRAPP, 1978, 1982). Based on this evidence and considering that *Macrovipera schweizeri* has been isolated since the Pliocene, it is plausible to believe that the species turned to alternative prey, adapting to hunting birds. If this is the case, the spring and autumn bird migrations would be of fundamental importance for the survival of this viper in the western Cyclades (NILSON, 2005) and SCHWEIZER (1957) claims that bird hunting occurs especially in the spring on Milos. It seems that *Macrovipera schweizeri*, after biting the bird, does not let go, but holds on and waits for the poison to have its effect and for the prey to die (whereas with micromammals, they are bitten and left to be found again later) (BRODMANN, 1987).

Concerning the prey observed during the present study in nature, see Tab. 3. SCHWEIZER (1957) also includes other snakes in the food range of this viper. In captivity, *Macrovipera schweizeri* of Milos proved to be essentially theriophagous.

Also in captivity, ritual struggles between ♂♂ of *Macrovipera schweizeri*,

Table 3

Prey found in some specimens of Macrovipera schweizeri *(Werner) on the islands of Sifnos and Milos (western Cyclades) (in brackets the number of specimens-prey).* * = incomplete tail

	PLACE	DATE	SEX	TL (cm)	PREY
SIFNOS					
1	Faros	22/04/1981	♂	107*	*Rattus* sp.
2	Kamares	24/04/1981	♂	82.2*	*Rattus* sp.
3	Faros	04/05/1981	♂	98*	Aves ad. indet.
4	Faros	06/05/1981	♂	97*	Aves juv. indet.
5	Plati Yalos	24/05/1985	♀	88*	*Rattus* sp.
6	Plati Yalos	24/05/1985	♂	93*	Rodentia sp. indet.
MILOS					
1	Adamas	06/05/1983	♂	73.4*	Aves ad. indet.
2	Zefiria	08/05/1983	♀	66	Aves ad. indet. (2), *Lacerta trilineata*
3	Parasporos	09/05/1983	♀	64.3*	Rodentia sp. indet.
4	Parasporos	09/05/1983	juv.	–	*Podarcis milensis*
5	Parasporos	10/05/1983	♂	67	Aves pullus indet. (3), *Mus* sp.
6	Zefiria	12/05/1983	♀	65	*Lacerta trilineata*
7	Parasporos	16/05/1983	♀	66	*Sylvia melanocephala* ad.
8	Agios Sosti	17/05/1983	♂	71.1	Aves ad. indet.
9	Tripiti	19/05/1983	♂	93*	*Lacerta trilineata*

similar to those that occur in nature during the breeding time, have been observed when in the presence of prey. The vipers concerned (two or more), after having manifested their excitement with vibrating tail motions, give life to a sort of "dance" around the mouse or rat that was killed by one of the contenders. This "dance" consists of rhythmic, undulating movements performed with the head and the front part of the trunk raised upwards. Finally, one of the vipers grasps the victim and carries it elsewhere, where it either devours it or, chased by the other contenders, begins a new "dance". I also observed this competitive behavior in *Vipera aspis* (L.) (cf. NAULLEAU, 1966). In sum, a ritual behavior similar to the one used for the right to mate is used for the possession of prey. If the prey is grabbed by two contenders at the same time with the teeth at each end (head, tail), cannibalism attempts may even occur. Sometimes, however, the dispute can be resolved with one contender biting the head of the other, which causes the competitors to withdraw and results in severe swelling, sometimes bleeding and, judging by the reaction, acute pain; these symptoms resolve after a few hours and show that the species is not totally immune to its own poison. During the bite, the venomous teeth can detach and remain fixed in the competitor. It is also not uncommon for lost teeth to grow back double, even two per side (*pers. obs*.). If the teeth are lost during predation, they can later be found in the stool (*pers. obs*.).

Perhaps the cause of the strong presence of *Macrovipera schweizeri* on Milos is the abundance of lizards *Podarcis milensis*, which are also favored by the absence of large herpetophagous snakes. This abundance could, in fact, lower the mortality rate of juveniles. Indeed, overall in ophidic species, the scarcity (up to the lack) of specific prey represents the most harmful limiting factor for the survival of young, which, compared to adults, are less experienced in obtaining food and, due to higher growth rates, less resistant to fasting (cf. SAINT GIRONS, 1951).

DEFENSE MECHANISMS – When menaced, *Macrovipera schweizeri* tends to flee; if escape is not possible, it hisses, sometimes tries to bite, but above all it swells excessively and stretches its ribs to the maximum, so as to appear considerably larger than normal. Sometimes, during escape, it raises up on the front part of the body and continues to stretch its ribs, but, in doing so, is unable to go very far despite wide undulating movements. It gives off the appearance of being very confident, for intimidation purposes, through its large size, enhanced by the increase in volume obtained by maximum lung inflation. It can emit defensive, odorous excretions similar to those of *Coluber* (s.l.).

In conclusion, the defense mechanisms of this viper do not appear sufficient to guarantee a long survival on the islands in question (in the Kamares valley on the island of Sifnos, where man is very present, it has very rarely

appeared). Furthermore, for the above cited reasons, the sexual phase makes it much more vulnerable. The only truly valid means that this viper has to combat the pitfalls brought about by its natural enemies (including man) are its mimetic qualities, given that it has a color that fits cryptically on many substrates.

PARASITES – Nematodes (cf. BUCHHOLZ, 1955) and Acari have been found.

POISON – In central western Asia, the bites inflicted on man by *Macrovipera lebetinus* (the closest species to *Macrovipera schweizeri*) seem to be frequent and sometimes fatal (WARREL, 2010). In these regions, people tend to adjust their activities in relation to the snake's rest periods (MALLOW *et al*., 2003). Its poison can kill men, horses, cattle and camels. Being a large viper with long fangs, its bite can cause physical trauma in addition to the chemical effects of the poison. Among the components of the poison, which has a mainly hemorrhagic, necrotic and proteolytic effects, L-amino acid oxidase, an enzyme also present and more active in the poison of *Vipera aspis*, is particularly effective (ZELLER, 1948).

There are no cases given in literature of man being poisoned from bites inflicted by *Macrovipera schweizeri* of the Cyclades islands. Incidents of this type do occur, but do not appear to have fatal outcomes (NILSON, 2005). I therefore find it relevant and useful to describe the consequences of a bite, inflicted by an adult *Macrovipera schweizeri* of Milos Island, on the right hand of a young woman - an incident that I was able to personally follow and monitor.

The patient was transported to hospital and subjected to sodium bicarbonate therapy and drugs designed to replenish electrolytes and body fluids, but not a specific serum. The affected limb swelled to the armpit and quickly became painful. The patient stayed in the hospital for two days, then was discharged. During the hospital stay there was an increase in blood sugar, a decrease in red blood cells, an increase in platelets, a slight hypotension and a decrease in heart rate. At discharge, the patient experienced intense thirst and neither the swelling nor pain in the affected limb had completely disappeared. In the following days, however, the effects subsided, and the affected person was able to return to his normal activity.

REYMOND (1956) defined the poison of the species of the *Macrovipera* genus of North Africa: "hemorrhagic proteolytic saliva". He also argued that saliva, like gastric juice, is digestive juice from the part of the digestive tract that precedes the duodenum; the enzymes contained in these juices act in an acidic medium. The long teeth of the viper inject the poison into the muscles of the victim, where lactic acid tends to create an acidic environment and therefore favor the poison's effect. Hence the importance of increasing the body's alkaline reserves in the case of a viper bite. In other words, given that

"le venin de Vipère lébétine agit moins comme un venin que comme une salive, il semble indiqué d'agir localement et généralement pour diminuer acidité locale au point mordu et augmenter le plus possible la réserve alkaline générale du sujet" (REYMOND, 1956). This further explains the use of sodium bicarbonate (antacid salt) in the therapy applied to the above patient.

Macrovipera schweizeri siphnensis

For "Habitat", "Man/viper relationship", "Active times", "Phenology", "Defense reactions", "Parasites" and "Poison" see *Macrovipera s. schweizeri*.

COEXISTING HERPETOLOGICAL TAXA - *Pelophylax kurtmuelleri*, *Mediodactylus kotschyi* cf. *skopjensis*, *Hemidactylus turcicus*, *Lacerta trilineata hansschweizeri*, *Podarcis erhardii*, *Ablepharus kitaibelii*, *Dolichophis caspius*, *Zamenis situla*.

FEEDING NOTES – Concerning the prey observed during the present study in nature see Tab. 3. In captivity, *Macrovipera schweizeri* of Sifnos also proved to be essentially theriophagous.

Macrovipera schweizeri and *Dolichophis caspius* have a substantially similar trophic spectrum. The ophidic species that can obtain homeothermic prey more easily and less dangerously (like most of those belonging to the family of Viperids) have an undoubted selective advantage in natural ecosystems compared to other coexisting species with a similar trophic niche, mainly if they find themselves operating in confined spaces, such as microinsular ones. On Sifnos, a situation of this kind could be reflected in the relationship between *Dolichophis caspius* and *Macrovipera schweizeri*, two sympatric and often syntopic species: *Macrovipera schweizeri* limits *Dolichophis caspius* and directs its diet towards alternative prey that are still suitable to its anatomical-functional characteristics (lizards). This would explain (at least in part) why a notoriously large species such as *Dolichophis caspius* (up to three meters in total length: WERNER, 1938) is represented on Sifnos by individuals that are no more than 150 cm long. In other words, the size of the coluber would be an expression of its trophic role. It would be plausible to believe that on Sifnos, that is, in a limited space (ca. 75 km^2), the overlap of the trophic niches has generated competitive interactions between the two species leading to a complementary division of space (see "Habitat" and Tab. 2) and food resources (Tab. 4) in the most congenial way for both, while also restricting them to relatively static roles. The competitive relationship would have resulted in a sort of spatial and trophic co-adaptation, without rigid adherence constraints. The interaction between the two species seems to be reflected not only in the size of the coluber, but also in that of the viper, which is usually

Table 4
Dolichophis caspius *(Sifnos)*/Macrovipera schweizeri *(Sifnos, Milos): comparative data on feeding in nature (the percentages refer to snakes with prey).*

	Dolichophis caspius	*Macrovipera schweizeri*	
	SIFNOS (April-May 1981; May 1985)		MILOS (May 1983)
	14/22 spec. with prey (63.6%)	6/16 spec. with prey (37.5%)	9/61 spec. with prey (14.7%)
LIZARDS	76.9%	-	42.8%
BIRDS	-	33.3%	42.8%
MICROMAMMALS	23.0%	66.6%	14.2%

larger than its congeners from Milos, as it is more strictly dependent on its different, more narrow, trophic role (homeothermic prey). On Milos, the lack of selective pressures due to the absence of competing snakes, could have induced the local population of *Macrovipera schweizeri* (*ecological release*: RICKLEFS, 1990), to have a trend towards a smaller size. We could be in the presence of a similar phenomenon to that occurred in *Elaphe quatuorlineata* on many Cyclades Islands (Mykonos, Ios, etc.) which led to the formation of the subspecies *muenteri*.

REPRODUCTION

Macrovipera schweizeri is oviparous. In the Viperidae family, the oviparous species are contained in the genera *Azemiops*, *Causus*, *Cerastes*, *Echis*, *Eristicophis*, *Daboia*, *Macrovipera*, *Pseudocerastes* and *Adenorhinos*.

On Milos, several ♀♀ were found with eggs in development (at least ten), some couples (♂♂ and ♀♀ paired) and, in at least two occasions, two ♂♂ together with one ♀. Both couples and groups of three individuals were in bodily, but not sexual, contact. On Sifnos, only three ♀♀ were encountered with well-developed eggs.

From 6th May (first day of research) to 15th May 1983 (ten days) *Macrovipera s. schweizeri* appeared in its sexual phase. During this period, it was extremely vagile (taking advantage of terrestrial thermal radiation and low winds, even in the early hours of the night), thus providing for a good genetic mixing, which, due to peculiar orographic conditions, perhaps cannot take place on Sifnos. A positive correlation has been noted between the end of this viper's sexual phase and the occurrence of particular astronomical events (new moon) and/or physical events (end of the strong Etesian winds).

Based on the data acquired from observation both in nature and in cap-

tivity, the reproductive cycle of *Macrovipera schweizeri* is summarized in the subsequent paragraph. For details regarding the number and characteristics of the eggs, the duration and average temperature of incubation, the birth and characteristics of the young, including their times of molting, see Tab. 5.

The reproductive ♀♀ would discard their *exuviae* between the end of June and the beginning of July (Tab. 5). The molting process, with various endocrine correlations, could be related to the occurrence of ovulation. In nature, therefore, independent of estrus times, egg maturation would last until about mid-June, when ovulation, and consequently fertilization, would occur. An intracorporeal incubation period would follow (initially characterized by the molting process), an eggshell would form, among other things, and at the end of this period (end of July) the eggs would be laid (Tab. 5).

In Colubrids, oviposition occurs about a month after ovulation (typically ovulation on 15th June, oviposition on 15th July: CATTANEO, 2017). At the time of spawning, the eggs of *Macrovipera schweizeri* have undergone about a month and a half of incubation in the womb (15 days more than reported for the Colubrids), and so it follows that the embryo is rather advanced (about 7 cm long). Another consequence is the relatively early hatching (45-50 days or less, depending on incubation temperatures). In Colubrids, for the same tem-

Table 5
Reproductive cycle of some female specimens of Macrovipera schweizeri *from the islands of Milos and Sifnos (western Cyclades). The molting indicates that ovulation has occured*. * = date of found.

	♀ Milos 10/05/1983*	♀ Milos 12/05/1983*	♀ Milos 21/05/1983*	♀ Sifnos 24/05/1985*
Molting	04/07/1983	29/06/1983	01/07/1983	02/07/1985
Egg deposition	31/07/1983	27/07/1983	27/07/1983	30/07/1985
Number of eggs	10	7	9	10
Average dimensions and egg color	35 x 25 mm; 10 g ivory with dark spots and star-shaped concretions			40.5 x 24.5 mm; 13.5 g ivory with blood red swirls and calcareous concretions
Incubation length	47-50 days	46 days	46-47 days	31 days
Average incubation temperature	26.5 °C	27.1 °C	26.6 °C	29.5 °C
Birth date of offspring	16-19/09/1983	11/09/1983	11-12/09/1983	30-31/08/1985
Number of offspring	5	6	7	4
Offspring size	18.7-21.1 cm; - g			21-22.5 cm; 7 g
Offspring molting	30/09-03/10/1983	25-28/09/1983	25-27/09/1983	10-11/09/1985
Interval birth-molt	13-15 days	14-17 days	14-15 days	10-12 days

peratures, there is an incubation period of 60-70 days or more. Delayed egg laying and a thinner egg shell compared to Colubrids show that we are in the presence of an adaptation to oviparity in a dynamic phase. The low altitudes, the particular latitude, as well as the hot-dry climate in which the Aegean populations of this viper live, represent suitable conditions for its maintenance.

The Cyclades viper appears to have a two-year reproductive cycle (NILSON *et al*., 1999). This seems to be due to its specialized feeding regime, which is based on migratory passerine birds; the abundance of this type of prey can vary from year to year and this can negatively affect the energy levels of the vipers, making them unable to accumulate the vitelline reserves necessary for an annual maturation of the eggs. As in all ophidic species with strong sexual dimorphism (♂♂ larger) copulation is preceded by ritual fighting between ♂♂ (WESTRIN, 1983). The sex ratio appears to be close to 1:1 (NILSON *et al*., 1999).

It should be noted that the eggs laid by the ♀♀ of Milos were not very large and contained less developed embryos than those laid by the ♀♀ of Sifnos (eggs opened immediately after being laid: see "Material and Methods") (Fig. 7); moreover, the egg shell was thinner than that of the eggs laid by the ♀♀ of Sifnos. The embryos from the eggs laid by the Sifnos ♀♀ (about 7 cm long) had a comparable developmental stage to the eggs that had been deposited for 15-20 days of some Colubrid species (*Elaphe quatuorlineata*, *Zamenis longissimus*).

It seems that vipers of the genus *Pseudocerastes* also lay eggs in an advanced stage of development, with hatching that would occur around the 30th day of incubation. However, the average incubation period for most oviparous vipers is 45-80 days (PHELPS, 2010).

Based on the fact that at the same site several *exuviae* of young specimens and egg shell remains were found, it is plausible to deduce the existence of common places of egg deposition where the newborns remain at least until the postnatal molt is complete (STUBBS, 1985). The use of the same site by several specimens of the same, and also of different species, is a frequent occurrence in Serpentes (KABISCH, 1978; GOLDER, 1985; CATTANEO, 2017).

MOLTING

Macrovipera schweizeri schweizeri

Twelve *exuviae* were found in nature from 7th to 20th May 1983. In captivity, the first seasonal change of the ♂♂ occurred at the end of March; which indicates that the Cyclades viper has the "*berus*" type of reproduction; in this type of reproduction sperm are mature in the spring, coincid-

Fig. 7 — Macrovipera schweizeri embryos from the islands of Milos (below) and Sifnos (above) extracted from freshly laid eggs. Note the more advanced stage of development of the Sifnos embryos (Photo A. Colasanti).

ing with the molting of the ♂♂, which therefore triggers the mating phase. Always in captivity, the second and last annual molt typically occurred in the summer (July).

Macrovipera schweizeri siphnensis

Two *exuviae* were found in the months of May, as well as a specimen in molting on 24th April 1981. In captivity the first seasonal change of the ♂♂

occurred between the end of March and the beginning of May, the second typically in July (see *Macrovipera s. schweizeri*).

TAXONOMIC NOTE

Macrovipera schweizeri of Sifnos Island differs from that of Milos Island for the peculiarities shown below.

– Trend for larger dimensions (see text and Tab. 1 and 3). This divergence reflects the different role that each viper population plays in their respective inhabited islands.

– Higher number of ventral scales (see text).

– Faded coloring. In the population of Milos the back design essentially consists of marks in the shape of subrectangular bars; in the population of Sifnos the bars are almost always faded to pale and blurred spots ("with faded or absent design", WETTSTEIN, 1953). While on Sifnos there are two quite distinct phenotypes (*grayish* and *ocher*) represented in equivalent quantities, in Milos there is only one phenotype (*grayish*) and a rare variant (*reddish*).

– On spawning, the (larger) eggs of the Sifnos ♀♀ have a thicker shell and more developed embryos.

The above-mentioned divergences support the need to validate the taxonomic distinction between the two populations of *Macrovipera schweizeri*: typical form in Milos and subspecies *siphnensis* on Sifnos. WERNER (1935) was the first to note the need for this distinction, declaring: "The snakes of Sifnos are to be understood as a particular race"; and by his own hand wrote on the specimen label of the Sifnos viper typus: "*Vipera lebetina siphnensis* Werner, typus, Siphnos, May 1934" (WETTSTEIN, 1953).

FINAL CONSIDERATIONS

Sifnos and the Milos archipelago have separated during the Pliocene, about 1.6 million years ago (DERMITZAKIS, 1989). This explains the diversity in the herpetological composition of the two islands, for example the presence of *Podarcis erhardii* on Sifnos and *Podarcis milensis* on Milos, or that of *Dolichophis caspius* on Sifnos and its absence on Milos. Based on purely biogeographical considerations, different colonization routes could be hypothesized. At least with regards to Sifnos, from the north (*Podarcis erhardii* and *Dolichophis caspius* are distributed in the more northern Cyclades Islands). Certainly, the presence of *Dolichophis caspius* on Sifnos must have led to the establishment of interactive balances with *Macrovipera schweizeri* that were

very different from those operating on Milos between the viper and the other components of reptile community there. The interaction with the coluber, at least, must have contributed to directing the viper towards a more homeothermic-prey-aimed diet, with consequences on size and habitat (see "Feeding notes"/*M. schweizeri siphnensis*). The different interspecies relationships, fueled by long isolation, are probably responsible for the morphological and functional divergences between the two populations. Similar considerations have led NILSON (2005) to argue that: "*M. schweizeri* and *M. siphnensis* could even be considered evolving species".

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Author's address – A. CATTANEO, Via Cola di Rienzo, 162 – 00192 Rome (I); email: augusto-cattaneo@hotmail.com