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In memory of Augusto Cesare Ambrosi (Casola in Lunigiana, 30.V.1919 – Firenze, 29.III.2003) eminent Tuscan historian and archaeologist, discoverer of the stelae-statues of Lunigiana and of *Speleomantes ambrosii.*

In memoria di Augusto Cesare Ambrosi (Casola in Lunigiana, 30.V.1919 – Firenze, 29.III.2003) eminente storico e archeologo toscano, scopritore delle statue-stele lunigianesi e dello *Speleomantes ambrosii.*

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A REVIEW OF SYSTEMATICS, TAXONOMY, GENETICS, BIOGEOGRAPHY AND NATURAL HISTORY OF THE GENUS *SPELEOMANTES* DUBOIS, 1984 (AMPHIBIA CAUDATA PLETHODONTIDAE)

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Abstract - A review of systematics, taxonomy, genetics, biogeography and natural history of the genus *Speleomantes* Dubois, 1984 (Amphibia Caudata Plethodontidae).
Outside the American continent the family Plethodontidae includes only the south Korean *Karsenia koreana* Min, Yang, Bonett, Vieltes, Brandon et Wake, 2005, and the European genus *Speleomantes* Dubois, 1984, whose systematics and taxonomy have rather recently been object of a morphologic and genetic review, which allowed to recognize 3 continental species [*S. strinatii* (Aellen, 1958); *S. ambrosii ambrosii* (Lanza, 1955) and *S. ambrosii bianchii* Lanza, Cimmaruta, Forti, Bullini et Nascetti, 2005; *S. italicus* (Dunn, 1923)] and 4 Sardinian ones [*S. flavus* (Stefani, 1969); *S. supramontis* (Lanza, Nascetti et Bullini, 1986); *S. imperialis imperialis* (Stefani, 1969) and *S. imperialis sarrabusensis* Lanza, Leo, Forti, Cimmaruta, Caputo et Nascetti, 2001); *S. genei* (Temminck et Schlegel, 1838) with subsp A and subsp. B]. Until recently the knowledge of *Speleomantes*' eco-ethology has been widely lacunose and specific research on this topic started only in the nineties. The present paper summarizes the current knowledge on the European plethodontid salamanders, genus *Speleomantes*. The authors deal with systematics, taxonomy, geographical and altitudinal distribution, genetics (two keys to species and subspecies are given: one based on morphology and geographical distribution, the other based on genetic characters), biogeography, ecology (habitats, herpetocoenosis, predators, parasites, food), ethology (feeding behaviour, activity, habitat use, displacement, antipredatory adaptations, communication), reproduction (sexual dimorphism, gametogenesis, mating behaviour, oviparity, ovoviviparity, parental cares), development, population dynamics, conservation (abundance, threats, conservation guidelines), as well as with research prospects. The quoted bibliography includes **564** titles.
Key words: Amphibia, Plethodontidae, *Speleomantes*, systematics, taxonomy, keys, genetics, biogeography, biology, conservation, France, Italy.

Riassunto: Revisione della sistematica, tassonomia, genetica, biogeografia e storia naturale del genere *Speleomantes* Dubois, 1984 (Amphibia Caudata Plethodontidae).
Al di fuori del continente americano la famiglia Plethodontidae conta solo la specie sud coreana *Karsenia koreana* Min, Yang, Bonett, Vieltes, Brandon et Wake, 2005, e il genere europeo *Speleomantes* Dubois, 1984, la cui sistematica e tassonomia, oggetto di una relativamente recente revisione su basi genetiche e morfologiche, ha portato a riconoscere 3 specie continentali [*S. strinatii* (Aellen, 1958); *S. ambrosii ambrosii* (Lanza, 1955) e *S. ambrosii bianchii* Lanza, Cimmaruta, Forti, Bullini et Nascetti, 2005; *S. italicus* (Dunn, 1923)] e 4 sarde [*S. flavus* (Stefani, 1969); *S. supramontis* (Lanza, Nascetti et Bullini, 1986); *S. imperialis imperialis* (Stefani, 1969) e *S. imperialis sarrabusensis* Lanza, Leo, Forti, Cimmaruta, Caputo et Nascetti, 2001); *S. genei* (Temminck et Schlegel, 1838) con le sottospecie A e B]. Sino a poco tempo fa le conoscenze sull'eco-etologia dello *Speleomantes* sono rimaste ampiamente lacunose e ricerche approfondite in proposito sono state avviate solo a partire dagli anni '90. Il presente contributo riassume le attuali conoscenze sui Pletodontidi europei del genere *Speleomantes*. Gli autori trattano sistematica, tassonomia, distribuzione geografica ed altitudinale, genetica (vengono fornite due chiavi per l'identificazione delle specie e sottospecie: una basata sulla morfologia e la distribuzione geografica, l'altra basata sulle caratteristiche genetiche), biogeografia, ecologia (habitat, erpetocenosi, predatóri, parassiti, dieta), etologia (comportamento predatòrio, attività, uso dell'habitat, spostamenti, adattamenti antipredatòrî, comunicazione), riproduzione (dimorfismo sessuale, gametogenesi, corteggiamento, oviparità, ovoviviparità e cure parentali), sviluppo, dinamica di popolazione, conservazione (abbondanza, minacce, linee-guida per la conservazione) e prospettive di ricerca. La bibliografia citata comprende **564** titoli.
Parole chiave: Amphibia, Plethodontidae, *Speleomantes*, sistematica, tassonomia, chiavi, genetica, biogeografia, biologia, conservazione, Francia, Italia.

CONTENTS

1. INTRODUCTION

Plethodontidae is the largest family of the order Urodela, including about 362 species in 28 genera, corresponding to nearly 70% of the 535 species of extant salamanders (cf. FROST, 2004; LANZA et al., 1995; MIN et al., 2005). The family is found mostly in the Americas from Nova Scotia and southwestern British Columbia to central Bolivia and eastern Brazil, through Central America and Colombia; it is also found with at least seven species in southwestern Europe (LANZA et al., 1998), and with the newly described *Karsenia koreana* Min, Yang, Bonett, Vieltes, Brandon et Wake in southern Korea (MIN et al., 2005) (see also 11 «Addendum»).

The present paper aims at summarizing and updating what has been extensively treated by LANZA et al. (1995) and LANZA (1999a-h) on the systematics, taxonomy, genetics, biogeography and biology of the European plethodontid salamanders, genus *Speleomantes* Dubois, 1984. Concerning morphology, the reader must refer to LANZA (1999a-h) and especially to LANZA et al. (1995) where the topic has been exhaustively treated.

2. MATERIALS AND METHODS

The morphological and genetic research is based respectively on the examination of about 3,000 and 600 specimens; ca. 1,100 of them were measured and/or radiographed and treated statistically.

Morphological methods and techniques for multilocus allozyme electrophoresis and RFLP (restriction fragment length polymorphism) of mtDNA have been more or less extensively described in NASCETTI et al. (1996), LANZA et al. (1995; 2005) and RUGGI et al. (2005).

The distributional maps are updated and redrawn versions of those published in LANZA et al. (1995), and LANZA (1999c-h); references have been quoted only for *Terrae typicae* and new localities: for others the reader may refer to the above mentioned papers. We did not consider the recent splitting of the former 4 Sardinian provinces (Cagliari, Nuoro, Oristano, Sassari) in the current 8 provinces. Until rather recently the European plethodontids were regarded as belonging to a single species or two species, one from France and continental Italy, another from Sardinia. MERTENS & WERMUTH, for example, treated them as a single species until 1960 and MATZ shared this opinion until 1976. The first paper on the occurrence of six species (actually seven ones) goes back to a few years ago (LANZA et al., 1982). The erroneous convinction that only one or two species occurred induced many authors to either consider it unnecessary to specify the origin of the material studied or to retain, as sufficient, indications «Italy» or «Sardinia». By doing so they automatically made it impossible, or extremely difficult, to assign their data to the right species. Luckily, in several instances it has been possible to identify certainly or almost certainly the species concerned by indirect methods: personal communications, subsequent specification by the same or, exceptionally, by another author, etc.; MERTENS (1923: 173, unnumbered fig.) and FRANZ (1934: 1083, fig. 910), for example, specify that SCHMALZ's (1916) figure refers to a specimen from Genoa. *When the species has been identified indirectly, the quotation is marked by the exponent* [i](= indirect): e.g.: SCHMALZ (1916[i]).

The bibliography includes **564** quoted titles, and the paper is updated to December 2006.

3. SYSTEMATICS TAXONOMY AND GENETICS

3.1 Systematics, taxonomy and geographical distribution.

The genus *Speleomantes* groups all the European members of the family and inhabits Sardinia, the province of Sassari excluded, southeastern France and northwestern and central Italy from the Ligurian Alps to the central Apennines as far south as the province of Pescara (Abruzzi) (LANZA et al., 1995) (see also Fig. 1).

The genus belongs to the subfamily Plethodontinae and the tribe Bolitoglossini, the only one able to colonize the Neotropical Region and Europe; all its members do not produce any aquatic larvae, apart from the recently described *Pseudoeurycea aquatica* Wake & Campbell, 2001 from the Mexican state of Oaxaca (WAKE & CAMPBELL, 2001). For further data on the family see LANZA et al. (1995: 16-24).

See LANZA et al. (1995: 21) also about the distinction between the European genus *Speleomantes* and *Hydromantoides*, a genus proposed by LANZA et VANNI (1981) for the American species and now considered junior synonym of *Hydromantes* due to a rather anomalous decision of the Commission on Zoological Nomenclature (ANONYMOUS, 1997). The above-mentioned Commission's Opinion (March 1997) is here defined «anomalous» since it should be more logic to consider as type species of the genus *Hydromantes* the European and first described species *Salamandra genei* Temminck et Schlegel, 1838, instead of the American *Spelerpes platycephalus* Camp, 1916. Also the research carried out by NASCETTI et al. (1996: 170), who found a huge genetic distance between the Californian «*Hydromantoides*» *shastae* and the Sardinian *Speleomantes genei* (D_{Nei} 3.38) and *Speleomantes imperialis* (D_{Nei} 3.92), appears to be consistent with the splitting of «*Hydromantes*» in two genera.

Furthermore *S. genei* is so different from all its congeners, from which it is separated by a large Nei's distance (NASCETTI et al., 1996), and in fact the species was recently assigned to the distinct subgenus *Atylodes* Gistel, 1868, by WAKE et al. (2005).

The cytomolecular studies by NARDI et al. (2000), according to which all the three repetitive DNA families found in the European plethodontids lack in the American *Hydromantes shastae* (see also § 3.4 «Genetics»), seem to lead up to the same conclusions. Further data on the painful nomenclatural sequence of

Geotriton, *Hydromantes, Hydromantoides*, and *Speleomantes* in LANZA et al. (1995: 21), LANZA (1999b: 81), and DUBOIS (1998: 179).

Last morphological and genetic studies of European plethodontids allowed to clear to a large extent the taxonomic status of the group. To date seven species of *Speleomantes* have been recognized: three continental ones and four inhabiting Sardinia. One mainland and two Sardinian species turned out to be polytipic, each with two subspecies (LANZA et al., 1986; LANZA et al., 1995; NASCETTI et al., 1996; FORTI et al., 1998; CIMMARUTA et al., 2002; LANZA et al., 2001; LANZA et al., 2005). These taxa are listed hereunder in alphabetic order, together with their ranges [cf. also BOLOGNA & SALVIDIO (2006), LANZA & SALVIDIO (2006), and LANZA et al. (2006; 2006a-d)].

Speleomantes ambrosii (Lanza, 1955): eastern Liguria and northeastern Tuscany, from the extreme southwestern end of La Spezia province (close to the Passo del Bracco, 44°15'N-09°30'E) and southern province of La Spezia to the southern Massa-Carrara province (Map. 1).

Speleomantes ambrosii ambrosii (Lanza, 1955): Ligurian range of the species West of La Magra River. In eastern Liguria the taxa is parapatric [not «sympatric» as stated by MAZZOTTI et al. (1999: 36) and by BRACCHI & POGGI (2006: 159)] with *S. strinatii* (cf. FORTI et al., 1998; CIMMARUTA et al., 1999).

Speleomantes ambrosii bianchii Lanza, Cimmaruta, Forti, Bullini et Nascetti, 2005: Tuscan range of the species East of La Magra River and, presumably, Ligurian areas (province of La Spezia) East of this watercourse.

Speleomantes flavus (Stefani, 1969): northeastern Sardinia (province of Nuoro), on the Monte Albo chain and its hilly extension between Siniscola and the Posada River, at least as far as 3-4 km as the crow flies N of Siniscola (cave Pozzo II di Posada, opened in an unspecified spot of the Mt Sasia) (Map 3).

Speleomantes genei (Temminck et Schlegel, 1838): southwestern Sardinia (province of Cagliari), in the territory known as Sulcis-Iglesiente (Map 6).

Speleomantes genei subsp. A: same range of the species, that of the subsp. B excluded.

Speleomantes genei subsp. B: municipality of Carbonia [northern slope of Mt Tasua (39°13' N - 08°33' E), ca. 4 km as the crow flies NE of Barbusi (39°13' N - 08°31' E); left and right sides of the stream Canale Peddori (ca. 39°12'07" N - 08°31'11" E), about 1 km as the crow flies ENE of Barbusi; hill Serra de Mesu (39°11'32" N - 08°31'19" E), near Carbonia, 1.5 km as the crow flies SE of Barbusi; locality Su Niu 'e s'Achili (ca. 39°10'17" N - 08°32'12" E), in the Rio Cannas Valley]. *This taxon could turn out to be a full species.*

Speleomantes imperialis (Stefani, 1969): central, central eastern and southeastern Sardinia, in the provinces of Nuoro, Oristano and Cagliari, roughly between 40° N (localities close to the lago Omodeo, Oristano) and 39°12' N [Castiadas, Minniminni Forest (39°12'37" N; Monte dei Sette Fratelli's group), Cagliari], westwards as far as 08°52' E [tunnel in the Santa Chiara dam, on Lago Omodeo, ca. 08°52'10" E, Oristano; MUCEDDA, 2005], 08°55' E [municipality of Genoni, on the Giara di Gèsturi, close to the pond Paùli Maiori (39°47’ N - 08°55’ E), Oristano] and 08°57’ E [municipality of Samugheo, Castello di Medusa (39°53’ N - 08°57’ E), Oristano], eastwards to about the coast (Map 5).

Speleomantes imperialis imperialis (Stefani, 1969): same range of the species, that of the subsp. *sarrabusensis* excluded.

Speleomantes imperialis sarrabusensis Lanza, Leo, Cimmaruta, Caputo & Nascetti, 2001: Monte dei Sette Fratelli, in the territory known as Sarrabus. *This taxon could turn out to be a full species.*

Speleomantes italicus (Dunn, 1923): northern (Appennino Tosco-Emiliano, Apuan Alps partly included) and central Apennines (Appennino Umbro-Marchigiano; Appennino Abruzzese) between 44°27’ N [Valestra (44°27’ N - 10°36’ E), province of Reggio Emilia] or possibly 44°38’ N [Mt Prinzera (44°38’ N - 10°06’ E), province of Parma] and 42°15’ N [Mount La Queglia, near Pescosansonesco (42°14’ N-13°52 E), province of Pescara], in the Republic of San Marino and the provinces of Parma (? see above), Reggio Emilia, Lucca, Modena, Pistoia, Ravenna, Forlì-Cesena, Florence, Prato, Arezzo, Pesaro-Urbino, Perugia, Ancona, Macerata, Ascoli Piceno, Teramo and Pescara; westwards to about the Tyrrhenian coast of the province of Lucca [environs of Seravezza, ca. 44°00’ N-10°16’ E]; eastwards to the environs of Pescosansonesco (see above) (Map 2).

Speleomantes strinatii (Aellen, 1958): southeastern France [easternmost regions of the Departement des Alpes-de-Haute-Provence (formerly Basses-Alpes); Departement des Alpes-Maritimes] and northwestern Italy from the Ligurian Alps to the Appennino Settentrionale (Appennino Ligure and extreme northwestern Appennino Tosco-Emiliano), in the provinces of Cuneo (southern part), Imperia, Savona, Alessandria (southern part), Genoa, La Spezia (north-western part), Massa-Carrara (northwestern part), Pavia (southern part), Piacenza and Parma; westwards to the Gorges de Daluis (ca. 44°04’ N - 06°49’ E) and Saint-Benoit (near Annot, ca. 43°58’ N-06°40’ E); eastwards to the environs of Morfasso (ca. 44°43’ N - 09°42’ E; province of Piacenza), Rocca di Bardi (44°38’ N - 09°44’ E; province of Parma), and environs of Codolo (ca. 44°22’ N - 09°50’ E; extreme northwestern part of the province of Massa-Carrara) (Map 1). The statement by BRACCHI & POGGI (2006) according to which the species inhabits Mount Prinzera (province of Parma) is wrong. Actually it is not sure if the only one known specimen from that locality is to be ascribed to *S. strinatii* rather than to *S. italicus* (cf. LANZA et al., 1995; LANZA, 1999c).

Speleomantes supramontis (Lanza, Nascetti et Bullini, 1986): territories of the central eastern Sardinia around the Gulf of Orosei, roughly between the sea, the Rio di Oliena-Cedrino Valley and 40° of latitude N, in the province of Nuoro (Map 4).

The genus has been up to now introduced and has become successfully established in three localities more or less far from its natural range, as well as in a zone of parapatry (see also Fig. 1).

Before the discovery on the Apuan Alps of a hybrid zone between *S. ambrosii* and *S. italicus*, Lanza attempted to obtain in nature their hybridization by introducing in a Monte Maggio's cave (province of Siena), on 1983, 13 adult ♂♂, 14 ad. ♀♀ and 3 subadults of *S. italicus* from Pian di Mugnone (near Fiesole, Florence) and 16 ad. ♂♂ and 14 ad. ♀♀ of *S. ambrosii ambrosii* from the environs of Pegazzano, near La Spezia; more information in LANZA et al. (1995), LANZA (1999c: 102), and especially FORTI et al. (2002b, 2005b).

Prof. J.-P. Durand (personal comm., 12.IV.1996, published by LANZA, 1999c: 105; see also LANZA, 1997, map of p. 38) introduced specimens of *S. strinatii* from the French Maritime Alps and the province of Genoa in a secret cave of the French Pyrenees (in the Salat Valley, Ariège, according to SALVIDIO, 2003); however, we think that hereafter should be advisable to check genetically these animals, since Durand presumably used for his studies also specimens of *S. ambrosii* and/or *S. italicus*.

At the end of 70s some individuals (at least a pair) of *S. strinatii* from the Grotta di Bossea (cadastral No. 108 Pi/CN, 44°14'28"N-07°50'21"E, municipality of Frabosa Soprana, provincia di Cuneo, 836 m a.s.l.) were introduced by unknown speleologists in the Grotta Regina del Carso di Cotici (cadastral No. 4760 VG/GO; municipality of Savogna d'Isonzo, province of Gorizia, 196 m

Fig. 1. Range of the genus *Speleomantes* (dark grey). The boundaries of Italian regions and neighbouring countries are represented. The arrows indicate the sites in which the genus has been introduced and naturalized outside its natural range, except for that on Pyrenees, that is out of the geografical range covered by the map.

a.s.l.), where they are still present (N. Bressi, A. Dall'Asta & L. Lapini, pers. comm., XI.2005) and, according to us, definitely naturalized.

To investigate spatial distribution and competition between parapatric sibling species, a field experiment was started in summer 1991 by FORTI et al. (1997) and CIMMARUTA et al. (1999) making samples of *S. ambrosii ambrosii* and *S. strinatii* artificially syntopic in the wild. One hundred and ten adults of native *S. strinatii* inhabiting a cave on the Mount Pietra di Vasca (44°15'35" N - 09°33'23" E, province of Genoa) were removed and replaced with 51 males and 59 females of *S. ambrosii* adults from the environs of Cassana (44°12'37" N - 09°51'27" E, province of La Spezia).

Finally, according to BASSI & FABBRI (2006), in the 60s some specimens of *S. italicus* from the cave «Grotta Grande di Giugnola» (northern Apennines, province of Bologna) has been introduced by speleologists at the entrance of the cave «Buco del Noce» (Brisighella, province of Ravenna), perhaps without naturalization.

3.2 Altitudinal distribution.

As a whole, the genus *Speleomantes* appears to be euryzonal, ranging from almost sea level up to elevations exceeding 2000 meters (LANZA et al., 1995).

Speleomantes strinatii is the most euryzonal species of the genus, as it has been collected from almost sea level (m 20 at Imperia: BOLOGNA & BONZANO, 1975) to over 2000 metres, since BONZANO (1984), in August 1984, found 2 juveniles in the cave «Grotta Sing-Sing», at about 2280 m (locality Gias dei Puffi; group of the Pianballaur; Ligurian Alps) and sighted the species in another cave, designated as «S6», in the same area, at about 2290 metres. According to BOLOGNA & BONZANO (1975; see also BONZANO, 1984), the late, skilled speleologist L. Ramella sighted some very young specimens in the abyss Abisso dei Caprosci at 2432 m on Mount Mongioie, ca. 30 km as the crow flies SE of Cuneo (southern Piedmont); howewer BONZANO (1977) failed to find the species either in this or in other caves of that area (LANZA et al., 1995).

Also *Speleomantes ambrosii* is rather euryzonal as it is known to occur from close to sea level (between Fezzano, 26 m, and Portovenere, 37 m, province of La Spezia, according to SOCHUREK, 1952, who does not specify the altitude; cave Grotta della Madonna, 30 m, near Rebocco, La Spezia) up to about 1730 m on the southern slope of Monte Tambura, in the cave Buca Tamburello, near Resceto, municipality and province of Massa-Carrara (CALANDRI, 1980; BONZANO et al., 1983; LANZA et al., 1995).

Speleomantes italicus is a rather euryzonal species such as *S. ambrosii*, so far known as inhabiting from 80 m in Garfagnana (cave Grotta della Cartiera, near Anchiano, on the left side of the Serchio R., municipality of Borgo a Mozzano, province of Lucca) up to 1598 m on the Apuan Alps (cave Buca dei Gracchi di Monte Corchia, municipality of Stazzema, province of Lucca) (LANZA et al., 1995).

Speleomantes flavus has been collected between 40 (cave Grotta di Cane

Gortoe, in the town of Siniscola) and 1040 m (cave Conca 'e Crapa, in the southern end of the Monte Albo chain) (LANZA et al., 1995).

S. supramontis has been found between 106 m (on the bottom of the Voragine del Golgo) and ca. 1360 m (in a cave of the Supramonte di Orgosolo) (LANZA et al., 1995).

S. imperialis ranges from 7 m (cave Grutta de Giuanniccu Mene, at the foot of the Mount Castello di Quirra, province of Cagliari) and 1170 m [cave Buca del Diavolo (=Su Stampu), locality Gea su Fossu, on the monte Tonneri, municipality of Seui, province of Nuoro] (LANZA et al., 1995).

S. genei has been collected between 8 m (cave and mine gallery Grotta di Gutturu Pala, locality Pubusino, municipality of Fluminimaggiore, province of Cagliari] and 600 m (cave Grotta delle Mura, on the northern slope of a nameless mountain, 646 m high, on the western slope of Punta Sebera, on the right side of the Canale Scioppadroxiu, between Santadi and Pula, municipality of Teulada, province of Cagliari), but probably it also inhabits higher localities (LANZA et al., 1995) since the highest mountains of its range reach 1236 m (Mt Linas; Iglesiente) and 1116 (Mt is Caràvius; Sulcis).

3.3 Morphological-geographical key to species and subspecies (subadults and adults).

As stated by NASCETTI et al. (1996) «Plethodontid salamanders have provided instances of high genetic divergence associated with low morphological differentiation (WAKE, 1981; BULLINI, 1983; WAKE et al., 1983; WAKE & LARSON, 1987). Accordingly, morphological characters used for species recognition can be of poor diagnostic value, and sometimes morphological diagnoses became possible only after isozyme analysis […]. Recent revisions of plethodontid taxonomy in the light of molecular data have therefore generated long lists of both synonymies and new species in many genera […] see also WAKE, 1981 and LARSON & CHIPPINDALE, 1993 for review». As pointed out by LANZA et al. (1995), another difficulty for a correct identification arises from the frequent occurrence of allometric growth (see f.i. LANZA, 1991); thus, while the adults of the three «giant» eastern Sardinian species (*S. flavus*, *S. supramontis*, *S. imperialis*) have a significantly larger foot than the adults of the «normal» species (*H. genei*, *H. strinatii*, *H. ambrosii* and *H. italicus*), this difference attenuates or disappears when animals of the same size are compared (i.e. halfgrown specimens of the «giant» species with fully developed specimens of the «normal» ones).

By making the necessary changes, the same applies to some meristic characters that, such as theet, are ontogenetically variable in salamanders; the eastern «giants», for instance, have a statistically higher number of premaxillary, prevomerine, maxillary and mandibular teeth than *H. genei*, *H. strinatii*, *H. ambrosii*, and *H. italicus* in both sexes, but this does not occur when fully developed specimens of the latter ones are compared with halfgrown «giants» of similar size. In practice, preserved specimens from unknown localities, especially if faded, are often unlikely to be correctly identified, even taking their osteology into consideration. On the other hand, identification *ex patria* is obvious for allopatric taxa (*S. genei* versus *S. imperialis*; *S. flavus* versus *S. supramontis*; *S. imperialis imperialis* versus *S. imperialis sarrabusensis*) or for the specimens of parapatric species collected outside the zone of parapatry (*S. strinatii* versus *S. ambrosii*, *S. ambrosii* versus *S. italicus*, *S. supramontis* versus *S. imperialis*). However, the parapatric taxa may be sometimes identified with an acceptable degree of accuracy also where their ranges meet, since, at least along some tracts of the border, they may show morphological and/or chromatic differential characters [see CIMMARUTA (1993) for *S. ambrosii ambrosii* versus *S. strinatii*, and CIMMARUTA et al. (2002), LANZA et al. (2005) for *S. ambrosii ambrosii* versus *S. ambrosii bianchii*, and the next key].

Consequently, as in the case e.g. of the genus *Podarcis* Wagler, 1830, the key must be used with extreme caution.

1 - From southeastern France to central Italy (province of Pescara, Abruzzo) along the Ligurian Alps and the northern and central Apennines (Fig. 1; Maps 1-2); belly usually on the whole dark as the light markings generally do not overwhelm the dark ground colour; trunk dorsal markings sometimes reddish (Figs 8-14); dorsal and loreal surfaces of the snout almost always merging into each other rather abruptly, thus forming a somewhat blunt *canthus rostralis*; septomaxilla present or absent; tongue usually shorter, the ratio snout-vent length[1]: snout tip-epibranchial tip[2] averaging more than 2 (1.83-2.78); tibial dorsomedial crest sometimes ending proximally in a spur; digits not enlarged to slightly enlarged at tips, their apices sometimes bluntly pointed but usually more or less obtusely truncate; bone phalanx of the first digit feebly to moderately enlarged, truncate conic or conic at tip; total length not exceeding 13 cm; no scent emission as consequence of handling; (heteromorphic sex chromosomes present)…………………………………………..….. **2**

- Sardinia (Fig. 1; Maps 3-6); belly on the whole light (excluding the transparence through the skin of some dark abdominal organs and contents) with only a few isolated melanophores or dark dots, spots or small blotches; usually no reddish trunk dorsal markings; dorsal and loreal surfaces of the snout almost always gently merging into each other without forming a *canthus rostralis* (slightly indicated only in some specimens, especially of *S. genei*); septomaxilla present or absent; tongue usually longer, the ratio snout-vent length[1]: snout tip-epibranchial tip[2] averaging 2 or less (1.58-2.23); tibial dorsomedial crest always ending proximally in a spur; digits always more or less strongly truncate at tips; bone phalanx of the first digit always more or less strongly enlarged at tip; total length sometimes exceeding 13 cm; a strong scent emission sometimes present as consequence of handling; (heteromorphic sex chromosomes present or absent) ………………………………………………………………………..…..…..…..… **4**

2 – Southeastern France, Liguria, southern Piedmont, southern Lombardy, Emilia-Romagna [eastwards as far as to the environs of Morfasso (ca. 44°43’ N - 09°42’ E; province of Piacenza) and Rocca di Bardi (44°38’ N - 09°44’ E;

province of Parma)], and northwestern Tuscany (province of Massa-Carrara) (Map 1); dorsal colouration and pattern extremely variable individually and/or geographically; septomaxilla always present and rather well-developed (n=16); pars frontalis of the premaxilla always reaching the frontal (n=15); dorsomedial surface of the tibia almost always with a crest ending proximally in a spur (n=17), lacking or feebly developed only in specimens of *S. ambrosii bianchii* whose genome is introgressed by genes of *S. italicus* (n=15); bone phalanx of the first finger usually feebly to moderately enlarged at tip, sometimes truncate conic, in a few cases conic …………………………………………………..…. **3**

- Northern (Appennino Tosco-Emiliano, Apuan Alps partly included) and central Apennines (Appennino Umbro-Marchigiano; Appennino Abruzzese) in the Republic of San Marino and the provinces of Parma (? perhaps on the Mt Prinzera, 44°38'N-10°06'E), Reggio Emilia, Lucca, Modena, Pistoia, Ravenna, Forlì-Cesena, Florence, Prato, Arezzo, Pesaro-Urbino, Perugia, Ancona, Macerata, Ascoli Piceno, Teramo and Pescara (Map 2); a hybrid zone, commanding at least a part of the Apuan Alps watershed between the provinces of Massa-Carrara and Lucca, is inhabited by populations whose genome is more or less introgressed by genes of *S. ambrosii bianchii*; dorsal colouration and pattern extremely variable within the hybrid zone as well as in the northernmost section of the range, whereas they are usually rather monotonous from the provinces of Bologna, Pistoia, Prato and Florence southwards (dorsal dark ground colour with reddish or yellowish ochre blotches or marblings); septomaxilla absent (50%) or poorly developed and sometimes (20%) on one side only (n= 11); *pars frontalis* of the premaxilla reaching the frontal in about 40% of the specimens (n= 10); dorsalmedial surface of the tibia with a low crest and no spur (n= 20) [spur sometimes feebly or normally developed in the specimens whose genome is more or less introgressed by genes of *S. ambrosii bianchi* (n=15)]; bone phalanx of the first finger usually conic, sometimes feebly to moderately enlarged at tip …………..……….. …………..……..…..…..….... ***Speleomantes italicus***

3 - Southeastern France and northwestern Italy from the Ligurian Alps to the Northern Apennines (Appennino Ligure and extreme northwestern Appennino Tosco-Emiliano), in the provinces of Cuneo, Imperia, Savona, Alessandria, Genoa, La Spezia, Massa-Carrara, Pavia, Piacenza and Parma; eastwards to the environs of Morfasso (ca. 44°43' N - 09°42' E; province of Piacenza), Rocca di Bardi (44°38' N - 09°44' E; province of Parma), and environs of Codolo (ca. 44°22' N - 09°50' E; extreme northwestern part of the province of Massa-Carrara) (Map 1); dorsal pattern and colouration extremely variable both intra- and interpopulationally (Figs 8-9), but usually differing from that of the parapatric *S. ambrosii* at least in the Passo del Bracco area, where the dark dorsal ground colour is overwhelmed by small ochreous yellow spots scattered all over the dorsum (see below at *S. ambrosii*); in the same area most specimens have a more or less obtusely pointed snout (almost always obtusely truncate in *S. ambrosii ambrosii*) ……………………….…………………….***Speleomantes strinatii***

- Eastern Liguria and northwestern Tuscany, from the extreme southwestern end of the province of La Spezia (close to the Passo del Bracco, 44°15'N - 09°30'E) to the southern province of Massa-Carrara (Map 1); a hybrid zone, commanding at least a part of the Apuan Alps watershed between the provinces of Massa-Carrara and Lucca, is inhabited by populations whose genome is more or less introgressed by genes of *S. italicus*; dorsal parts with the dark ground colour more or less reduced by ochreous yellow (occasionally ochreous reddish) spots, patches or marblings, but sometimes completely spottless or almost so; two light, usually ochreous yellow, often more or less discontinuous dorsolateral stripes occur in many specimens and are especially sharp in the zone of La Spezia (Figs 10-12); an albino ♀ of *S. a. ambrosii*, the only one case of complete albinism known for the genus, was found in a cave of La Spezia province (CORSINI et al., 2002; FERRETTI et al., 2002) ……………………………………*Speleomantes ambrosii*

a **-** West of La Magra River (Liguria) …………………………………… ……………………………………………*Speleomantes ambrosii ambrosii*

b **-**East of La Magra River (Tuscany) and presumably, also in the Ligurian areas East of the same river …………………………………… ……………………………………………***Speleomantes ambrosii bianchii***

4 – Southwestern Sardinia (Iglesiente and Sulcis) (Map 6); total length not exceeding 13 cm; a slight *canthus rostralis* sometimes present; septomaxilla always present and well developed (n= 5) according to LANZA et al. (1995), but not found (n= 3) by GREVEN et al. (2003); tongue usually shorter, the ratio snout-vent length[1]: snout tip-epibranchial tip[2] averaging more than 1.9 (1.81-2.23); foot usually smaller [snout-vent length[1]: foot length[3] ♂♂7.01(8.00)9.15, ♀♀ 6.78(8.08)9.78]; mental gland usually smaller [snout-vent length[1]: mental gland width[4] 12.56(16.82)25.45; snout-vent length[1]: mental gland length[5] 18.00(23.69)33.48]; number of visible maxillary and mandibular teeth[5] usually lower [maxillary teeth (per side) ♂♂ 14(20.90)27, ♀♀ 17(25.02)33; mandibular teeth (per side) ♂♂ 17 (25.75) 34, ♀♀ 22 (29.89)38]; always 13 trunk vertebrae (n=119); no scent emission as consequence of handling; (no heteromorphic sex chromosomes) ………………………………………………… ***Speleomantes genei***

a **-** Same range of the species, range of the subsp. B excluded ………………………………………………***Speleomantes genei*** subsp. **A**

b **-** Municipality of Carbonia [northern slope of Mt Tasua (39°13'N-08°33'E), ca. 4 km as the crow flies NE of Barbusi (39°13'N-08°31'E); left and right sides of the stream Canale Peddori (ca. 39°12'07"N-08°31'11"E), about 1 km as the crow flies ENE of Barbusi; hill Serra de Mesu (39°11'32"N-08°31'19"E), near Carbonia, 1.5 km SE of Barbusi; locality Su Niu 'e s'Achili (ca. 39°10'17"N-08°32'12"E), in the Rio Cannas Valley] …………………………… ***Speleomantes genei*** subsp. **B**

- Central and eastern Sardinia; total length sometimes exceeding 13 cm; *canthus rostralis* absent or, rarely, feebly developed; septomaxilla present or absent; tongue usually longer, the ratio snout-vent length[1]: snout tip-epibranchial tip[2] averaging less than 1.9

(1.58-2.17); foot usually larger [snout-vent length[1]: foot length[3] in *S. flavus* ♂♂ 6.51(6.78)7.33, ♀♀ 6.09(6.85)7.63; in *S. supramontis* ♂♂ 6.11(6.75)7.29, ♀♀ 5.50(6.87)8.37; in *S. imperialis* ♀♀ 6.02(7.12)7.85, ♂♂ 6.48 (7.20)7.70]; mental gland usually larger [snout-vent length[1]: mental gland width[4] in *S. flavus* 11.51(13.25)16.00; in *S. supramontis* 11.69(14.34)18.05; in *S. imperialis* 10.62(12.83)18.93; snout-vent length[1]: mental gland length[5] in *S. flavus* 16.25(19.09)24.54; in *S. supramontis* 16.43(20.71)26.50; in *S. imperialis* 15.90(20.18)28.69]; number of visible maxillary and mandibular teeth[6] usually higher [maxillary teeth (per side) in *S. flavus* ♂♂ 22(26.62)31, ♀♀ 29(35.50)40; in *S. supramontis* ♂♂ 23(28.23)35, ♀♀ 23(31.66)38; in *S. imperialis* ♂♂ 18(28.15)35, ♀♀ 24(33.09)41; mandibular teeth (per side) in *S. flavus* ♂♂ 28(35.09)43, ♀♀ 33(41.82)48; in *S. supramontis* ♂♂ 30(37.82)45, ♀♀ 32(40.45)49; in *S. imperialis* ♂♂ 26(39.71)47, ♀♀ 33(43.44)50]; almost always 13 trunk vertebrae, sometimes 12 or 14 (n = 228); a strong scent emission sometimes present as consequence of handling (heteromorphic sex chromosomes present) …………………………………………………...…...………...……………………... **5**

5 - Monte Albo and hills between Siniscola and Posada River (northeastern Sardinia) (Map 3); anterior palatal area corresponding to the openings of the intermaxillary gland usually very large and extensively hollow; septomaxilla (n= 6) always present and well developed; no scent emission as consequence of handling ……………………………………………………..…………... ***Speleomantes flavus***

- Central and eastern Sardinia, south of the Rio di Oliena-Cedrino Valley; anterior palatal area corresponding to the openings of the intermaxillary gland usually smaller and flat, with a pit only where the ducts open; a strong scent emission sometimes present as consequence of handling..………..……………………….. **6**

6 - Central eastern Sardinia around the Gulf of Orosei, roughly between the Rio di Oliena-Cedrino Valley and 40° of latitude N (Map 4); no scent emission as consequence of handling; trunk sometimes very stout, especially in the females (Fig. 3); septomaxilla (n= 8) always present and well developed; tongue usually longer [snout-vent length[1]: snout tip-epibranchial tip[2] ♂♂ 1.67(1.77)1.91, ♂♂ 1.58(1.67)1.78; in *S. imperialis imperialis* ♀♀ 1.72(1.89)2.17, ♂♂ 1.67(1.87)2.15; in *S. imperialis sarrabusensis* ♂♂ 1.78(1.89)1.99, ♀♀ 1.68(1.82)1.96]; foot usually larger [snout-vent length[1]: foot length[3] ♂♂ 6.11(6.75)7.29, ♀♀ 5.50(6.87)8.37; in *S. imperialis imperialis* ♂♂ 6.02(7.12)7.85, ♀♀ 6.48(7.20)7.70; in *S. imperialis sarrabusensis* ♂♂ 7.29(7.65)8.06, ♀♀ 6.98(7.74)8.62] ………….. ***S. supramontis***

- Central, central eastern and southeastern Sardinia roughly between 40°05'N and 39°12'N, westwards as far as 08°52'E and 08°57'E, eastwards to about the coast (Map 5); a strong scent emission as consequence of handling usually occurring in the nominate subspecies; septomaxilla (n= 9) sometimes absent mono- or bilaterally (44.44%); tongue usually shorter, trunk slender, foot smaller (comparative data under *S. supramontis*) ……………….…………………***Speleomantes imperialis***

a* -** Central, central eastern and southeastern Sardinia, in the provinces of Nuoro, Oristano and Cagliari, roughly between 40°10'N (municipality of Sèdilo, Oristano) and 39°29'N (municipality of Villasalto, Cagliari); total length up to 133 (♂) and 150 (♀) mm; dorsal pattern and colouration moderately variable: ground colour dark brown to blackish with ochreous yellow, yellowish or greenish occasionally reddish blotches, marblings or roundish spots overwhelming ("*imperialis*"-type, in the southern part of the range) or not ("*funereus*"-type, in the northern part of the range) the ground colour (Figs 18-20); a strong scent emission as consequence of handling, lacking only in the northernmost populations inhabiting the localities close to the Lake Omodeo ………………………………………….. ***Speleomantes imperialis imperialis

b – Extreme southeastern Sardinia, roughly between 39°15'N and 39°12'N, Monte dei Sette Fratelli's group, in the territory known as Sarrabus (province of Cagliari); total length up to 111 (♂) and 123 (♀) mm; dorsal pattern of the "*funereus*"-type (of the "*imperialis*-type in the closest populations of the nominate form) (Figs 20-21); scentless (the occasional emission of a light scent to be checked) ……………...………………………***Speleomantes imperialis sarrabusensis***

[1]*Snout-vent length*: from the snout tip to the anterior end of the vent. [2]*Snout tip-epibranchial tip*: distance between the tip of the snout and the posterior end of the epibranchial sheat with the tongue at rest position (the end of the sheat exposed by dissection). [3]*Foot length*: from the inner border of the foot to the tip of the 4th toe, the latter at 90° against the inner margin of the foot (cf. LANZA et al., 1995, Fig. 2 hereunder). [4]*Mental gland width*: its greatest width. [5]*Mental gland length*: from the anterior midpoint, just behind the mandibular symphysis, to the midpoint of the posterior border (when the latter is concave, to the midpoint of the tangent touching its posteriormost points. [6]*Teeth number (approximate)*: tooth counts are based on the visible teeth, i.e. on the functional, ankylosed teeth, as well as on those not yet functional but almost piercing the mucous membrane and about to replace the lost ones (on one side; of course teeth lacking due to traumatism were also counted as present).

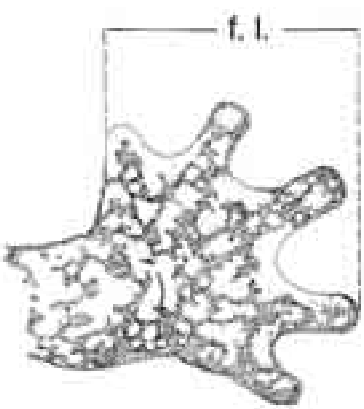

Fig. 2. Right foot of a *S. italicus* from the cave «Buca delle Fate di Coreglia Antelminelli», cadastral number 141 T/LU, 44°02'45''N – 10°31'26'' E, 270 m a.s.l., Coreglia Antelminelli, Lucca.
f. l. = foot length (from LANZA et al., 1995).

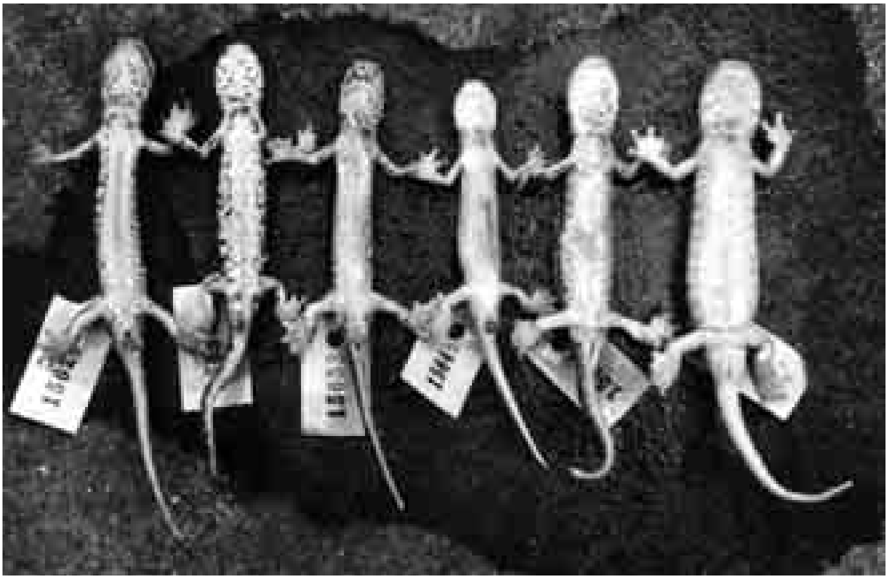

Fig. 3. *S. supramontis.* Left to right: ♂ (holotype), 3 ♂♂ (paratypes) and 2 ♀♀ (paratypes), see Map 4, loc. A. Note the light belly colour, typical of the Sardinian species (cf. Fig. 11). Photo by Marco Borri.

3.4 Genetics

Plethodontid salamanders frequently show high genetic divergence among taxa along with a scarce morphological differentiation (WAKE et al., 1983a; WAKE & LARSON, 1987). Fossils of *Plethodon*, a still living genus, are known from Oligocene (TIHEN & WAKE, 1981); they are impressively similar in osteology to the extant species.

A relevant feature of *Speleomantes* species is their large genome, about 76 pg per haploid nucleus (BATISTONI et al., 1991; SESSION & KEZER, 1991), among the largest in animals. Once again, plethodontids show peculiar genetic features, with congeneric species having similar morphology and kariology but multiple amount of DNA, as for example *Plethodon* species (MACGREGOR, 1982; MIZUNO & MACGREGOR, 1974). It is therefore not surprising that plethodontid salamanders, and particularly *Speleomantes*, have been deeply studied using genetic approaches both for taxonomic and evolutionary purposes.

3.4.1 Diagnostic loci and biochemical key

The most extensive taxonomic study to date carried out on the whole genus is reported in NASCETTI et al. (1996), where 33 putative gene loci were scored by means of allozyme electrophoresis in 32 samples belonging from the entire genus range. Only one locus (*Gpi*, E.C. 5.3.1.9) did not show diagnostic power among taxa, being the other 32 able to discriminate one or more pair of taxa: *a-Gpdh* (1.1.1.8), *Ldh-1, Ldh-2* (1.1.1.27), *Hbdh* (1.1.1.30), *Mdh-1, Mdh-2* (1.1.1.37), *Mdhp-1, Mdhp-2* (1.1.1.40), *Idh-1, Idh-2* (1.1.1.42), *6-Pgdh* (1.1.1.44),

Table 1 - Diagnostic loci at 99% level between *Speleomantes* taxa.

Taxon	*S. italicus*	*S. a. bianchii*	*S. a. ambrosii*	*S. strinatii*	*S. flavus*	*S. supramontis*	*S. i. imperialis*	*S. i. sarrabusensis*	*S. genei A*
S. ambrosii bianchii	*α-Gpdh, Ldh1, Ldh2, Mdhp2, NADH, Ck, Pgm2, PepC, Ca3*	----							
S. ambrosii ambrosii	*α–Gpdh, Ldh1, Ldh2, Mdhp2, Ca3, Idh2, Sod1, Pgm2, Ck, PepC, Ada1*	*Idh2, NADH, Sod1, Ada1*	----						
S. strinatii	*α–Gpdh, Ldh1, Ldh2, Mdh2, Ca3, NADH, Ck, Ada1*	*Mdh2, Mdhp2, Pgm2, PepD, Ada1*	*Mdh2, Mdhp2, Idh2, NADH, Sod1, Pgm2, PepD*	----					
S. flavus	*Ldh1, Ldh2, Hbdh, Idh2, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Adk, PepC, PepD Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Hbdh, Mdhp2, Idh2, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Adk, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Hbdh, Mdhp2, Idh2, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Adk, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Hbdh, Mdh2, Idh2, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Adk, PepC, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	----				

Table 1. (Following)

Taxon	*S. italicus*	*S. a. bianchii*	*S. a. ambrosii*	*S. strinatii*	*S. flavus*	*S. supramontis*	*S. i. imperialis*	*S. i. sarrabusensis*	*S. genei A*
S. supramontis	*Ldh1, Ldh2, Hbdh, Mdhp2, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum*	*Ldh1, Hbdh, Mdhp2, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Fum*	*Ldh1, Hbdh, Mdhp2, Idh2, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum*	*Ldh1, Hbdh, Mdh2, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat2, Ck, Adk, Est4, PepC, Lap, Ada1, Ada2, Ca3, Ca4, Fum*	*Idh2, 6Pgdh, Gapdh, PepC, Ada2, Fum*	----			
S. imperialis imperialis	*Ldh1, Ldh2, Hbdh, Mdhp2, Idh1, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Adk, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*Ldh1, Ldh2, Hbdh, Mdhp2, Idh1, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdhp2, Idh1, Idh2, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Adk, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*Ldh1, Ldh2, Hbdh, Mdh2, Idh1, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Adk, PepC, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*Ldh2, Hbdh, Idh2, 6Pgdh, Gapdh, PepC, Ca4, Fum*	*Ldh2, Hbdh, Gapdh, Aat2, PepC, Ada2, Ca4*	----		

Table 1. (Following)

Taxon	*S. italicus*	*S. a. bianchii*	*S. a. ambrosii*	*S. strinatii*	*S. flavus*	*S. supramontis*	*S. i. imperialis*	*S. i. sarrabusensis*	*S. genei A*
S. i. sarrabusensis	*Ldh1, Ldh2, Hbdh, Mdhp2, Idh1, Idh2, 6Pgdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Adk, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*Ldh1, Ldh2, Hbdh, Mdhp2, Idh1, Idh2, 6Pgdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdhp2, Idh1, Idh2, 6Pgdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Adk, PepC, PepD, Lap, Ada1, Ada2, Ca3, Fum, Mpi*	*Ldh1, Ldh2, Hbdh, Mdh2, Idh1, Idh2, 6Pgdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Adk, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*Ldh2, Hbdh, 6Pgdh, Gapdh, Aat2, Ca4, Fum*	*Ldh2, Hbdh, Idh2, Aat1, Aat2, PepC, Ada2*	*Idh2, 6Pgdh, Gapdh, Aat2, PepC, Ca4*	----	
S. genei A	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh2, Mdhp1, Idh1, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh2, Idh1, Mdhp1, 6Pgdh, Gapdh, NADH, Np, Sod1, Sod2, Pgm1, Pgm2, Aat1, Aat2, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh2, Idh1, Idh2, Mdhp1, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh2, Mdhp1, Idh1, 6Pgdh, Gapdh, NADH,, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Adk, Est4, PepC, PepD, Lap, Ada1, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Hbdh, Mdh2, Idh2, Mdhp1, Fum, 6Pgdh, Gapdh, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Est4, PepC, PepD, Lap, Ada2, Ca4, Fum*	*α–Gpdh, Ldh1, Hbdh, Mdh2, Mdhp1, Mdhp2, 6Pgdh, Gapdh, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Est4, PepC, Lap, Ada2, Ca4, Fum*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh2, Mdhp1, Mdhp2, 6Pgdh, Gapdh, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Est4, PepC, PepD, Lap, Ada2, Ca4, Fum*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh2, Mdhp1, Mdhp2, Idh2, 6Pgdh, Gapdh, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Est4, PepC, PepD, Lap, Ada2, Ca4, Fum*	----

Table 1. (Following)

Taxon	*S. italicus*	*S. a. bianchii*	*S. a. ambrosii*	*S. strinatii*	*S. flavus*	*S. supramontis*	*S. i. imperialis*	*S. i. sarrabusen-sis*	*S. genei A*
S. genei B	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh1, Mdh2, Mdhp1, Idh1, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh1, Mdh2, Mdhp1, Idh1, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Hbdh, Mdh1, Mdh2, Mdhp1, Idh1, Idh2, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Adk, Est4, PepC, PepD, Lap, Ada1, Ada2, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh1, Mdh2, Mdhp1, Idh1, 6Pgdh, Gapdh, NADH, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Adk, Est4, PepC, PepD, Lap, Ada1, Ca3, Ca4, Fum, Mpi*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh1, Mdh2, Mdhp1, Idh2, 6Pgdh, Gapdh, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Est4, PepC, PepD, Lap, Ada2, Ca4, Fum*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh1, Mdh2, Mdhp1, Mdhp2, 6Pgdh, Gapdh, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Ck, Est4, PepC, Lap, Ada2, Ca4, Fum*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh1, Mdh2, Mdhp1, Mdhp2, 6Pgdh, Gapdh, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Est4, PepC, PepD, Lap, Ada2, Ca4, Fum*	*α–Gpdh, Ldh1, Ldh2, Hbdh, Mdh1, Mdh2, Mdhp1, Mdhp2, Idh2, 6Pgdh, Gapdh, Sod1, Sod2, Np, Pgm1, Pgm2, Aat1, Aat2, Ck, Est4, PepC, PepD, Lap, Ada2, Ca4, Fum*	*Ldh-1, Ldh2, Mdh1, Mdhp1, Est4*

Gapdh (1.2.1.12), *NADH-dh* (1.6.99.3), *Sod-1, Sod-2* (1.15.1.1), *Np* (2.4.2.1), *Aat-1, Aat-2* (2.6.1.1), *Ck* (2.7.3.2), *Adk* (2.7.4.3), *Pgm-1, Pgm-2* (2.7.5.1), *Est-4* (3.1.1.1), *Pep C* Leu-Ala (3.4.11.), *Pep D* Phe-Pro (3.4.11.), *Lap* (3.4.11.), *Ada-1, Ada-2* (3.5.4.4), *Ca-3, Ca-4* (4.2.1.1), *Fum* (2.1.2), *Mpi* (5.3.1.8).

A biochemical key to species identification was already reported in LANZA et al. (1995) but the following Table 1 allows the identification of all the taxa (species and subspecies) so far described.

3.4.2 Genetic differentiation (allozymes and mitochondrial DNA)

Early studies on the genetic structure of *Speleomantes* carried out using allozymes provided evidence of a wide variation within the genus allowing identifying genetically divergent population groups. Accordingly, the taxonomy of the genus changed till to the present arrangement (see § 3.1 «Systematics, taxonomy and geographical distribution»; NASCETTI et al., 1996).

Concerning the levels of differentiation observed, the most divergent taxon is the southern Sardinian *S. genei,* showing a mean genetic distance (NEI, 1972) of 2.4 (±0.5) with respect to the mainland taxa (*S. italicus, S. ambrosii, S. strinatii*) and 1.7 (±0.4) with respect to the eastern Sardinian taxa (*S. flavus, S. supramontis, S. imperialis*). A comparable differentiation is observed between mainland and eastern Sardinian *Speleomantes,* showing a mean distance of 1.5 (±0.4). The mainland species have a mean D_{Nei} of 0.37 (±0.1) with a range between 0.34 and 0.41 (FORTI et al., 1998). Within the single species the genetic structuring is quite different and related to the local orography and palaeoclimatic history. *S. italicus* is genetically highly homogeneous through its whole range (D_{Nei} between 0.002 and 0.046) and has low genetic variability values, specially in the southern part of the range where for example the observed heterozygosity ranges between 0.000 and 0.054 (FORTI et al., 1998). Within *S. ambrosii,* the small range hosts two geographically separated and genetically well differentiated subspecies: *S. a. ambrosii* and *S. a. bianchii* (LANZA et al., 2005). The two subspecies have four diagnostic loci (*Idh*-2, *NADH-dh, Sod-1 and Ada-1*) and a D_{Nei} of 0.19. As reported in LANZA et al. (2005) «As already hypothesized by NASCETTI et al. (1996:165), the evident lack of gene exchange between the two subspecies of *S. ambrosii* seems to be related to the extrinsic geographic barriers represented by the Magra River and, probably, by unfavourable ecological conditions in the upper course of the river, as suggested by the presumable absence of the genus *Speleomantes* from the Pontremoli's area E of the Magra River». As to *S. strinatii,* the data presented in CIMMARUTA et al. (2005) show that this species includes three genetically and geographically characterised population groups. The eastern part of the species range is inhabited by a genetically quite homogeneous group of populations that are also genetically close to those from the Roburent area and the province of Cuneo, Piedmont. A second group includes the populations from the western part of the range, the French Alpes-Maritimes and the province of Imperia (Liguria, Italy), which are genetically highly fragmented. The third group includes the populations from the «Finalese» in the province of Savona (Liguria), which are the most genetically differentiated within the species in spite they are located in the middle of the species range. The differentiation between the three groups of *S. strinatii* is reported in Table 2, see CIMMARUTA et al. (2005) for further details.

Table 2 – Mean genetic distances (D_{Nei}, Nei, 1972, below the diagonal) and divergence times in years (*t*, Nei, 1975, above the diagonal) between the three genetically characterised forms identified within *S. strinatii*.

As shown in the Table 2, the genetic subdivision of this species seems to be

Population group	«Eastern»	«Finalese»	«Western»
«Eastern»	---	t = 590.000	t = 375.000
«Finalese»	**0.118**	---	t = 500.000
«Western»	**0.075**	**0.100**	---

related to the influence of glacial events (see chapter 4 «Biogeography»), according to FORTI et al. (1998) and CIMMARUTA et al. (2005).

As frequently in plethodontid salamanders, the same level of divergence between pair of species could lead to different degrees of reproductive isolation (TILLEY et al., 1990; ARNOLD et al., 1993). The three mainland species have two contact zones so far identified and studied: one between *S. italicus* and *S. a. bianchii* in the Apuan Alps (Tuscany) and another between *S. a. ambrosii* and *S. strinatii* in easten Liguria. In the first case the two taxa met and hybridized, generating a hybrid zone characterised by a strongly asymmetric introgression, with the alleles of *S. ambrosii* entering the *S. italicus* gene pool for long distances but not viceversa. The *S. ambrosii* alleles of two of the nine discriminating loci *(Mdhp-2* and *Ca-3)* can be found over 90 km from the contact zone. On the contrary the alleles of *S. italicus* barely move 15 km away from the hybrid zone in the *S. ambrosii* range (CIMMARUTA, 1993; FORTI et al., 1998).

The study of the hybrid zone using direct sequencing and Restriction Fragment Length Polymorphism (RFLP) of the mitochondrial gene cytochrome-b showed a different pattern with respect to the allozymes. The different haplotypes coexist in a single sample and show a clean-cut geographical subdivision between *S. a. bianchii* and *S. italicus* haplotypes (RUGGI et al., 2005 and unpublished data; cf. also CIMMARUTA et al., 2006). A complete different picture comes from the analysis of the contact zone between *S. a. ambrosii* and *S. strinatii*: the two taxa show a parapatric distribution, with the closest populations at less than 1 km (a distance that can be covered by *Spleleomantes*, stated the absence of local barriers) that show alternative fixed alleles at 10 allozyme loci without any evidence of hybridization (CIMMARUTA et al., 1999). In this case competitive interactions seem to originate and maintain the observed distribution (CIMMARUTA et al., 1999).

The three eastern Sardinian species are all parapatrically distributed (based on the present knowledge) and show a comparable level of genetic differentiation, with D_{Nei} between 0.46 and 0.49 (CIMMARUTA et al., 1998). All the three species are genetically quite structured, with intraspecific differentiation never lower than D_{Nei} 0.05 (CIMMARUTA et al., 1998). The high intraspecific differentiation observed witin both *S. imperialis* and *S. supramontis* (D_{Nei} intraspecific range 0.047-0.282 and 0.066-0.069, respectively) is maybe due to a progressive differentiation of the populations following the base of the Gennargentu Mountain where they both live. Moreover, *S. imperialis* has been shown as including two different subspecies: *S. i. imperialis* and *S. i. sarrabusensis* (LANZA et al., 2001). All the three eastern Sardinian species have high levels of genetic variability, with heterozigosity values between 0.06-0.10 in *S. flavus*, 0.06-0.12 in *S. supramontis* and 0.09-0.11 in *S. imperialis* (CIMMARUTA et al., 1998). The southern Sardinian *S. genei* shows two well differentiated population groups (*S. genei* A, from Iglesiente and Sulcis and *S. genei* B from Sulcis, D_{Nei} 0.25) exhibiting 5 loci with fixed alternative alleles (*Ldh–1*, *Ldh–2*, *Mdh–1*, *Mdhp–1*, *Est–4*) in spite the two population groups reach a distance of 7 km only. While *S. genei* B lives in a small area, and therefore is genetically quite homogeneous, *S. genei* A can be further subdivided in two population groups inhabiting northern and southern Cixerri region, respectively (D_{Nei} 0.12, CIMMARUTA et al., 1998).

3.4.3 Karyology and repetitive DNA

Number and shape of chromosomes are quite uniform in the plethodontid salamanders, in spite the high genetic variation usually observed (LARSON, 1984). The bolitoglossine tribe has a chromosome formula $2n$=26 but *Speleomantes* constitutes an exception, having n=14 as demonstrated by STEFANI (1969) and confirmed by Kezer (MORESCALCHI, 1973) and the subsequent studies (see LANZA et al., 1995). Since only two haploid chromosome numbers can be found in plethodontids, n=13 and n=14, *Speleomantes* karyotype can be considered as primitive (NARDI, 1991).

According to the overall uniformity of the family, all the *Speleomantes* species share very similar karyotypes and C-banding patterns which are also resembling those observed in the American *Hydromantes*. The only exception is the XIV pair, which is asymmetrical in the European species while metacentric in the American ones (SESSIONS, 1984). Another relevant feature concerning the chromosome pair XIV is their differentiation as sex chromosomes of the XX/XY type (NARDI et al., 1986). In the females the two chromosomes are similar and both subtelocentric as it is one of the sex chromosomes in the males (X sex chromosome) which have the second sex chromosome (Y) submetacentric and therefore differing from the X chromosomes by the centromeric index, having the short harm slightly longer (from LANZA et al., 1995 pag. 113-115 where can be found a summary of *Speleomantes* chromosomes features). Interestingly in *S. genei* there is no sex chromosome heteromorphism, being the chromosomes of pair XIV subtelocentric and homomorphic in both males and females, similar to the X chromosomes of the other *Speleomantes* species. For this reason the karyotype of *S. genei* is considered as ancestral (NARDI, 1991).

The studies on repetitive DNA by BATISTONI ET AL. (1991, 1992, 1995), DELUCCHINI et al. (1978), MARRACCI et al. (1996), NARDI ET AL. (1982, 1986, 1999) have been summarized by NARDI et al. (2000). They wrote: «We have studied three DNA families (named Hy/Pol III, Hsrl and Hy 500), belonging to three distinct classes of repetitive DNA. [...] In conclusion, our cytomolecular results are in agreement with electrophoretic and morphological data (LANZA et al., 1995, NASCETTI et al., 1996) and support the view that *H. genei* is more distantly related to all the other European species» and «[...] all the three repetitive DNA families, we have studied, are absent from the American species *H. shastae*».

4. BIOGEOGRAPHY

What follows is mainly an updated version of LANZA et al. (1995) and NASCETTI et al. (1996), who treated the subject extensively.

WILDER et al. (1920) and DUNN (1926) proposed for Plethodontidae an origin from Appalachian mountain-stream dwellers; they suggested that the proto-plethodontids with reduced or no lungs were less likely floated away in the swift mountain streams where they lived. Moreover, selection for lung reduction or loss seems most likely to have occurred in urodeles living in cool, fast, oxygen-rich waters: a trend shown by other non-plethodontid salamanders (such as some Hynobiidae, Salamandridae and Ambystomatidae) more or less associated to cool mountain brook habitats. Several evidence support an Appalachian origin: «the present distribution of the family centers around Appalachia; here occur the most primitive forms, while not all are found elsewhere; some of them are very specialized» (DUNN, 1926). According to RUBEN & BOUCOT (1989), these basic assertions were widely accepted and WAKE (1966) further suggested a late Mesozoic (Cretaceous) Appalachian mountain-brook origin of the Plethodontidae, by quoting as fundamental supporting evidence for this expanded scenario the description (ESTES, 1964) of the Cretaceous «desmognathine» *Prodesmodon* from the upper Cretaceous - lower Paleocene of North America, now considered a batrachosaurid (DUELLMAN & TRUEB, 1986). Moreover the Appalachian mountain habitats have been relatively stable for a very long time, at least since the mid-Mesozoic. However, «as logical as the classic scenario apparently seems», RUBEN & BOUCOT (1989) regard it as incorrect, since «geological and paleontological evidence suggest that Appalachia in the middle to late Mesozoic had a warm, subtropical environment of low elevation and low relief»; moreover, STOKES (1966) and STANLEY (1986) consider the present Appalachian topography as largely Tertiary in origin. Therefore RUBEN & BOUCOT (1989) conclude that, «as a Cretaceous Appalachian origin does seem most consistent with the distribution of extant plethodontids, they may have arisen instead from terrestrial or semi-aquatic proto-plethodontids» and suggest that the respiratory modifications found in some North American Ambystomatidae «may provide insight into the origins of plethodontid lunglessness» (refer to the original paper for further details). Further evidences supporting an Appalachian origin of plethodontids arised recently from the analysis of mitochondrial genomic sequences (MACEY, 2005).

The alternative hypothesis, which cannot be ruled out, is that a mountain-brook origin of Plethodontidae could be searched for in western North America and eastern Asia, where extensive mountain regions apparently occurred in the late Mesozoic (RUBEN & BOUCOT, 1989). We find this hypothesis scarcely convincing and implicitly, to a certain extent, neither RUBEN & BOUCOT (1989) seem to give it much credit.

From the hypothetical but almost certain Appalachian center of origin the Plethodontidae invaded, as terrestrial forms, western north America, central and southern America, Europe (DUNN, 1926) and, according to some authors, Asia as well. According to WAKE (1966; see also LARSON, 1984) «Bolitoglossines probably reached the West Coast of North America some time in early Tertiary via terrestrial forest corridor routes. Subsequent divergence of the plethodontine terrestrial species may have brought plethodontines and bolitoglossines into competition, with resultant extinction of the less well adapted bolitoglossines in Appalachia and surrounding eastern North America».

The European plethodontids are likely to have in California their closest relatives, belonging to the genus *Hydromantes*: three species on the western slope of the Sierra Nevada (and possibly also one or more up to now undescribed species), as well as, according to JENNINGS (1987), a new, undescribed species inhabiting East of the same mountain chain. Almost certainly *Speleomantes* and *Hydromantes* belong to a monophyletic supergenus *(Hydromantes)*, although a *very remote* possibility exists that it may be polyphyletic «[…] with the convergence depending on rather close habitat affinities, of Mediterranean type» (LANZA & VANNI, 1981), an hypotesis that seems to be discarded also according to the most recent research (JACKMAN et al., 1997).

The present, disjunct and clearly relict distribution of *Speleomantes* and *Hydromantes* «has been tentatively interpreted in different ways. Some authors simply admit that the plethodontids were once widely distributed also in Eurasia (e.g. DARLINGTON, 1957) or in Europe (e.g. STEWARD, 1969) without taking a stand on the family's origin, whether Palaearctic or Nearctic. SCHMIDT (1946), pointing out that "the faunas of western Europe and western north America have a considerable number of forms in common and confined to these two areas", that "among vertebrates, by far the most striking case is that of the plethodont salamanders of the genus *Hydromantes* [at present splitted in *Hydromantes* and *Speleomantes*]" and that during the Pleistocene "North America and Europe are shown to have been heavily glaciated, *while northern Asia was almost entirely free from ice* [our italics]", seems to implicitly suggest that the supergenus *Hydromantes* would have repopulated western North America and western Europe from its northern Asiatic refugia. However, even if suitable for other groups, SCHMIDT'S hypothesis cannot be applied to *Speleomantes* and *Hydromantes*, as their lineages splitted about 28 (WAKE et al., 1977 and 1978) or 50 (LANZA and VANNI, 1981) million years ago.

Other authors, explicitly or implicitly assuming a Neartic origin, suggested that Plethodontidae may have reached Europe or Eurasia by moving eastwards across Greenland and Iceland during periods which differ for the different authors: *undefined period* (CAMERANO, 1885; NOBLE, 1931; VANDEL, 1964); *late Mesozoic* (LAURENT, 1975 and 1986; CASALE, 1987); [late Mesozoic: Jurassic ?; BALLETTO, 2005] *late Mesozoic (Cretaceous) to Tertiary* (DEHAUT, 1911); *early Tertiary* (JEANNEL, 1943); *Tertiary* (DEHAUT, 1920; BRANGHAM, 1962); *pre-Miocene age* (PUDDU & VIARENGO, 1988); *before early Eocene* (LANZA and VANNI, 1981; actually "late Eocene", "early Eocene" being a *lapsus calami*); *late Miocene to Pliocene* (DUNN, 1926).» (LANZA et al., 1995). The figure of 350 Myr ago, quoted by Gruppo Speleologico C.A.I. Bolzaneto for the origin of *Speleomantes*, is wrong and actually refer to the origin of the whole amphibians.

«Another hypothesis expects Plethodontidae to have moved westwards, through the Bering land bridge during different periods: *undefined period* (GORMAN, 1964); *early Eocene* (WAKE, 1966); *late Oligocene or Oligocene* (WAKE et al., 1977 and 1978; BOLOGNA, 1978 [actually published 1982, cf. Bibliography], BANI, 1984 and 1985; DUELLMAN and TRUEB, 1986; SAGE et al., 1982). MANSUETI (1950) mentions the two possibilities and rules out that plethodontids reached Europe by human transport. The above-mentioned hypotheses are mainly based on paleogeographic data, with the exception of that by WAKE et al. (1977; 1978), based on immunological research; WAKE and coworkers assume that albumin has evolved at about 1.7 immunological distance units every million years in *Hydromantes*, so that Californian and European lineages would have separated about 28 million years ago, during the late Oligocene; these authors also admit that, should their chronology be true, plethodontids could not have used the migration route from West to East, as north America completely detached from Europe during the early Eocene, about 50 million years ago (WAKE et al., 1977, 1978). LANZA & VANNI (1981) considered the proposal of DUNN (1926), NOBLE (1931) and especially LAURENT (1975) as the best grounded, particularly supposing that the plethodontid dispersal may have involved only western Europe (see also LANZA et al.. 1992 and 1993). SAGE et al. (1982) completely disagree with LANZA & VANNI (1981) as "their arguments are based solely on what they find credible about distributional patterns, rather than on any data, and thus cannot be considered further". Notwithstanding this criticism, we still consider the Bering alternative to be highly unreliable as: 1) taking into account the trend toward a morphological stasis clearly shown by the Plethodontidae, a topic brilliantly treated by WAKE et al. (1983a), the morphological differences existing between the Californian and European species [...] [cf. LANZA et al., 1995: 22-24] appear to be less trivial than have been postulated and sufficiently consistent with a divergence time longer than that proposed by WAKE et al. (1977 and 1978); 2) the same applies to the biochemical and karyological data [...] [cf. LANZA et al., 1995: 23-24, NASCETTI et al., 1996: 170, and NARDI, 2000]; 3) it appears hardly credible that a whole family evolutionary "healthy", "successful" and including "both highly evolved specialists and little evolved, essentially static, generalists" (WAKE et al., 1983a) could have disappeared from almost all of Europe and Asia, or at least from all of Palearctic Asia, all the more so because wide portions of the latter (SCHMIDT, 1946) surely felt no or only slight effects of the Pleistocene glaciations» (LANZA et al., 1995). About the successfulness of the family and particularly of the tribe Bolitoglossini, to which *Hydromantes* and *Speleomantes* belong, it is noteworthy to point out that nearly one half of the approximately 400 [actually 535 (cf. Introduction)] species of living salamanders are just members of this latter! (JACKMAN et al., 1997).

«In conclusion, the European plethodontids, all belonging to the relatively thermophilic tribe Bolitoglossini, could be, according to a vicariance model, the relict heirs of the well-known rich faunal contingent of American origin inhabiting a part of the "future" Europe during the warm and humid Eocene» (LANZA et al., 1995).

The recent discovery of the first Asian plethodontid salamander, *Karsenia koreana* (MIN et al., 2005), adds new data to the problem of the origin of the European plethodontids. The external morphology and osteology are very close to those of the American *Plethodon* even if tarsus and vomer are more similar to those of *Aneides* (MIN et al., 2005). The analysis of the nuclear gene Rag-1 places *Karsenia* in a clade that includes desmognathine salamanders and has strong affinities with *Ensatina* and *Hydromantes*. As a consequence of this discovery, plethodontids are «now seen to have a Holarctic distribution, although it is impressively disjunct […] to the west, no plethodontids are known until central Italy» (MIN et al., 2005). Disjunctions for North America and Asia are known for many taxa but the patterns are not similar to those shown by plethodontids, being the Asian species in the clades usually the most numerous (here the largest species number is in eastern North America) (XIANG et al., 2004). According to MIN et al. (2005), «mammalian fossils indicate strong physical and phylogenetic connections between east Asia and North America at least until the late Miocene (WALLACE & WANG, 2004), and polar sea temperatures are estimated to be averaged about 15°C 70 millions years ago and more than 20°C at 90 million years ago. Such temperatures would have been favourable for plethodontid salamanders. Accordingly, there have been many opportunities for early migrations between the continents. An important implication of current distributions is that the Old World plethodontids have had lower rates of speciation than those in the New World, but also may have been disproportionately subject to extinction». This last sentence suggests that the relationships between the Asian *Karsenia* and the European *Speleomantes* should be deeply investigated before ruling out whatever paleobiogeographic scenario.

However, the disagreement between the holders of the two biogeographic theories persists. Recently, for instance, JACKMAN et al. (1997) supported the westwards way (Bering), DELFINO et al. (2002; 2005) the eastwards one (Greenland). The only way to validate the hypothesis of Eurasia invasion and subsequent subtotal extinction would be the discovery of living or fossil plethodontids in central and/or southern Eurasia. Therefore, we consider it is right to keep supposing that *Speleomantes*' ancestor(s) actually have a western origin and hypothesizing that *Karsenia*'s one(s) reached eastern Asia by dispersal through the Bering Bridge. *Consequently we think that the present range of* Speleomantes *arised from a vicariance process, while* Karsenia *originated from* a *dispersion process*.

According to LANZA et al. (1995), «the plethodontids known as fossils belong to six recent genera ranging from the lower Miocene to Pleistocene of North America (DUELLMAN & TRUEB, 1986); to these are to be added the remains of a late Pleistocene "*Hydromantes*" recently discovered in the south central Sierra Nevada, California (MEAD et al., 1985), and those of *Hydromantes* [now *Speleomantes*] from the Sardinian Pliocene (SANCHÍZ, 1983; MARTIN & SANCHÍZ, 1987). The latter ones were found in a layer at San Giovanni (Domusnovas, SW Sardinia) and in three layers at Siniscola (NE Sardinia) (MARTIN and SANCHÍZ, 1987, and personal communication, 13.XII.1991). Because of their relatively recent origin, they probably belong to *S. genei* and *S. flavus* respectively, or to their direct ancestors». Further fossil records of *Speleomantes* are the following ones: Late Pleistocene and Holocene of the cave Grotta Corbeddu (Oliena; central eastern Sardinia; province of Nuoro) (SONDAAR et al., 1984, 1988; CALOI et al., 1986); Plio-Pleistocene of Monte Tuttavista (Orosei, central eastern Sardinia; province of Nuoro) (DELFINO, 2002; ABBAZZI et al., 2004); middle Pleistocene of the cave Grotta di Valdemino (municipality of Borgio Verezzi; province of Savona; Liguria) (DELFINO, 2002, 2004); Early Pleistocene of the cave Grotte du Vallonnet (Alpes-Maritimes, France) (Salvador BAILON, pers. comm. to Massimo Delfino, 18.IV.2002). One may suppose that these remnants belong to *S. supramontis* [Oliena and Orosei; already quoted as *Hydromantes* sp. n. by SONDAAR et al., 1984 and 1988, as *Hydromantes supramontis* by CALOI et al., 1986, as *Speleomantes* sp. 1 (Orosei) by DELFINO, 2002], and *S. strinatii* (Savona, quoted as *Speleomantes* sp. 2 by DELFINO, 2002; Alpes-Maritimes) or to their direct ancestors. DELFINO et al. (2002; 2005) rightly pointed out that these palearctic fossils, scarce and occurring only within the present range of the family, cannot make any effective suggestion on the origin of European Plethodontidae. The recent finding of a fossil plethodontid salamander from Middle Miocene of Slovakia (VENCZEL & SANCHÍZ, 2005) does not alter the evolutionary scenario (vicariance model) proposed before.

«On the basis of paleogeographic, anatomicocomparative, cytogenetic and biological data, STEFANI (1969) considered the southwestern Sardinian form (*Speleomantes genei*) as the most primitive and its range (Iglesiente and Sulcis) as the secondary diffusion center of the European plethodontids. He hypothesized two migratory routes: one to Provence, probably through a very wide late Miocene land connection (with a question mark represented by Corsica, where the family is absent), the other to eastern Sardinia; finally *Speleomantes* probably spread from Provence to central Italy with a Pliocene and Quaternary migration along the Apennines» (LANZA *et al.*, 1995).

However, further paleogeographic and taxonomical evidence has shown that Stefani's views must be partly modified since: 1) it is now sure that, as first supposed by ARGAND (1924) in an often overlooked paper, the Sardinian block detached from southern France during the Tertiary (see f.i. ALVAREZ, 1972 and 1973) to reach its present position, according to AZZAROLI et al. (1986), about 19 million years ago; 2) the «giant» eastern Sardinian forms are full species (*S. flavus, S. supramontis, S. imperialis*) and more closely related to the continental ones (*S. strinatii, S. ambrosii* and *S. italicus*) than to *S. genei* (LANZA et al., 1982; NARDI et al., 1982; LANZA, 1983: 726 and 744; LANZA et al., 1986; NASCETTI et al., 1996).

In the light of the above-mentioned data we may infer (see also LANZA, 1983) the existence of two relict, secondary southern French diffusion centers, a possibility already mentioned by LANZA & POGGESI (1971: 662). We may hypothesize that one of these centers, inhabited by the ancestor of *S. genei* which has no heteromorphic sex chromosomes (NARDI et al., 1982 and 1986) -what indicates a primitive condition- detached from the European continent later than the middle Oligocene, probably in the lower Miocene, during the Aquitainian (begun 23 Myr ago)-Burdigalian (ended 16 Myr ago) stages (MONTIGNY et al., 1981), and migrated together with the Cyrno-Sardinian microplate. It is dutiful to recall that this hypothesis, arising from ARGAND's (1924) studies, had already been suggested by CEI (1941b: 291-292). On the other hand, the ancestral form inhabiting the second continental Provençal center perhaps gave rise to *S. strinatii* which, in turn, gave rise to *S. ambrosii* and *S. italicus*, during the Pliocene or Quaternary, as well as to the ancestor of the three eastern Sardinian species, during an unknown, probably earlier period. The last ones could have reached Sardinia in the late Miocene, during the Messinian salinity crisis. In this case, since the genus does not occur in the non-Apennine zones of central Italy, the ancestor of *S. flavus*, *S. supramontis* and *S. imperialis* would not have migrated through Tuscany or Latium, but through a northern connection including Corsica, a migration route between continental Europe and the Cyrno-Sardinian complex which, according to some authors, had been followed by numerous plant and animal species. *Speleomantes* might have become extinct in Corsica for climatic reasons, as this island was glaciated to some extent during the Pleistocene; cf., e.g., THORPE (1973: 90 and fig. 5.1), who consequently hypothesized a Sardinian refuge and a secondary post-glacial range extension to Corsica for *Natrix natrix cetti.* LANZA & POGGESI (1971) were very skeptical about this possibility especially because of the global physiographic and environmental characteristics of this island. However, this hypothesis is consistent with the estimated evolutionary divergence of about 6 million years between the mainland and the eastern Sardinian species [calculated according to NEI's formula (1975)]. Moreover, the absence of plethodontids' fossils in Corsica is not in contrast with the use of this island as a bridge to Sardinia during the Messinian epoch. The southward migration of species at this time should have been quite rapid, without the settlement of stable and wide populations, because occurring only during the final phase of the Messinian. Only at that time, indeed, the climate turned to be cold, allowing to use the bridges previously formed but scarcely exploitable till that moment because of the very hot and dry climate, making them very harsh habitats during the Early and Middle Messinian. On the other hand, many different bridges emerged during the Messinian, connecting the mainland to Sardinia and therefore not requiring a passage through Corsica to reach the latter. In conclusion, any definitive hypothesis concerning the migration routes of *Speleomantes* appears presently hard to be defined.

As to the origin of the extant taxa NASCETTI et al. (1996) agree with LANZA (1983) in indicating the presence of the ancestor of *S. genei* on the Corsica-Sardinia microplate when it separated from the Spanish-French continental margin during late Oligocene, 27-30 Myr ago. In conclusion, any convincing hypothesis on this subject appears presently impossible. According to a hypothesis by NASCETTI et al. (1996), in a period following the separation of Corsica and Sardinia from the continental margin, a new karyological *Speleomantes* form evolved, presumably on the mainland, characterized by heteromorphic sex chromosomes. This form apparently replaced the ancestral one, with undifferentiated sex chromosomes (never found today on the mainland), and extended its range on the continent. During the Messinian (about 6 Myr ago), a salinity crisis led to a partial desiccation of the Mediterranean basin, with the formation of broad, stable land-bridges, which allowed mainland heterochromosomic *Speleomantes* to colonize eastern Sardinia. The progressive cooling of the climate in the last part of the Messinian (BERTOLANI-MARCHETTI, 1985), possibly triggered a southward migration of *Speleomantes*, leading to a restriction of *S. genei*-like populations in southwestern Sardinia, while allowing the mainland heterochromosomic *Speleomantes* to colonize eastern Sardinia.

An alternative scenario considers more recent datings (NASCETTI et al., 1996: 169-170): the first colonization of Sardinia from the mainland by a *S. genei* ancestor would have taken place during the Messinian salinity crisis (about 6 Myr ago); the colonization of eastern Sardinia by mainland heterochromosomic *Speleomantes* would have occurred about 1-2 Myr ago throught the bridge formed by Argentario promontory, a «fossil island» of the Tuscan Archipelago, whereas the extant eastern Sardinian and mainland taxa would have speciated during Pleistocene glaciations, about 500,000 years ago.

This second scenario was however discarded by NASCETTI et al. (1996: 170), because the use of the «Argentario bridge» would imply a «recent» divergence between mainland and eastern Sardinian taxa which is not supported by the high genetic distances recorded among these taxa (around 1.5). Furthermore, the scenario proposing more ancient dating (the first reported by NASCETTI et al., 1996) is strongly supported by the comparison with other amphibians from the same area. For example *Euproctus* Gené, 1838 mountain newts, which inhabits the Pyrenean region, Corsica, and Sardinia as a result of the microplate disjunction (SBORDONI et al., 1991; CACCONE et al., 1994) shows a genetic divergence (D_{Nei} = 1.7-1.8) comparable to that found between *S. genei* and the other European *Speleomantes*. Other relevant data come from toads of the genus *Discoglossus*, inhabiting the Cyrno-Sardinian region with two endemic species, the more ancient *D. montalentii*, a taxon perhaps facing extinction, and the more recent *D. sardus* (LANZA et al., 1984). The first species presumably colonized this region during the Messinian, and shows a Nei's average D of 1.06 from the *D. pictus*; the second one, which reached the Cyrno-Sardinian region through the Argentario bridge, has a D of 0.42 from *D. pictus* (CAPULA ET AL., 1985; ZANGARI ET AL., 2006). The first value is rather similar to that *found between* mainland versus eastern Sardinian *Speleomantes* (1.5), whereas the latter (0.42) is significantly lower, allowing us to rule out the possibility that *Speleomantes* successfully used the Argentario bridge 1-2 Myr ago. Comparable values (D_{Nei} from 0.37 to 0.47) are indeed found between mainland *Speleomantes* taxa and between eastern Sardinian taxa, but never between Sardinian and mainland taxa.

As to the divergence of mainland-eastern Sardinian taxa, a new scenario was recently proposed by DELFINO et al. (2005) based on the observation that «the European fossils are found only inside the present range and mostly in Sardinia (where they are not rare!), a fact suggesting relatively recent expansion of the range on mainland Italy and France». Based on this remark and on the conservative power of islands, DELFINO et al. (2005) hypothesize that «*S. genei*, or its forerunner, entered Sardinia in Oligocene, survived there while mainland (at least Pyrenean) populations went extinct, giving rise to the rest of Sardinian species (3) which are responsible of the further spread into Peninsular Italy (3 species)». It is quite surprising that such statement is based on only six fossil records: four from Sardinia and two from mainland, a very low number of cases to support the strong assertion that in Sardinia fossils «are not rare». Indeed, in the same paper the authors (p. 48) affirm that «the fossil record of plethodontids is astonishingly poor and recent». If this is a general trend, why would it assume a particular relevance for the mainland European species? Moreover, the recent finding of a fossil plethodontid salamander from Middle Miocene in Slovakia (VENCZEL & SANCHÍZ, 2005) unhinges the assumption that European fossils are found in the present range only. Another problem with this scenario is that it does not date divergence times. If the splits are assumed to be those proposed in NASCETTI et al. (1996), it is difficult to imagine a northward migration (from Sardinia to mainland) during the last cooling part of the Messinian which triggered southward movements of faunas (BERTOLANI-MARCHETTI, 1985). Also, as DELFINO et al. (2005) pointed out, mainland and eastern Sardinian species share similar parasite taxa while *S. genei* does not (LANZA et al. 1995). State the growing evidence of the host-parasite coevolution and the increasing use made of parasites as «biological tags», the parasitological data strongly contradict the idea of a «Sardinian origin» of the eastern Sardinian species which in this case are expected to bear Sardinian (not mainland) taxa of parasites. Another remark concern the idea that the scenario proposed by DELFINO et al. (2005) «would fit the antiquity of *S. genei*, its lower genetic distance from the other Sardinian species than from the continental ones (LANZA et al. 1995: 240; NASCETTI et al. 1996: table 3 and 5) […]». The antiquity of *S. genei* is beyond all dispute but its lower genetic distance with respect to the eastern Sardinian species is not significant (as stated by NASCETTI et al., 1996: 168) as shown by the high values of the standard errors reported (in the already cited table 5). This is not surprising because of the long diverge times involved, causing a saturation of the evolutionary signal in allozymes and making the absolute values poorly informative: this is why neither MAXSON & MAXSON (1979) nor NEI (1975) calibration were able to perform reliable divergence times estimates for both the oldest events (*S. genei* ancestor isolation and eastern Sardinian vs. mainland ancestors isolation) and the more recent ones (origin of the extant taxa), as discussed by NASCETTI et al. (1996: 170). Finally, the different separation times of the eastern Sardinian species between each other (Late Pliocene) and of the mainland species (Early Pleistocene) is seen by DELFINO et al. (2005) as a confirmation that mainland Italy and France have been recently colonized. This is a forcing in data interpretation, because what the data show is simply that the climatic oscillations combined with the orographic features in producing different genetic patterns. For example, *S. flavus* resulted more differentiated with respect to the other two Sardinian species than are *S. supramontis* and *S. imperialis* among them (CIMMARUTA et al,. 1998), as a result of the presence of the Gennargentu Massif within their range: the two species show an intergradation around this mountain with many loci showing a clinal variation along its base (CIMMARUTA et al,. 1998: 188-190).

Ice ages surely had a decisive influence on the evolution and present distribution pattern of *Speleomantes* [see: LANZA et al., 1995; LANZA, (1999c, 1999g) and particularly CIMMARUTA et al., 1998, FORTI et al., 1998, CIMMARUTA et al., 2002 and 2005].

This is because the ecological requirements of these animals (see chapter 5 «Ecology») suggest that glacial stages would have promoted fragmentation and isolation at the population level. Indeed ice ages were characterized not only by low temperature but also by a dry climate, being precipitation mainly due to snow (BERTOLANI-MARCHETTI, 1985). Fragmented and declining populations would persist only in association with surviving woods, confined at low altitude and/or along the coasts (FORTI et al., 1998). On the contrary, during the inter-glacial stages, the warmer and humid climate would have promoted populations expansion, moving at higher altitudes together with the vegetation plans (PIGNATTI, 1994). These considerations lead to hypothesize a «flush and crash» mechanism bringing to both the extant species origin and the intraspecific population genetic structure. Allozyme data were used to calculate the times of divergence between closely related species inhabiting the same geographical region (i.e., the three mainland and the three eastern Sardinian species). The results obtained corroborate the idea of glacial stages as a «crash» period, being the divergence time of the mainland species between 1.7-2.1 Myr ago (FORTI et al., 1998) and that among the eastern Sardinian ones 2.3-2.4 Myr ago (CIMMARUTA et al., 1998). In both cases the late Pliocene glaciations started the divergence process between all the considered taxa, because of the temporary unfavourable environmental conditions. On the other hand, the genetic structure at the intraspecific level was influenced by the alternation of glacial and interglacial stages that characterized the Pliocene and Pleistocene epochs. The «flush» occurring during interglacials brought in contact populations isolated during the previous glacials, generating a number of «micro secondary contacts» mixing the different alleles originated during the allopatric (glacial) stage. The finding that areas surrounded by orographic boundaries are now hosting populations characterised by high levels of genetic variability supports this hypothesis. In Sardinia the pattern of genetic differentiation recorded within eastern Sardinian species is in agreement with this scenario: sampled populations of each species are genetically well differentiated (D_{Nei} up to 0.05) as expected from repeated isolations and fragmentations. Moreover, the highest values of genetic variability are recorded in the zones characterized by the most complex orography (CIMMARUTA et al., 1998). Also the mainland species show a pattern of genetic structure according to the above mentioned paleogeographic hypothesis. *S. strinatii* hosts well differentiated population groups in the western part of its range (FORTI et al., 1998). In particular, the most divergent group from the «Finalese» lives in a small area isolated by relatively high mountains that turned in geographic barriers during glacial stages. The times of divergence of this group with respect to the other *S. strinatii* population clusters date back to two Pleistocene glaciations: Günz and Mindel (CIMMARUTA et al., 2005), confirming the important role played by these events in subdividing *Speleomantes* populations. *S. ambrosii* is divided in two allopatric subspecies (LANZA et al., 2005) whose glacial refuges are identified in the Apuan Alps (*S. a. bianchii*) and in the Southern Ligurian Apennines (*S. a. ambrosii*) (FORTI et al., 1998). This picture matches with previous studies, identifying these areas as refuges for other organisms (LA GRECA, 1970; MARIOTTI, 1984), and is supported by recent molecular data highlighting two remnant nuclei in the Apuan Alps, where two genetically distinct and geographically apart haplotypes have been identified using mtDNA RFLP (RUGGI et al., 2005).

According to LANZA et al. (1995: 122), *S. italicus* is absent from the higher part of the northern [as Monte Cimone (2165 m)] and central Apennines [as Monti Sibillini (2476 m), Gran Sasso d'Italia (2912 m), Parco Nazionale d'Abruzzo (2242 m), etc.], even at elevations which, at present, would appear to be perfectly suitable to its ecological requirements. This could be due to the heavy glaciations which affected the above-mentioned mountains during the Quaternary. It could be objected that the species should have had enough time to regain the lost territories during the thousands years elapsed since the last Ice Age, but, as an alternative possibility, we could hypothesize that *S. italicus* might be a species not so euryzonal as *S. strinatii* and consequently unable to populate areas higher than about 1600 m. The same applies to the Sardinian Mount Gennargentu massif (1834 m) where up to now the genus is known to occur only in the zone of Aritzo (840-890 m), on the SW slope of the mount, and has not be found even in caves and abandoned mines around 1100 m of elevation, in the environs of Passo Correboi, on its NE slope (LANZA et al., 1995: 162, 291; 1999h: 180).

5. ECOLOGY

5.1 Habitats

Many authors have dealt with the habitat characteristics of the continental *Speleomantes*, but their data are usually second-hand and sometimes either partly or completely wrong; one may quote e.g. SAVI (1838), DE BETTA (1864; 1874), CAMERANO (1885), SCHREIBER (1875; 1912), PERACCA (1885), FISCHER (1887), BERG (1893), TRAMBUSTI (1896), BEDRIAGA (1897), VANDONI (1914), SCHMALZ (1916), SCHREITMULLER (1916), HOLDHAUS (1924), JEANNEL (1942), LANZA (1946; 1986; 1999b-h), ANGEL (1946), BECK (1950; 1967), KOLAR (1952), SOCHUREK (1952), VANDEN EECKHOUDT (1954), SCORTECCI (1957), ELKAN (1958A), GHIGI & PASQUINI (1958), GHIDINI & ORSINI CAPOCACCIA (1959), VEROLE (1962), THORN (1965; 1969), STEFANI (1969), DURAND (1970; 1973), MELODIA & PASTORINO (1971), ANELLI (1971), BOLOGNA (1972), SERRA (1972B), FRETEY (1975), BRICOUX (1975), AELLEN & STRINATI (1975; 1976), EWALD (1977; 1989), ARNOLD & BURTON (1978; 1979), MORISI (1980; 1983a), CASALE & SBORDONI (1983), MATZ (1983a-b), RAFFAELLI (1983), RUBBI & TASSINARI (1983), BONZANO et al. (1983), BANI (1984), BALLASINA (1984a-d), RABACCHI (1984), ANELLI et al. (1985), SUTTO & PAOLI (1985), TASSI (1985), ENGELMANN et al. (1985), BOGLIANI & BARBERI (1986; 1988), DIESENER & REICHHOLF (1986), MONGUZZI (1986), SWEET (1986), MAZZOTTI (1988; 1989), CAPULA (1989), CORTESOGNO & BALLETTO (1989), SAUER (1989), VANNI & NISTRI (1989), SPAGNESI (1989), SALVIDIO (1990; 1991; 1992; 1993a-b; 1998; 2001), NÖLLERT & NÖLLERT (1992), SALVIDIO (1994), SALVIDIO et al. (1994; 2002), FERRI (1996), SCARAVELLI & TEDALDI (1996), TEDALDI et al. (1997), TEDALDI (1998; 2000), TEDALDI & LAGHI (1998), CIMMARUTA et al. (1999), THORN & RAFFAELLI (2001), LEONARDI (2001), ARNOLD (2002), CASALI et al. (2002a), PIEROTTI (2002), ONETO et al. (2003), ACEMAV COLL. et al. (2003).

Being euryzonal, totally terrestrial, and consequently not linked to any body of water for reproduction, the genus *Speleomantes* occurs, according to LANZA (1999c; modified, updated and freely translated from German) «in extremely diverse habitats, from coniferous forests and overall hardwoods, mixed woods and maquis to open, sometimes seminaked rocky territories, from areas with a rich surface hydrography to barren localities, from sea level up to elevations close to or, in the case of *S. strinatii*, exceeding 2000 metres. The widespread misconception according to which the genus is mandatorily or almost mandatorily linked to caves and as a consequence especially to the calcareous rocks either of metamorphic (as the famous Apuan Alps marbles) or sedimentary origin arises mainly from its ethological characteristics and the self-evident truth that the caverns are the only natural subterranean cavities on a human scale. Actually the *conditio sine qua non* for the survival of these plethodontids is the occurrence of adequate natural or artificial complexes of underground spaces offering the animals a favourable environment (moisture, temperature, and possibly food) during the more or less long periods when the conditions above ground are prohibitive, i.e., too cold, too hot or too dry. Though it cannot be denied that such complexes reach their greatest extent in the limestone substrata, they nevertheless occur everywhere, allowing *Speleomantes* to inhabit regions of almost any lithological and geological nature. Till now it has been found, besides on limestone, gypsum [*S. italicus* in a cave of Mount Rontana, in the environs of Brisighella (province of Ravenna): MAZZOTTI & STAGNI, 1993; *S. italicus* from a cave near Ponte S. Maria Maddalena (province of Pesaro-Urbino): GUIDUCCI, undated, quoted by BASSI, 1999; *S. italicus* from a cave near Montescudo (province of Rimini): BAGLI, 2001], sandstones (many localities), conglomerates (e.g. *S. strinatii* from Scrivia and Vobbia valleys, province of Genoa: MELODIA & PASTORINO, 1971), colluvial and alluvia1 deposits, marls (e.g. *S. strinatii* from the Torrente Bisagno, ca. 20 km NE of Genoa: SALVIDIO, 1990), shales and schists (e.g. *S. imperialis* on the Aritzo micaschists, in the province of Nuoro: LANZA, 1986), granites (*S. supramontis* from the environs of the Cantoniera di Genna Scala, province of Nuoro: LANZA et al., 1995; *S. imperialis sarrabusensis* from Monte dei Sette Fratelli's group, in the province of Cagliari: LANZA et al., 2000 and 2001), ophiolites (e.g. *S. strinatii* from Sassi Neri, municipality of Romagnese, province of Pavia: COVA, 1981; *S. a. ambrosii* from the Passo del Bracco, municipality of Deiva Marina, province of La Spezia), and volcanic rocks (*S. supramontis* from the environs of Dorgali, province of Nuoro: LANZA et al., 1986; *S. imperialis* from the Giara di Gèsturi, municipality of Genoni, province of Nuoro: CAMBONI, 1989; *S. genei* from Montessu, province of Cagliari: LANZA et al., 1995)».

Speleomantes frequents indifferently both natural and artificial environments; among the last ones any suitable underground cavities (abandoned mine galleries, cellars, etc.) as well as surface structures (dry-walls, retaining walls, etc.).

However, though seemingly euryoecius as tolerant of a wide range of habitats, actually *Speleomantes* is fundamentally a stenoecious genus, which, as already been told, is able to survive only in humid and cool environments, which it can found in any season (and almost everywhere within its range) penetrating more or less deeply into the ground.

Since European plethodontids are fully terrestrial their occurrence in the water is to be considered accidental (see § 6.2 «Activity, habitat use and displacement»). UVA et al. (2005), who studied kidney and osmoregulation in *S. genei*, conclude «that *Speleomantes*, that spends its life on land, reasorbs from the preurine, by means of the collecting ducts cells, water and, moderately, ions from the proximal and distal segments. A similar function is seen in te segments of the kidney of some Birds and in Mammals».

According to SALVIDIO (1991), *Speleomantes strinatii* is commonly found *inter alia* beneath leaf litter and in talus, mainly beside streams, in hygrophilic woods dominated by *Alnus glutinosa* (L.) Gaertner and *Ostrya carpinifolia* Scop., but also in mesophilic chestnut woods (*Castanea sativa* Miller), at relatively long distance from any watercourses.

Other vegetational characteristic of the same areas inhabited by the genus are quoted e.g. by VOESENEK et al. (1987), CIMMARUTA et al. (1999), PASTORELLI et al. (2001), and FORTI et al. (2005a).

CIMMARUTA et al. (1999), by analyzing vegetational-climatic conditions of 24 eastern-Ligurian sites inhabited by *S. strinatii* and *S. a. ambrosii*, pointed out that in allopatric conditions both the species are mainly found in mesic environments (i.e. with low mean annual temperature and moderate, all year precipitation) with an high percentage of plant cover (70% to 100%), characterized by mixed deciduous woodlands dominated by chestnut trees (*Castanea sativa*) and mesophilic oak [*Quercus petraea* (Mattuschka) Liebl. and *Q. cerris* L.], *Ostrya carpinifolia, Sorbus aria* (L.) Crantz, *Acer pseudoplatanus* L., *Corylus avellana* L., *Quercus pubescens* Willd., and *Fraxinus ornus* L. But in parapatric conditions with *S. strinatiii*, *S. a. ambrosii* has been found in xeric environments with a scarce plant cover (30% to 70%) such as Mediterranean maquis, garigue, and sclerophyll woodlands with predominant evergreen oaks (*Quercus ilex* L.) and pines (*Pinus pinaster* Aiton and *P. halepensis* Miller), associated with acidophilous bushes of *Arbutus unedo* L., *Erica arborea* L., *Cistus salvifolius* L., *Ulex europaeus* L., *Juniperus communis* L., and the fern *Pteridium aquilinum* (L.) Kuhn (see also § 6.2 «Activity, habitat use and displacement»).

PASTORELLI et al. (2001), by studying the habitat preferences of *S. italicus* on the Appennino Tosco-Romagnolo (provinces of Forlì-Cesena and Rimini), found that the species occurs between 175 [LANDI, 2000; but, according to us, most probably its spreading toward lower spots is locally prevented by pedological constraints (clays, alluvial deposits, a.s.o.)] and 1200 m, mostly between 600 and 1200 meters a.s.l., in mixed mesophilic woods dominated by *Quercus cerris* L. and *Ostrya carpinifolia* (50%) or chestnut tree (*Castanea sativa*) (4%) as well as in microthermic beechwoods (*Fagus sylvatica* L.) (38%) and in the association *Fageto-Abietum* (8%) (of course, these percentages have only a relative value since it was impossible to correlate them with the area effectively covered with the different vegetational formations). Actually, according to our measurements by means of both barometric and GPS instruments, the figure «175 m a.s.l.» given by LANDI (2000) is inaccurate, hence the lower altitudinal limit of *S. italicus* in the studied area should be corrected in about 230 m a.s.l.

The main vegetational characteristics of three localities studied by FORTI et al. (2005b) are outlined hereunder. **1)** locality Colle Matellina, «frazione» Pegazzano, municipality and province of La Spezia, E Liguria, 200-220 m a.s.l., inhabited by *S. a. ambrosii*: a relatively xeric station on limestone covered by an oak-wood of *Quercus ilex* with some plants of *Castanea sativa*, of anthropogenic origin, and *Quercus pubescens* Willd.; underwood with *Viburnum tinus* L., *Rubia peregrina* L., *Hedera helix* L., *Rubus* sp., *Smilax aspera* L., *Asparagus acutifolius* L., etc. **2)** northern slope of the hill «Colle di San Francesco», close to Pian di Mugnone, municipality of Fiesole, province of Florence, Tuscany, 170-190 m a.s.l., inhabited by *S. italicus*: a relatively mesic station on sandstone (arenaria macigno) covered by a rather thick mixed wood, largely of anthropogenic origin, of *Castanea sativa* (dominant) and *Robinia pseudoacacia* L., with some saplings or shrubs mainly growing at its edges [*Fraxinus ornus* L., *Acer campestre* L., *Ostrya carpinifolia, Cornus sanguinea* L., *Sambucus nigra* L., *Ailanthus altissima* (Miller) Swingle, etc.], and an underwood with *Hedera helix* L. (dominant), *Clematis vitalba* L., *Rubus* sp., etc. **3)** southern slope of Monte Maggio, just S of Fungaia, municipality of Monteriggioni, province of Siena, Tuscany, 315 m a.s.l., inhabited by an allochthonous population of *S. a. ambrosii* and *S. italicus*, introduced respectively from the localities 1) and 2), and their hybrids: a relatively xeric station on limestone covered with a rather thick mixed oak-wood of *Quercus ilex* (perhaps dominant) and *Quercus pubescens*, with *Juniperus communis*, *Fraxinus ornus* L., *Rubus* sp., *Crataegus monogyna* Jacq., *Acer monspessulanum* L., *Ligustrum vulgare* L., *Coronilla emerus* L., *Phyllirea latifolia* L., *Smilax aspera*, *Ruscus aculeatus* L., *Asparagus acutifolius*, etc.

CASALI et al. (2002a-b, 2005), in San Marino Republic, found *S. italicus* in a mixed mesophilic wood, dominated by *Ostrya carpinifolia*, *Fraxinus ornus* and *Acer* spp. and with a rich herbaceous undergrowth and scarce shrubs.

In Sardinia the surface habitats frequented by *Speleomantes* range from almost naked rocky zones and maquis to holm-oak (*Quercus ilex*) woods; e.g. VOESENEK et al. (1987), in the Gulf of Orosei, found *S. supramontis* on the northern slope of a hill covered by a holm-oak wood with *Quercus suber* L., *Pistacia lentiscus* L., and *Arbutus unedo.*

According to LANZA (1999c), the range of the continental and Sardinian *Speleomantes* roughly falls within the climatic parameters reported in Table 3. Worth mentioning is that, at low altitudes, the air temperature may exceed 40 °C and, on the continent, go beyond -20 °C; but, of course, *Speleomantes* can easily escape all the climate extremes by going underground. Wind, even if rather strong, is well-tolerated provided that the relative humidity is at -or close to- saturation, as one of us (BL) observed especially on the Apuan Alps (*Speleomantes ambrosii bianchii – S. italicus* hybrid zone; near the northern opening of the Galleria del Cipollaio, m 750-850 a.s.l., 11. XI, at night, under the rain) and in NW Sardinia (*S. genei* subsp. A; mine gallery at Su Corovau, near Domusnovas, m 286 a.s.l., in which, at least in August there is a constant strong draft).

Table 3. Climatic parameters in *Speleomantes* range.

ISOTHERMS	
January	July
a) continent: 4-7 °C	continent: 24-27 °C
b) Sardinia 8-11 °C	Sardinia: 25-28 °C
ANNUAL PRECIPITATION	
a) continent: between 600 and more than 2000 mm (up to more than 3000 mm in some areas, as for instance at Campagrina on the Apuan Alps)	
b) Sardinia: between 600 and 1500 mm	
DE MARTONNE's ARIDITY INDEX [(1)]	
a) continent: between 20 and more than 60.	
b) Sardinia: between 15 and 60.	

[(1)] $I = 12\ P\ (T+10)$ where P is the average monthly rainfall in mm, T the average monthly temperature in °C, and 10 a constant; values less than 20 indicate increasing dryness, greater than 20 increasing wetness.

5.2 Herpetocoenosis

Underground, *Speleomantes* could potentially be in contact with all the local herpetofauna in which all the sympatric amphibians and reptiles spend much of their life there. In the easily accessible surface hiding-places, and often under the same shelters, have been found *Anguis fragilis* L., 1758 (LANZA, 1946 and 1948: with *S. ambrosii bianchii* on the Apuan Alps), *Coronella austriaca* Laurenti, 1768 (LANZA, 1946: with *S. ambrosii bianchii* on the Apuan Alps), *Timon lepidus* (Daudin, 1802) (EWALD, 1977: with *S. strinatii* in the Alpes-Maritimes), *Salamandra salamandra* (L., 1758) (LANZA, unpublished: with *S. ambrosii bianchii*, near Forno, province of Massa-Carrara). P. Laghi & C. Pastorelli (unpublished) found *Salamandra salamandra* with *S. italicus* (near Campigna, on the Apennines, province of Forlì-Cesena), *Salamandrina perspicillata* (Savi, 1821), with *S. italicus* (near Campigna and in the environs of Bagno di Romagna, on the Apennines, province of Forlì-Cesena), *Hemidactylus turcicus* (L., 1758) with *S. flavus* (near Siniscola, province of Nuoro), *Chalcides chalcides* (L., 1758) with *S. i. imperialis* (Castello di Quirra, province of Cagliari), *Algyroides fitzingeri* (Wiegmann, 1834) with *S. flavus* (near Siniscola, province of Nuoro) and *S. genei* subsp. A (near Iglesias, province of Cagliari), and *Natrix natrix* (L., 1758) with *S. italicus* (near Campigna, see above). Riccardo Jesu (pers. comm., 26.X.2002) observed at night *S. strinatii* close to *Tarentola mauritanica* (L., 1758); both the species were in activity on a dry-stone wall at Nervi, near Genoa. SALVIDIO (1991, 1998) reports that in the Bisagno Valley (near Savignone, province of Genoa) *S. strinatii* is often syntopic with *Salamandra salamandra*, *Salamandrina perspicillata*, *Bufo bufo* (L., 1758) and *Rana italica* Dubois, 1987, rarely with *Podarcis muralis* (Laurenti, 1768), *Anguis fragilis*, and *Natrix natrix*.

In caves the genus has been found, in the same rooms and passages but not in mutual contact, with: *Salamandrina perspicillata* (LANZA, 1947: *S. italicus*, Monti della Calvana, province of Prato); *Salamandra salamandra* (BOLOGNA & VIGNA TAGLIANTI, 1985: *S. strinatii*, in Ligurian Alps, province of Imperia; LANZA, 1999c: *S. strinatii*, Arroscia Valley, province of Imperia); *Discoglossus sardus* Tschudi, 1837 (LANZA, 1999c: *S. genei* subsp. A, near Domusnovas, province of Cagliari); *Pelodytes punctatus* (Daudin, 1802) (BOLOGNA & VIGNA TAGLIANTI, 1985: *S. strinatii*, municipality of Pamparato, Province of Cuneo); *Bufo bufo* (LANZA, 1947: *S. italicus*, Monti della Calvana, province of Prato; VANNI & MAGRINI, 1986: *S. italicus*, Monte Morello, province of Florence; BOLOGNA & VIGNA TAGLIANTI, 1985: *S. strinatii*, in Ligurian Alps, province of Imperia; P. Laghi & C. Pastorelli, unpublished: *S. italicus*, on the Apennines, provinces of Modena and Forlì-Cesena); *Hyla sarda* (De Betta, 1857) (LANZA, 1999c: *S. genei* subsp. A, in the above mentioned mine gallery at Su Corovan, near Domusnovas, province of Cagliari); *Rana temporaria* L., 1758 (BOLOGNA & VIGNA TAGLIANTI, 1985: *S. strinatii*, municipality of Triora, province of Imperia; LANZA, unpublished: *S. strinatii*, Arroscia Valley, province of Imperia); *Rana dalmatina* (P. Laghi & C. Pastorelli, unpublished: *S. italicus*, on the Apennines, provinces of Modena and Forlì-Cesena); especially frequent the rather troglophilic *R. italica* (LANZA, 1947: *S. italicus*, Monti della Calvana, province of Prato; VANNI & MAGRINI, 1986: *S. italicus*, Monte Morello, province of Florence; VANNI, 1997: *S. italicus*, near Piteccio, municipality and province of Pistoia; P. Laghi & C. Pastorelli, unpublished: *S. italicus*, on the Apennines, provinces of Modena and Forlì-Cesena, and *S. strinatii* near Savignone, province of Genoa); *Anguis fragilis* (BOLOGNA & VIGNA TAGLIANTI, 1985: *S. strinatii*, municipality of Bardineto, province of Savona), *Natrix natrix* (LANZA, 1947: *S. italicus*, Monti della Calvana, province of Prato; LANZA 1948a: *Speleomantes ambrosii bianchii – S. italicus hybrid* zone, Garfagnana, province of Lucca; BOLOGNA & VIGNA TAGLIANTI, 1985: *S. strinatii*, municipality of Pamparato, Province of Cuneo); *Vipera aspis* (L., 1758) (BOLOGNA & VIGNA TAGLIANTI, 1985: *S. strinatii*, Monte Camoscere, province of Cuneo, and municipality of Rocchetta Nervina, province of Imperia).

Considering the term herpetocoenosis *sensu strictiori*, i.e. as an assemblage of amphibians and reptiles having similar ecological preferences, one may assert that *Speleomantes* actually does not share its niche with any other amphibian and reptile species.

5.3 Predators

According to BERG (1893), who raised specimens from the environs of Genoa (*S. strinatii*) and Florence (*S. italicus*), cave salamanders are eaten willingly by *Natrix natrix* (Linné, 1758) (cf. also SALVIDIO, 1997), *N. tessellata* (Laurenti, 1768) and *N. maura* (Linné, 1758); LANZA (1946; 1948a) found a specimen of *S. ambrosii bianchii* 104 mm long in the stomach of an *Anguis fragilis* Linné, 1758, 330 mm long on the Apuan Alps in the province of Massa-Carrara; a specimen of *S. genei* (subsp. A, near Iglesias) eaten by a small *Natrix natrix cetti* Gené, 1839 is quoted by GENÉ (1839); PUDDU & VIARENGO's (1988) statement according to which *Speleomantes* fall victim to many small mammals and night birds of prey must be considered as an arbitrary inference, partially suggested by the prevalently nocturnal habits of the genus. On two occasions PASTORELLI et al. (2006) first observed *S. italicus* small juveniles preyed by the big troglophilous spider *Meta menardi* (Latreille, 1804) (17.V.1999 and 22.X.2000; cave «Grotta del Tritone», Savio Valley, Forlì-Cesena). For cannibalism and oophagy see under § 6.1 «Feeding behaviour»; for antipredatory adaptations, see at the homonymous § 6.3.

5.4 Parasites

Speleomantes is mainly parasitized by endoparasites, owing to the noxious secretions that avoids approaches by other organisms to its skin. The only one known ectoparasites of the genus is *Batracobdella algira* (Moquin-Tandon, 1846). This greenish, small leech inhabits North Africa, Iberian Peninsula, Balearic Islands, Corsica, Sardinia and perhaps Crimea, parasitizing urodeles and a few anurans such as *Discoglossus* and *Rana* (MINELLI, 1977, 1979); it has been frequently found on the three «giant» eastern Sardinian *Speleomantes* species: *S. flavus* (FURREDDU and MAXIA, 1964; LANZA, 1956; LANZA et al., 1986, Fig. 10; LANZA, 1999d), *S. supramontis* (MINELLI, 1979; LANZA, 1999h; P. Laghi & C. Pastorelli, unpublished), and *S. imperialis* (PUDDU & PIRODDA, 1974; BOCCONE, 1981; PUDDU, 1984; LANZA, 1999f).

In *9 S. italicus*, 10 *S. flavus*, 20 *S. supramontis*, 14 *S. imperialis* and 32 *S. genei* RICCI (1988) found the following parasites: *Chondrostagon haematicum* Babudieri, 1931 (BABUDIERI, 1930; 1931), an enigmatic blood parasite discovered in *S. strinatii* from the environs of Genoa and found also in *S. flavus* and *S. supramontis*, 2 Trematoda [*Brachycoelium salamandrae* (Froelich, 1789) in *S. italicus* and *S. imperialis*; *Halipegus* Loos, 1899 sp. in *S. flavus*], 1 Cestoda (*Nematotaenia minor* Ricci, 1988, in *S. italicus* and *S. flavus*), 6 Nematoda [*Oswaldocruzia filiformis* (Coeze, 1782), in *S. genei*; according to B. Lanza, *O. bonai* Slimane & Durette–Desset, 1995, parasite of *S. genei*, is possibly a synonym of *O. filiformis.*; *Pharyngodon italicus* Ricci, 1988, in *S. imperialis*; *Archeonema lanzai* Ricci, 1988, in *S. supramontis*; *Cosmocerca sardiniae* Ricci, 1988, in *S. supramontis*; *Cosmocercoides speleomantis* Ricci, 1988, in *S. flavus*); *Oxymatium brevicaudatum* (Zeder, 1800) in *S. italicus*], and 1 Acanthocephala [*Acanthocephalus falcatus* (Froelich, 1789) in *S. genei*]. Some Cestoda (family Nematotaeniidae) of problematic systematic allocation, have been found recently in a dozen specimens of *S. strinatii* from the province of Genoa (BURIOLA et al., 2002), and described as *Distoichometra italica* Buriola, Pastorino & Bona, 2005 (BURIOLA et al., 2005; cf. ONETO et al., 2005), belonging to a genus so far known only for America. In the intestine of *S. strinatii* from the province of Genoa STREIFF (1930), SALVIDIO (1990) and PASTORINO (1974) found respectively Cestoda, Nematoda and worms probably belonging to Nematoda (cf. also to DE MARTINI et al., 2004).

At the present stage of research parasitological evidence also seems to confirm that continental and eastern Sardinian *Speleomantes* are closer to each other than to *S. genei*, as the two groups have no genera in common (LANZA et al., 1995).

5.5 Food

Almost all the authors dealing with *Speleomantes* give information on the feeding habits of continental *Speleomantes*; to them one may add WEISMANN (1876), BERG (1896), LANG (1950), HELLMICH (1956, 1962), BRANGHAM (1962), BATINI (1969), GROSSE (1983); however only three papers, all dealing with *S. strinatii*, report detailed data on European Cave Salamanders (MORISI, 1981; SALVIDIO, 1990 and 1992); a fourth contribution by BRUNO (1973, pp. 384-385) cannot be taken into consideration as it is totally and demonstrably a figment of imagination (criticism in LANZA, 1986, p. 311, note 8). For three years MORISI (1981) examined the droppings deriving from more than 300 «feeds» of the animals inhabiting the cave Grotta del Bandito, m 726 a.s.l., in a karstic area near Cuneo (Piedmont), while SALVIDIO analysed the stomach contents of 30 adults and 18 juveniles (1990), and those of 51 mature and 44 immature individuals (1992) in epigean activity, all inhabiting a marl caveless area along a small tributary of the Bisagno Stream, m. 380 a.s.l., 20 km NE of Genoa (Liguria); he used both dissection and stomach flushing, and the two tecniques proved quantitatively equivalent.

According to MORISI (1981) *S. strinatii* does not show any specialization in preying on the organisms characteristic of the deep biocoenoses, as the troglobies and troglophiles represent only 1.27% and 3.36% of the diet, respectively, while the regular trogloxenes (i.e. the elements most typical of the vestibular tract of a cave) and the extracavernicolous forms represent respectively 35.36% and 60%. MORISI (1981) and SALVIDIO (1990; 1992) completely agree in considering *S. strinatii* as an opportunistic predator able to seize all invertebrates of the right size: Oligochaeta, Gastropoda Pulmonata (also the naked ones) Crustacea Isopoda, Araneae, Pseudoscorpiones, Opiliones, Acari, Diplopoda, Chilopoda, Thysanura, Collembola, Blattaria, Mantoidea, Orthoptera, Dermaptera, Hemiptera, Neuroptera, Mecoptera, Trichoptera, Lepidoptera, Diptera, Coleoptera, and Hymenoptera.

The most common faecal remains, found more than 50 times by MORISI (1981), are comprised of the Isopoda, Araneae, Opiliones, Orthoptera (especially the troglophilic *Dolichopoda,* a classic element of the cave parietal fauna), Hemiptera, Diptera, Lepidoptera, and Coleoptera, mainly Carabidae; Hymenoptera were represented by only 14 entire specimens of ants which, according to BERG (1896; quoted also by SCHREIBER, 1912), are deadly if not vomited at once, which is clearly valid only for some species. The taxa most frequently found by SALVIDIO (1990) are Acari, Isopoda and Collembola (56%) in the juveniles, Isopoda, Araneae, Collembola and Diptera (62%) in the adults; the largest volume is represented by Isopoda (ca. 55%), Chilopoda (ca. 10%) and insect larvae (ca. 10%) in the juveniles, and by Isopoda (more than 30%), Chilopoda (more than 20%), Araneae (about 20%) and insect larvae (ca. 10%) in the adults. According to further research made by SALVIDIO (1992) in the same locality, «The utilization of prey taxa by number of specimens and by volume varies seasonally and between size classes, whereas prey volume spectra appear to remain constant within each size group. In mature individuals energy requirements are fullfilled mainly by large food items, whereas small prey are relatively more important in the diet of immature salamanders. Adults have a broader and a more varied trophic niche than juveniles. Values of trophic niche overlap are higher when calculated on prey volume categories rather than on taxonomic categories.» In particular, data show that the taxa more frequently preyed by juveniles are Acarina (28.6%), Isopoda (24.7%), Collembola (15.4%) in Spring, and Pseudoscorpionida (27.1%), Acarina (10.0%), and Diptera (10.0%) in Autumn while adult salamanders forage mainly on Isopoda (18.6%), Araneida (17.5%), Diptera (13.4%), and Collembola (12.4%) in Spring, on Araneida (14.9%), Diptera (14.9%) and Phalangida (8.9%) in Autumn. The analysis of food volume categories provides more informative data, showing that juveniles forage mostly on Isopoda (67.8%), Araneida (8.9%) and Insect larvae (6.2%) in Spring, on Araneida (27.3%), Insect larvae (23.5%), and Myriapoda (11.9%) in Autumn; adult salamanders eat mainly Isopoda (35.6%), Myriapoda (22.3%), Araneida (21.4%) and Insect larvae (11.9%) in Spring, Myriapoda (39.7%), Araneida (22.2%), Isopoda (14.3%) and Gastropoda (7.5%) in Autumn.

SALVIDIO et al. (1994) studied by means of stomach flushing the food habits of *S. strinatii* in an artificial tunnel near Besolagno (Scrivia Valley, province of Genoa). Data from 60 stomach contents showed that foraging occurred mainly on tunnel walls, since more than 80% of the ingested volume was represented by a crowd of the dipteran *Limonia nubeculosa* Meigen, 1804, an element of the parietal cave fauna that does not penetrate into small fissures. Nonetheless, juveniles prey significantly also on coleopterans and myriapods (17% of ingested volume) proving to have a broader trophic niche than adults, a result seemingly contrasting with that obtained with animals feeding on the rock face of a caveless area (see before: SALVIDIO, 1992). According to the author, this could be explained taking into account the spatial segregation that constrains juveniles near the entrance of the cavity and its immediate outside vicinity, where they can prey on a more diversified invertebrate fauna (cf. § 6.2 «Activity, habitat use and displacement»). Recently VIGNOLI et al. (2006) studied the trophic niche of *S. italicus* in central Italy, with similar results to those obtained for *S. strinatii*.

Robert Wiedersheim (personal communication to WEISMANN, 1876) found that the stomachs in specimens from some caves of La Spezia and/or Carrara were filled mainly with scorpions, a statement questioned by HERTER (1941); small scorpions are eaten according to BEDRIAGA (1897) as well. The stomach of several specimens of *S. italicus* from Monte Ceceri, N of Florence, contained small snails, beetles (especially Carabidae and Curculionidae), caterpillars, myriapods and terrestrial isopods; that of a female 108 mm long was misshaped by two sandstone splinters, the largest one 6.5x4 mm, which had surely been swallowed accidentally (LANZA, 1946); also SALVIDIO (1990; 1992) and SALVIDIO et al. (1994) found occasional substances in the stomach contents examined: sand, vegetal fragments, and pieces of exuviae.

The droppings, roughly fusiform, measure 10-12x2.5-4.5 mm in the adults (LANZA, 1999c).

6. ETHOLOGY

6.1 Feeding behaviour

The Cave Salamander's tongue is a morphologically very complex specialized mechanism which enables the animals to catch prey situated at some distance even if fast moving. In fact, adult *S. italicus, S. ambrosii, S. strinatii* and *S. genei* can project their tongue up to a distance of about 4.5 cm and the three «giant» eastern Sardinian species even farther, *S. supramontis* the farthest of all as it has the longest tongue (LANZA et al., 1995; LANZA, 1999h; see also under § 3.3 «Morphological-geographical key to species and subspecies»); their tongue can be projected for a distance only slightly shorter than their body length (cf. ELIOT, 1998), up to 80% of this latter in *S. supramontis* (DEBAN et al., 1997).

The skeletal and muscular mechanisms involved in the tongue projection have been thoroughly studied by SERRA et al. (1991, 2000), by LOMBARD & WAKE (1976) and DEBAN et al. (1997); the latter ones found that the tongue skeleton leaves the mouth completely, so that the tongue protraction is truly ballistic.

The motion picture analyses (ROTH, 1976) show that in *S. italicus* «the tongue projection from mouth to the prey over an average shooting distance of 2.5 cm takes about 1/100 s, the gluing of the prey and the retraction of the tongue lasts about 1/13-1/11 s». As the *Speleomantes* feed either in the light or total darkness, «there are two guidance systems of prey catching behaviour: one visual and one olfactory […]. The visually guided prey catching behaviour is determined by the stimulus parameters: velocity, size, contrast and ambient illumination. Continuously moving objects are effective within a velocity range of 0.05 to 6 cm/s with an optimum at 1.25 cm/s» (ROTH, 1976). *S. genei*, in comparison to *S. italicus*, shows a clear preference for the highest stimulus velocity (3.125 cm/s), which «strikingly corresponds to differences in the general prey catching behaviour of the two species: *Hydromantes genei* responds far more quickly to natural prey and to test stimuli than *H. italicus*» (ROTH 1978, 1987). «Stimuli moving stepwise elicit fixation of the prey and complete approach more frequently than continuously moving stimuli. The prey size which elicits prey catching ranges from 0.5 to 10 mm^2 with an optimum size between 2.5-5.0 mm^2 […]. The prey catching behaviour is hardly impaired by a decrease in ambient illumination down to 0.03 cd/m^2. Beyond 0.03 cd/m2, prey catching activity decreases sharply, but there are still responses at an illumination level of 0.003 cd/m^2. […] *H. italicus* also responds to stationary non-smelling visual stimuli following stimulation by smell or movement». This species is «able to detect prey by smell only both in total darkness and in the light […]. In the light, the prey catching behaviour with regard to smelling objects is inhibited by the absence of visual contrast» (ROTH, 1976). Anyway *Speleomantes* probably prefer to catch prey mainly by means of the visually guided behaviour; studying in the wild *S. italicus* PASTORELLI et al. (2001, 2002a) found that salamanders frequent almost esclusively the lighted part of the cave, and only few individuals were found beyond the point in which light reach 0.0 lux value. Also ONETO & SALVIDIO (2005) confirm that light intensity plays an important role in affecting *S. strinatii* spatial distribution inside a cave.

According to SERRA et al. (1995), who studied retinic photoreceptors of *S. genei* and *S. italicus*, the eyes of the Sardinian species are «[...] particularly fit to work in a scarcely lit surrounding, [...] they seem to be more fitted to adsorb great amount of light than to have a good resolution».

ROTH'S (1976) experiments on prey catching in darkness were carried out also using the pulp of dead flies, cooled down to the temperature of the terrarium so as to exclude shape detection as well infrared, sound and vibration localization. However «one cannot exclude the possibility of the interaction of other sense modalities, such as sound and vibration, to effect the localization of living prey in darkness» [ROTH, 1976; see also, concerning this possibility, SERRA's (1980[i]) and SERRA's et al. (1989[i]) papers on *S. genei*].

Further data on the function, evolution and phylogeny ot the plethodontid tongue as well as on the relationships between feeding mechanisms and nervous system are contained in the papers by LOMBARD and WAKE (1977; 1986), UVA et al. (1979), ROTH (1987), ROTH et al. (1983, 1988a-b, 1990), UVA and DEPLANO (1983), WAKE et al. (1983b), and LARSEN et al. (1989).

The visually guided prey catching behaviour in *S. italicus* (Roth, 1976) «can be divided into fixation, approach (with or without correcting turns of the head), a short stop at the shooting distance, and tongue projection. The fixation is achieved by a moderately quick turn of the head towards the object moving within the animal's visual field. Often the animals follow the prey for a certain time only with their heads. The velocity of the approach greatly depends on the velocity or the intensity with which the prey moves. After having reached the shooting distance (2-4 cm) the tongue projection does not occur immediately in most cases, but the animals wait in front of the prey, move their heads slowly forward for some mm, and only then project their tongues. If, however, a prey moves very quickly, the animals may shoot at it while they are in full motion. They may even catch a laterally passing prey, move their heads slowly forward for some mm, and only then project their tongues. If, however, a prey moves very quickly, the animals may shoot at it while they are in full motion. They may even catch a laterally passing prey by an abrupt turn of the head, in which case they very often project the tongue laterally, sometimes of an angle of more than 45° to the head axis».

Very often *Speleomantes* do not wander in search of prey but simply stay more or less motionless waiting for it, so practicing a low-energy «ambush strategy». FREYTAG (1967; see also DIESENER and REICHHOLF, 1986) writes that the Cave Salamanders «sometimes eat also with the jaws»; but almost surely a feeble protrusion of the tongue occurs in these cases as well; LANZA (1999c) observed this behaviour when the animals met and snapped an earthworm.

The «mysterious» disappearance of some very small *Speleomantes* reared by LANZA (1999c), without feeding, together with adults in small boxes at 4-5 °C raises a doubt about the occurrence of cannibalistic episodes. VOESENEK et al. (1987) observed that a subadult *S. supramontis* was vomited by an adult collected in a cave near Dorgali; they hypothesize that «This cannibalism can be caused by the presence of high densities in a limited optimal habitat as a cave».

With respect to oophagy see § 7.4 «Oviparity, ovoviviparity and parental cares».

According to FISCHER (1887) *Speleomantes* may fast 4-5 months during the winter; LANZA's (1999c) observations show that at 5 °C the fasting can be rather well-tolerated for as long as one year; the young individuals are very resistant as well.

6.2 Activity, habitat use and displacement

So far continental *Speleomantes* have been found active in the field at the air temperatures and relative humidities reported in Table 4.

Table 4. Temperatures and relative humidities values for continental *Speleomantes* activity.

Speleomantes strinatii					
Author (s)	**Date**	**Environment**	**Elevation (m)**	**Temp. (°C)**	**Rel. Hum. %**
CHERCHI 1952	I-XII	cave	-	7-15	88-99.5
CHERCHI 1952	-	cave	480	16	-
CHERCHI 1952	-	cave	35	14-15	98
TORCHIO 1963	24.IV	cave	ca. 100	11	-
THORN 1965	13.V	cave	640	22	100
BOLOGNA 1972	26.III	cave	850	7	-
BOLOGNA 1972	31.III	cave	270	7.5	-
BOLOGNA 1972	9.IV	cave	840	7.5-8.3	-
BOLOGNA 1972	1.V	cave	887	6.2	96
BOLOGNA 1972	20.IX	cave	443	8.3	90
MASSA 1975	-	cave	300	10-13	-
SALVIDIO 1991	8.XII	outdoor	520	8	84
SALVIDIO 1991	24.I	outdoor	520	8	95
SALVIDIO 1991	3.IV	outdoor	520	14	83
SALVIDIO 1991	8.IV	outdoor	440	10	86
SALVIDIO 1991	29.IX	outdoor	410	16	80
SALVIDIO 1991	16.VII	outdoor	380	10	87
SALVIDIO 1991	1.VIII	outdoor	380	19	88
SALVIDIO 1991	2. XII	outdoor	380	5	74
SALVIDIO 1991	26.XII	outdoor	270	8	76
SALVIDIO 1991	1.V	outdoor	220	14	90
SALVIDIO 1991	7.II	outdoor	170	9	80

Table 4. (Following)

Author (s)	Date	Environment	Elevation (m)	Temp. (°C)	Rel. Hum. %
SALVIDIO 1991	28.VI	outdoor	170	12	82
SALVIDIO 1991	1.XI	outdoor	170	16	96
SALVIDIO et al. 1994	I-XII	cave	392	6.7-12.5	>95
SALVIDIO 1998	Annual mean, 1993	outdoor	390	12.7	-
SALVIDIO 1998	Annual mean, 1994	outdoor	390	15	-
SALVIDIO 1998	Annual mean, 1995	outdoor	390	15.3	-
SALVIDIO 1998	Annual mean, 1996	outdoor	390	12.3	-
Speleomantes a. ambrosii					
GRUPPO SPELEOL. C.A.I. BOLZANETO (undated)	Range (IX.1995-XI.1997)	cave	320	13.5-15.0	-
Speleomantes italicus					
MARCHETTI 1931	6.VIII	cave	425	10.4	-
MARCHETTI 1931	25.VIII	cave	964	17.2	-
LANZA 1946	27.III	cave	760	3.8	-
LANZA 1946	10-14.IV	cave	760	4-4.5	-
LANZA 1946	24.VI	cave	760	10	-
LANZA 1946	21.VII-17.VIII	cave	760	11.9-12	-
LANZA 1946	26.X	cave	760	9	-
LANZA 1946	27.III-10.IV	cave	725	4-5.2	-
LANZA 1946	24.VI	cave	725	8	-
LANZA 1946	17.VIII	cave	725	7.5-10	-
LANZA 1946	26.X	cave	715	10	-
LANZA 1946	28.VII	cave	510	17.5	-
LANZA 1946	7.V	cave	610	15	-
LANZA 1946	30.VI	cave	778	9-10	-

Table 4. (Following)

Author (s)	**Date**	**Environment**	**Elevation (m)**	**Temp. (°C)**	**Rel. Hum. %**
LANZA & MARCUCCI 1953	14.IX	cave	430	13.3	-
BANI 1984	-	cave	1100	7	-
LANZA 1999c	31.I	cave	490	11.5	88
P. Laghi & C. Pastorelli (unpub.)	12.IX	cave	1100	12	-
P. Laghi & C. Pastorelli (unpub.)	19.V	cave	1200	10.5	85
P. Laghi & C. Pastorelli (unpub.)	19.V	outdoor	1200	11.3	67
P. Laghi & C. Pastorelli (unpub.)	4.X	cave	930	8.7	90
P. Laghi & C. Pastorelli (unpub.)	25.X	outdoor	1010	13	95
P. Laghi & C. Pastorelli (unpub.)	1.VII	cave	930	8	100
P. Laghi & C. Pastorelli (unpub.)	2.X	outdoor	1010	11	-
P. Laghi & C. Pastorelli (unpub.)	9.X	outdoor	495	16.5	95
P. Laghi & C. Pastorelli (unpub.)	9.X	outdoor	540	12.6	84
P. Laghi & C. Pastorelli (unpub.)	28.IV	cave and outdoor	700	13.0	85
P. Laghi & C. Pastorelli (unpub.)	Annual mean 1999	cave	810	9.5	95
P. Laghi & C. Pastorelli (unpub.)	Annual mean 2000	cave	810	8.9	96

Table 4. (Following)

Author (s)	Date	Environment	Elevation (m)	Temp. (°C)	Rel. Hum. %
P. Laghi & C. Pastorelli (unpub.)	Annual mean 2001	cave	810	9.1	96
P. Laghi & C. Pastorelli (unpub.)	Annual mean 2002	cave	810	9.1	95
CASALI et al. (2002a)	Spring and Fall samples (mean)	outdoor	ca. 550	13.0	-
CALDERA & BOLOGNA (2004)	Range (X.2003-III.2004)	caves	540-1385	2.6-11.3	95-100
SPILINGA et al. (2006)	Annual range (V.2005-IV.2006)	cave	ca. 900	10.1-18.2	83-100

According to these data the continental *Speleomantes* lead an active life between 2.6 and 22.0 °C and at a relative humidity between 67 and 100%, but almost surely their actual tolerance to these factors is a little wider, as the closely related Californian *Hydromantes platycephalus* (Camp, 1916) is active between -2.0 and 11.5 °C, according to field observations by Joe Gorman (unpublished, quoted by BRATTSTROM, 1963; Gorman observed also that this species shows a preference for 13-14 °C in a thermal gradient of 4 to 24 °C); according to DURAND (1970, 1973) continental *Speleomantes* cannot be reared for a long time at a relative humidity lower than 70%. In captivity it is advisable to maintain temperatures lower than 20 °C, even if healthy animals reared in optimal conditions (temperature apart) may tolerate at length temperatures as high as 25 °C [SCHMALZ (1916) in *S. strinatii*; the figure quoted by R. MERTENS (29 °C: 1918) is a misprint (cf. MERTENS 1923: 172, note)] or 23-27 °C [CEI (1942b) in *S. italicus*].

BRATTSTROM (1963), in a review of the thermal requirements of amphibians, draws the following conclusions that perfectly apply to *Speleomantes*: «Terrestrial salamanders are usually the same temperature as the substrate under objects where they are found, if the substrate is moist. Body temperatures of terrestrial salamanders away from hiding places may be as cold or colder than the air, and owing to evaporation from the skin approximate the temperature of a wet-bulb thermometer. As the limits of temperature and moisture are reached, terrestrial salamanders usually retreat deep underground».

On the basis of a series of experiments on the thermoregulation of *S. strinatii* from the province of Genoa, CHERCHI (1952) concludes that these animals: **1)** have a very poor thermoregulatory capability when adult, and a very slight one when young; **2)** tend to have a body temperature a little higher than the environmental one up to an air temperature a little lower than 24 °C, while when this latter exceeds 24 °C (which probably is close to the critical thermal maximum of the species) the opposite occurs; **3)** when the environmental temperature falls within safe limits they slowly adequate their body temperature to the environmental one, while when the latter is close or exceeds 24 °C their thermoregulatory capability decreases strongly and their body temperature rises quickly. In LANZA's (1999c) opinion these conclusions should be checked using a larger number of animals and maintaining them at a higher relative humidity, usually only a little more than 60 % in CHERCHI's (1952) terraria.

The continental *Speleomantes* may be therefore classified as eurythermic (rather oligothermic) and stenohygric animals (LANZA, 1999c). Sardinian species, presumably more warm-enduring than the continental ones (LANZA, 1999d), have been found active in the field at the air temperatures and relative humidities reported in Table 5.

Table 5. Temperatures and relative humidities values for Sardinian *Speleomantes* activity.

Speleomantes flavus					
Author (s)	**Date**	**Environment**	**Elevation (m)**	**Temp. (°C)**	**Rel. Hum. %**
FURREDDU & MAXIA (1964)	-	cave	980	16	75
FURREDDU & MAXIA (1964)	-	cave	700	17-18	87
FURREDDU & MAXIA (1964)	-	cave	710	11	92
LANZA 1999d	5.VIII	cave	1040	11	94
Speleomantes supramontis					
Author (s)	**Date**	**Environment**	**Elevation (m)**	**Temp. (°C)**	**Rel. Hum. %**
SCHWARZER et al. (1984)	III-IV	outdoor	-	12.5	-
MASA (1986)	V	cave	396	-	98
VOESENEK et al. (1987)	19, 20, 21.IV	cave	-	11.0	-
VOESENEK et al. (1987)	20.VI	cave	-	13.0	86
LANZA 1999h	VIII	cave	[142]	15-17.5	94-95
LANZA 1999h	VIII	cave	1227	19.0	90
Speleomantes imperialis					
Author (s)	**Date**	**Environment**	**Elevation (m)**	**Temp. (°C)**	**Rel. Hum. %**
LANZA 1999f	VIII	cave	180	18.5	95
LANZA 1999f	VIII	cave	1025	14.0	94
Speleomantes genei					
Author (s)	**Date**	**Environment**	**Elevation (m)**	**Temp. (°C)**	**Rel. Hum. %**
LANZA 1999e	VIII	cave	286	14.0	94

According to LANZA (1999h), some adult *S. supramontis* tolerated for 3 months, though showing some signs of suffering, daytime temperatures varying between a minimum of 15-23 and a maximum of 18-24 °C.

Following PAVAN's (1944) and RUFFO's (1959) ecological classification of the cavernicoles, LANZA (1999c) agrees with BOLOGNA (1972), GRAFITTI (1980), CASSOLA (1982), etc. in including *Speleomantes* among the troglophiles, i.e. in the category including the animals frequently found in underground caves or passages but not confined to them, and, more precisely, among the eutroglophiles, which -unlike the subtroglophiles- are able to reproduce underground. On the basis of other behavioural characteristics *Speleomantes* may be considered (LANZA, 1986) as «animals essentially rupicolous and nocturnal, as glaringly shown by the webbed limb extremities and the big size of the eyes» (see Fig. 4). LANZA (1991) also wrote: «During growth [...] Hands, feet and tail, for example, significantly increase in a positive allometric manner as to the body length. As the body volume and, consequently, body weight grow according to the third power and the surface of the extremities according to the second one, it is clear that the positive allometric growth of the hands and feet, which moreover are webbed, has an adaptive value in these typically rupicole animals. This type of growth reduces or counterbalances the handicap represented by a body that becomes heavier and heavier with age. The positive allometric lengthening of the tail (accompanied by an increase in the number of caudal vertebrae) has, *mutatis mutandis*, a similar adaptive significance as the Cave Salamander uses this prehensile and very sensitive organ largely when climbing (LANZA, 1991)».

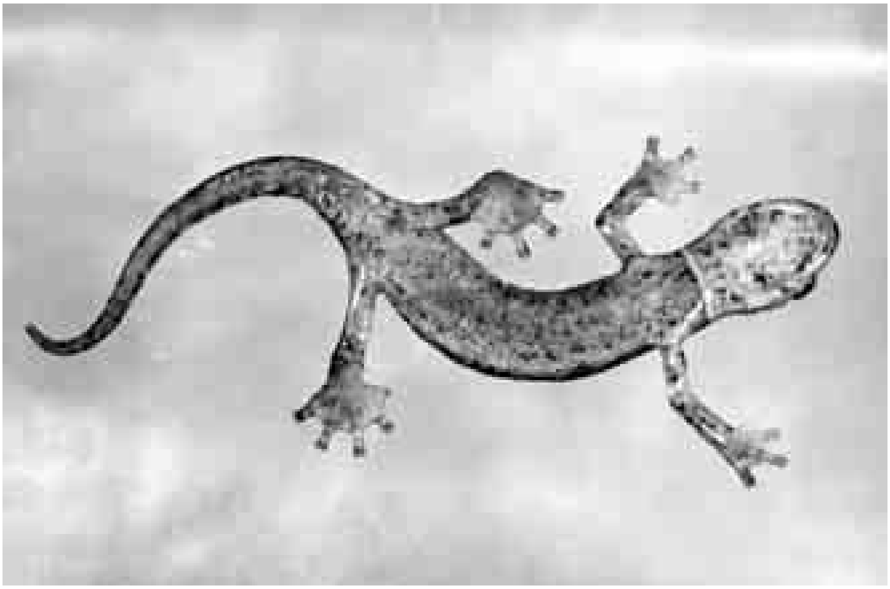

Fig. 4. *S. supramontis*. Ventral view of an adult ♀ from the cave «Grotta di su Bentu» (see Map 4, loc. 4) climbing on a glass. Note the webbed limb extremities. Photo by Isabelle Hunt Conant.

In caves *Speleomantes* frequent almost exclusively the parts not far from the outside; when in these latter the environmental conditions are always consistent with their needs, the animals remain active all year round. One may therefore infer that this should occur also where there are no caverns, as there as well the animals usually have access to a suitable environment in any season simply by means of short-range movements towards the subsoil. According to SALVIDIO (1998), thermal gradients recorded in a rocky zone in nortwestern Italy are comparable to those reported by FEDER (1982) for tropical and other temperate plethodontid microhabitats.

It is noteworthy that even though all the European Urodela (excluding *Proteus* Laurenti, 1768) spend long periods underground, no other salamander is found as often in caves as members of the genus *Speleomantes*, which partially justifies some of their rather misleading common names such as Cave Salamanders, Höhlensalamander, Höhlenmolche, peščernye salamandry, etc. All the above-mentioned eco-ethological characteristics probably work together, to a lesser or greater degree, to enhance the cavernicolous reputation of these plethodontids (LANZA, 1999c). One may suppose that their trend to frequent rocky seminaked or naked surfaces may be conditioned by the propensity to elect open space that allows an optimal utilization of the prey catching system mainly based on the tongue-protrusion mechanism.

On 5.VIII.1970, BOLOGNA (1972) found a male of *S. strinatii* underwater, on the bottom of a fountain of Viozene, a village near Ormea, in the province of Cuneo, m 1250 a.s.l.; on 7 July 1971, after two days of rain, he collected in the same place and situation, at a depth of about 35 cm, another specimen (female) which had been seen there by a farmer the previous evening; the fountain, surrounded by stalls, houses, vegetable gardens and a hazel thicket (*Cory1us avellana* L.), had only mosses along the walls and a thin sand layer on the bottom; the water temperature was 8 °C, and the air, at 07.30 a.m., had a temperature of 15 °C and a relative humidity of 82%. As already written the occurrence of the Cave Salamander in water at least of a certain depth must be considered as accidental; the animals may fall in during their wanderings and are destined to die if the walls of the «container» are too steep, as in water they cannot of course adhere to the substratum. PERACCA (1885) found a drowned specimen of *S. strinatii* in a pool along the road Ormea-Colle di Nava (Cuneo). The statement by LEONARDI (2001: translate from italian) according to which *S. i. sarrabusensis* «needs a lot of water, it is an animal that live in ponds» is completely wrong.

CEI (1941a), studying the water regulation in specimens of *S. italicus* from the environs of Florence, observed that they cannot spend more than 5-6 days in the water, after which they swell and die owing to osmotic troubles; GHIGI and PASQUINI (1958) found drowned Sardinian animals kept in captivity; also according to FISCHER (1887: *S. strinatii* from the environs of Genoa), Berg (1893[i]: *S. strinatii* from the environs of Genoa) and SAUER (1989), cave salamanders drown in water; however FISCHER (1887) observed that his reared animals occasionally, before moulting, willingly entered containers with a film of water and stayed there hours or days.

According to LANZA's (1999c) observations, in an aquarium with 20 or more cm of water, the animals swim rather nimbly with snake-like movements, either horizontally on the surface or otherwise in that direction; when they are tired they sink and stop or walk on the bottom. Animals, maintained underwater in an aquarium provided with an oxygenator and a submerged net preventing them from reach the surface, survive for a more or less long time also in accordance with the water temperature; two specimens (*S. italicus* from the Turrite Cava Valley, Apuan Alps, province of Lucca) submerged in such an aquarium, kept in a semi-dark room where the minimum and maximum temperature varied during the day between 5-9 and 13-19 °C (January-February), survived 29 and 37 days, while two others maintained in an aquarium whose temperature varied between 17-18 and 22-23 °C (May) died after 5 and 6 days.

For data on the longest survival of some completely submerged American terrestrial Plethodontidae see WHIPPLE (1906). The respiratory gular movements stop shortly after submersion (RICCIARDELLI, 1898).

WERNER (1912, quoted by HERTER, 1941: 144) writes that *Speleomantes* may run as fast as lizards; although this is surely an overstatement, cave salamanders -when strongly disturbed- are able to escape with swift snake-like movements. When caught in their shelters or on the wall of a cavern, they either remain motionless or, even if not touched but disturbed by human presence and light, go away slowly in search of another shelter or an inaccessible crevice.

According to PROCTER (1921), in Cave Salamanders the tail «is not only endowed with prehensibility but it has also another function to perform» (about the prehensibility see also BERG, 1893); she writes: «I have studied the habits of sixteen specimens for a period of eighteen months, and find that the end of the tail is largely used as a tactile organ, and that the terminal half or three-quarters of an inch is extremely sensitive. When climbing they frequently pause and feel about them with the end of the tail, using it as an insect uses its antennae [...]. In this manner they either find something to grasp with the tail, or else, satisfied that there is nothing suitable, progress, and then again grope about. They are extremely fond of climbing the plants of their vivarium, and when doing so this method of using their tails is plainly very helpful to them; they grope from side to side in a helpless manner when walking up glass [This groping has nothing to do with the tail movement performed by *Hydromantes*, which uses its tail as a walking stick when climbing (LANZA et al., 1995); see hereunder]. When taking a prolonged walk *Spelerpes fuscus* nearly always carries the tail clear off the ground, or with at least the end portion held well up. This is presumably to keep it from becoming callous or injured in any way by ostacles. In the young *Spelerpes fuscus* the tail is equally sensitive, if not more so. One born in my vivarium on May 8th, 1920, always lifted its tail off the ground when walking usually with the end curled upwards». When climbing, the American genus *Hydromantes*, contrary to *Speleomantes*, points the tail tip towards the substratum, using the tail as a walking-stick to support the body when the foot on the downhill is passed forward to a new position (cf. STEBBINS, 1947). According to the studies by SERRA & STEFANI (1974) and SERRA et al. (1991) this behaviour has its anatomical basis in a complex of muscular and cutaneous specializations: 1) distal insertion of the *ilio-caudalis* muscle reaching the tip of the tail (in *Speleomantes* the insertion is attached to the caudal vertebrae III-IV as well as to the transverse apophysis of the V caudal vertebra); 2) *caudali-pubo-ischio-tibialis* muscle attached to the distal third of the *pubo-ischio-tibialis* muscle (in *Speleomantes* to the proximal third); 3) skin of the tail tip provided with a number of papillae forming «a rough and strong cutaneous envelop» around the organ (any skin specialization in *Speleomantes*) (SERRA et al., 1991).

The way of life of the Plethodontidae is no doubt strongly conditioned by their lunglessness, which was discovered by WILDER (1894) in the American species and confirmed in the European ones by CAMERANO (1894a-c, 1895) and WILDER (1896). In the American species the cutaneous gas exchange may account for more than 90% as the percentage of capillaries in the buccal cavity is usually minute compared to that in the skin, respectively averaging 6.8% and 93.2% in the seven species studied [CZOPEK's (1962) data summarized by DUELLMAN & TRUEB (1986); see also FOXON, 1964]; according to WHITFORD & HUTCHINSON (1965), quoted by DUELLMAN & TRUEB, 1986) plethodontids may obtain up to 24% of their oxygen through the buccal mucosa. There are contrasting opinions about the European species. CAMERANO (1894b: species?; quoted also by LÖNNBERG, 1899 and SCHREIBER, 1912) observed that animals prevented from buccopharyngeal breathing died in a few hours at 14-16 °C and concluded that the skin breathing «gives no effective help». RICCIARDELLI (1898[i]) and GOGGIO (1903[i]) found respectively a survival of 24-50 hours and 15-19 days in specimens of *S. italicus* from the environs of Florence tested at 15-18 and 14-16 °C; according to RICCIARDELLI (1898) the skin breathing, even though about three times less intense than the buccopharyngeal one, represents an «effective he1p»; according to GOGGIO (1903) it is rather important to life at least up to temperatures just a little higher than 10 °C. Also SERRA & STEFANI (1981[i]: *S. genei* from the environs of Iglesias) and SERRA & MANCOSU (1984: *S. imperialis* from Aritzo) attach great importance to the buccopharyngeal breathing and think that the cutaneous one «could be sufficient only for a basal metabolism». On the contrary skin respiration is thought to be of paramount importance by BETHGE (1898), BRUNER (1901), DESPAX (1923), LANG (1950) and ELKAN (1955; 1958a), who even suggested (ELKAN, 1955) «that the gular vibrations are not concerned with exchange but with the sense of smell»; BETHGE (1898) pointed out that in *Speleomantes* the skin capillaries have an exceptionally large diameter of 24-30 µm, i.e. twice that in *Triturus* Rafinesque, 1815, and that the respiratory surface of the buccopharyngeal capillary net is less than a quarter of the skin net surface. The skin and/or buccopharyngeal vascularity has been studied by BETHGE (1898: *S. italicus* ?), CITTERIO (1930[i]: *S. imperialis* from Aritzo), ELKAN (1955; 1958a: unspecified species) and SERRA & STEFANI (1981[i]: *S. genei*). Data on the movements of the buccal floor may be found in BERG (1896[i]: *S. italicus* from Florence and/or *S. strinatii* from Genoa), RICCIARDELLI (1898[i]: *S. italicus*; the most important research, overlooked by the three following authors), GOGGIO (1903[i]: *S. italicus*) and SERRA & MANCOSU (1984: *S. imperialis*); the frequency of these movements, which can stop for longer than a day (RICCIARDELLI, 1898), is, to a certain extent, positively correlated with the temperature and activity degree.

Underground, temperature and moisture permitting, the animals tend to frequent the cavities closest to the surface or, within the caves, the semi-dark tracts near to or not too far from the opening, where are the spots which usually offer richer food resources than the deeper ones and at the same time ensure safety from the risks linked to outside environmental variations (cf. CIMMARUTA et al., 1999 and FORTI et al., 2002a, 2005a: *S. strinatii* and *S. a. ambrosii*; MORISI, 1981 and SALVIDIO et al., 1994: *S. strinatii*; GRUPPO SPELEOLOGICO C.A.I. BOLZANETO, undated: *S. a. ambrosii;* PASTORELLI et al., 2001, 2002a: *S. italicus;* CALDERA & BOLOGNA, 2004: *S. italicus*). Exceptions to the rule, more apparent than real, are subterranean tracts far from the main opening (or openings) but connected with the outside by relatively short secondary passages inaccessible to man, and large vertical potholes where daylight usually penetrates more deeply than into the horizontal caverns and which have plenty of food on the bottom, consisting not only of troglobies and troglophiles but also of a large number of trogloxenes, which have survived the fall. An impressive example is given by the abyss Voragine del Golgo, in the Orosei Gulf, where *S. supramontis* has been found on the bottom, at a depth of 290 m (MASA, 1986).

According to SALVIDIO et al. (1994: *S. strinatii*), PASTORINO et al. (1997: *S. strinatii*), GRUPPO SPELEOLOGICO C.A.I. BOLZANETO, (undated: *S. a. ambrosii)* PASTORELLI et al. (2001 and 2002a: *S. italicus*) and FORTI et al. (2002a: *S. strinatii* and *S. ambrosii*), young *Speleomantes*, when in caves, frequent the zones nearest to the opening, while adult ones are found in deeper zones. Spatial segregation between juvenile and adult terrestrial salamanders has been already reported for a number of American plethodontid genera, e.g. for *Desmognathus* (COLLEY et al., 1989: quoted by SALVIDIO S., 1996). With regard to *Speleomantes* such a segregation in cave environments was first suggested by LANZA (1946) for *S. italicus,* then by SALVIDIO et al., (1994) for *S. strinatii* and is pointed out by data on spacing of *S. italicus* published by PASTORELLI et al. (2001, 2002a: *S. italicus*); SALVIDIO & PASTORINO (2002) assessed the occurrence of such a segregation in *S. strinatii* inhabiting an artificial tunnel in northwestern Italy. They found that juveniles in their first and second years of life concentrate in the twiligt zone (i.e. the section receiving some illumination: in this case the first 7 m from the entrance) that is more exposed to environmental hazards, such as predation and disseccation. In contrast adult salamanders of both sexes were randomly dispersed in the darker and more stable zone. Spatial distribution of adult females and males sometimes don't differ statistically; nevertheless males are found at a higher mean distance from the entrance (cf. PASTORELLI et al., 2002a and 2005: *S. italicus*; SALVIDIO et al., 1994: *S. strinatii;* GRUPPO SPELEOLOGICO C.A.I. BOLZANETO, undated: *S. a. ambrosii*). Also subadults display a random dispersion, suggesting that they have already acquired adult–like spacing and microhabitat use. On the basis of data coming from individually marked females, SALVIDIO et al. (1994) reject the hypothesis that females aggregate near the entrance to lay and brood eggs and as a consequence they infer that the segregation may be caused by some kind of intraspecific behaviour, such as an active avoidance, interference or competition for space and food, both limited resources in the underground environment (cf. FORTI et al., 1997 and CIMMARUTA et al., 1999). According to SALVIDIO et al. (1994), juveniles, during humid periods could move towards the external subsurface environment to reduce interference with adults (including cannibalism: see § 6.1 «Feeding behaviour»), to forage and colonize new zones; this would confirm the statement by LANZA (1946) and ROTH (1976) that cave salamanders migrate from their subterranean habitat towards the epigean environment during spring and autumn.

In *S. italicus* PASTORELLI et al. (2001, 2002a; Savio Valley, province Forlì-Cesena) observed that salamanders frequent almost exclusively the half-lighted parts of the cave, and MORISI (1981) reported that captive *S. strinatii* keeped in total darkness refused any kind of prey; actually *Speleomantes*, though more successful catching in half-light, are able to feed also in complete darkness (ROTH, 1976).

SALVIDIO et al. (1994) pointed out that also microhabitat heterogeneity influences cave salamanders distribution inside a cave, since «Squares with cracks extending deeply into the rockwalls and with irregular surfaces were more frequently occupied than those without cracks and with smooth surfaces».

The distribution of salamanders inside a cave also changes seasonally. In summer, when external conditions are prohibitive, cave salamanders are found at higher distance from the entrance than in spring and autumn (FORTI et al., 2002a, 2005a: *S. strinatii* and *S. ambrosii*; PASTORELLI et al., 2002a, 2005: *S. italicus*; SALVIDIO et al., 1994: *S. strinatii*; VOESENEK et al., 1987: *S. supramontis*).

According to LANZA (1999c; updated and free translation from German), «with external favourable conditions *Speleomantes* move to the surface where they occur in protected (under stones, logs a.s.o.) or exposed positions (see below); such conditions coincide with night or twilight, high relative humidity or rain, and a temperature not -or barely- exceeding 20 °C, but, on occasion, with daylight under a cloudy sky; however, whether in caves or outdoor, activity usually reaches the highest values after the sunset (cf. also MORISI, 1981; SALVIDIO, 1991, 1994: *S. strinatii*; PASTORELLI et al., 2001, 2002a, 2005: *S. italicus*). The animals walk on the ground, preferably not densely herbose, even on paved or asphalted roads as reported by CASALI et al. (2002a: *S. italicus*), or lie in wait in open places such as on piles of stones or, especially, on rocky surfaces -which can be vertical or even projecting- or on comparable artificial structures such as drystone walls, ruins and the outer walls of old country houses.

According to PROCTER (1921), *Speleomantes* (unspecified species), at least in a terrarium, are extremely fond of climbing the plants. Protected surface positions chosen by the animals are underneath rock flakes, logs or rubbish (cardboard, boards, plates, etc.), rarely within fallen decaying trees. On 31.III.1979, by day and with an overcast sky, Luigi Benassi and Alberto Stagi (personal communication to B. Lanza) overtaked and photographed an adult male *S. italicus* on a leafless shrub, about 40 cm above the ground, at the foot of Monte Procinto, near Stazzema, province of Lucca, Apuan Alps». Similarly, on 9.X.2000, at dusk and with cloudy weather, P. Laghi & Dino Scaravelli found an adult male *S. italicus* on a tree trunk, about 50 cm above the ground, in locality Serre Samone, province of Modena, Northern Apennines. On X.2002, at night, P. Laghi & C. Pastorelli observed a subadult *S. strinatii* walking for about 1 m on a *Clematis vitalba* L. stem as thin as a pencil (Bisagno Valley, Savignone, province of Genoa). Further observations showed that *Speleomantes* habit to climb on trees is probably not to be considered so exceptional as presumed by LANZA (1999c). Actually, providing that environmental parameters are suitable for outside activity, *Speleomantes* don't make a difference between rocks, dry-stone walls, trees, poles, or any other kind of structure on which these animals can adhere and walk on. CASALI et al. (2002a-b, 2005) studied the «arboreal habits» of *S. italicus* in the Republic of San Marino, on a north facing slope covered by a mixed mesophilic wood, dominated by *Ostrya carpinifolia*, *Fraxinus ornus* and *Acer* spp. and with a rich herbaceous undergrowth and scarce shrubs. The site was visited at night, between 11 p.m. and 3 a.m., under diverse weather conditions, during foggy, rainy or cloudless days, and even with dry soil, at a mean air temperature of 12-13 °C. During four sampling sessions the authors were able to collect 128 findings of *S. italicus*, of which 83 on trees, 6 on iron poles, and 39 on the ground or on rocks. Salamanders were sighted on tree trunks up to over 3.50 m above the ground, mostly between 31 and 70 cm. No evidence was found on preferential tree use by the different size and sex categories; tree utilization resulted unrelated also to species, trunk diameter and bark characteristics.

SALVIDIO (1991; 1993a), who studied the activity of *S. strinatii* on humid rock surfaces along a small stream, found that above-ground activity of salamanders is strongly seasonal and positively correlated with monthly rainfall. Salamanders were most abundant in late spring (May) and in autumn (October) when temperature were moderated, while activity decreased in winter when temperatures were too low and in summer, when night temperatures were >19°C and relative humidity too low (<75%).

CIMMARUTA et al. (1999) studied ecological needs of *S. strinatii* and *S. a. ambrosii* both in allopatric and parapatric conditions in four different sites, three and one respectively in the provinces of La Spezia and Genoa. They found that «the environmental components having the main direct influence on the number of salamanders foraging on the ground are the external temperature and humidity and the density of invertebrates (mainly *Limonia* flies) inside the retreat [...] These preliminary data indicate that the two species are influenced in their activity on the ground by the same environmental parameters. In particular they need the same kind of retreat (moist and cool) at the same time i.e., under the same environmental conditions (hot and dry climate)» (cf. also FORTI et al. 2002a, 2005a).

In caves and cave-like spaces the *Speleomantes* activity pattern depends on a quantity of disparate parameters, such as the morphology of the cave itself, its geographic position, the nature of its environs, a.s.o.; this accounts for the seemingly contrasting results obtained by different authors and/or in different localities. It is, f.i., obvious that the initial part (i.e. that preferred by *Speleomantes*) of a cave with a large opening is likely to be dry during the summer, while a cave with a small one will usually be humid also in the driest periods of the year. Another important factor is the presence or absence of a parietal fauna on which *Speleomantes* feed; in fact, the animals inhabiting a cave with a rich parietal fauna will tend at a lesser extent to leave the underground environment even with suitable outer conditions (cf. FORTI et al., 2005a).

SALVIDIO et al. (1994), PASTORINO et al. (1997), and ONETO & SALVIDIO (2002, 2005), studied the activity cycle of *S. strinatii* in a artificial tunnel, about 30 m long, located near Besolagno (Scrivia Valley, province of Genoa); they found that hypogean observable activity of *S. strinatii* reaches maximum values in July and August, and show no significant relationship with rainfalls recorded 24 hours before samplings, while it is positively correlated with air temperatures. Both for juveniles and adults the highest correlation coefficients were obtained for temperatures recorded outside or near the tunnel entrance, although salamanders inhabit mostly the central part of the tunnel. PASTORINO et al. (1997) also found that the number of juveniles *S. strinatii* on cave walls decrease in the first hours of the day, while adult ones don't show circadian variations in the activity. In the same gallery ONETO et al. (2003) experimentally verified the occurrence of a meaningful correlation between the activity of *S. strinatii* and the abundance of its prey (mainly the dipteran *Limonia nubeculosa*, see also under § 5.5 «Food») inside the tunnel (cf. also to VIGNOLI et al. 2006). FORTI et al. (2002a, 2005a), studying both *S. strinatii* and *S. ambrosii*, observed summer maximum activity values inside caves, and winter ones outside (cf. also to GRUPPO SPELEOLOGICO C.A.I. BOLZANETO, undated).

PASTORELLI et al. (2002a), studying the seasonal activity of *S. italicus* in a natural cave in North Apennines (Savio Valley, province of Forlì-Cesena), found that *Speleomantes italicus* hypogean observable activity showed great variations throughout the year, with the highest number of salamanders captured in May and September and the lowest in January and December (cf. also SPILINGA et al., 2006), and that such variations were correlated with the inside temperature. SALVIDIO et al. (2001, 2002) observed a similar seasonal activity pattern, i.e. with a spring and a fall peak, also in three *S. ambrosii* populations inhabiting different natural karstic caves (Grotta del Papero, near Riccò del Golfo; Grotta Lunga di S. Antonio, near Pignone; Grotta di Cassana, near Cassana) of the province of La Spezia (E Liguria).

According to LANZA (1999c; updated and free translation from German) «No experimental data exist on the movement patterns, territoriality and orientation capability of the *Speleomantes* species. One may only maintain that they do not undertake any true migration and that their movements -in search of the relatively most favourable conditions, food and maybe partners- are of a "dispersion" type. Observations made in and around caverns have verified that the animals gravitating around a cave and populating it during some periods, sometimes in a very impressive manner, promptly leave it as soon as the environmental conditions become more suitable for them on -or close to- surface. For this reason it is improper (LANZA, 1946, 1991; cf. also FORTI et al., 2005) to distinguish between cavernicolous (let alone "hypogean") and non-cavernicolous (let alone "epigean") populations, as made for instance by BOLOGNA (1982), SALVIDIO (1990, 1991, 1992, 1996, 1998), SALVIDIO et al. (1994), ONETO & SALVIDIO (2005), SALVIDIO (2006), and VIGNOLI et al. (2006); at most, as pointed out by LANZA (1946), there might be a distinction between populations which, according to the geological nature of their home territory, have or do not have caves at their disposition. As a consequence, one may found a *continuum* between populations whose animals feed mainly in caves, and other ones whose animals are forced to go outside to find plenty of food, as there are no caves in the area. Finally, within the same population, one may found that most animals feed in caves in some given periods of the year, or outside in other periods. However, with or without caves, *Speleomantes* are relatively faithful to their subterranean retreats and probably even philopatric. Furthermore, notwithstanding LANZA's (1986) statement that cave salamanders possess much more vagility than is usually understood, they are not really vagil in the purest sense of word. The solution to these problems as well as the assessment of the different dispersion parameters (extent, direction, etc.) depends on badly needed painstaking research». The most important individual active displacement verified up to now has been quoted by FORTI et al. (2005a), who found a specimen 80 m far from the opening of the cave where it had been marked.

According to PASTORINO et al. (1997) *S. strinatii* seems to move from cracks towards the cave, rather than along cave walls, since the studied specimens remained in the same sector (or in contiguous ones) for long periods (a juvenile specimen stayed 24 hours in the same crevice!). Capture-recapture data coming from a sample of 13 *S. strinatii* (individually recognized by means of their hind limb dorsal patterns) showed little displacement; indeed, the animals were always found in an area of 4-8 m^2, and movement rate averaged only 7cm/day (SALVIDIO et al., 1994). According to PASTORELLI et al. (2005), who studied individual displacements of *S. italicus* in a natural cave in northern Apennines, «Home range size, calculated only for 11 individuals captured at least 4 times, averaged 21.75 ± 25.24 m^2 (range = 1.75-82.26 m^2). It goes without saying that the observed home range represents only a part of the actual one, this latter being larger, as it extends also in rock interstices».

SALVIDIO & PASTORINO (2002) state that «the random pattern of distribution characterising adult salamanders of both sexes may indicate a lack of territorial behaviour in *S. strinatii*, as is the case in *Plethodon vehiculum* (OVASKA, 1988)». ZANETTI & SALVIDIO (2006), who obtained preliminary data on the territorial behaviour of *S. strinatii* males in controlled conditions, found no evidence of overtly aggressive behaviours in the tested specimens. They also wrote: «both residents and intruders displayed only exploratory, sensitive or avoidance behaviours» (see also § 6.4 «Communication»).

CIMMARUTA et al. (1999) studied habitat repartition between parapatric *S. strinatii* and *S. a. ambrosii* in eastern Liguria, both at macro- and microenvironmental scale. At a larger scale no syntopic populations exist in the area: *S. strinatii* is found in mesic environments, while *S. ambrosii* in more xeric, and hence less suitable, habitats (see also under § 5.1 «Habitats»); but in allopatry, though *S. ambrosii* and *S. strinatii* clearly prefer mesic environments, both taxa could be found either in mesic or xeric situations. «At a smaller scale, a field experiment artificially created a syntopy, putting together specimens of both species in the same micro-environment [But see also § 9.2 «Threats and conservation guidelines» for criticism to this kind of experiments]. This allowed the study of the spatial distribution of the two species within the environmental micro-patches observed in the caves that *Speleomantes* use as a retreats». About half of the adult population of *S. strinatii* inhabiting a cave sited on Pietra di Vasca Mountain (province of Genoa) was removed and replaced with 51 males and 59 females of *S. a. ambrosii* from a cave near Cassana (province of La Spezia). «The censuses carried out in the cave during the years following the transplantation showed that 44% of the adult specimens belong to *S. ambrosii*. From spring 1993 *S. ambrosii* was reproducing in the site: 56 of the 135 observed newborn were *S. ambrosii*. These data show that the experiment has made the two taxa actually syntopic, and that *S. ambrosii* has settled down in the site. […] *S. ambrosii* was again found mainly in the micro-patches that were less effective as refuges, while *S. strinatii* occupied the patches with steady favourable environmental conditions and abundant prey. The comparison of the two sets of results obtained suggests that the two species compete for cover (i.e., a micro-habitat providing high humidity, low temperature and prey availability even during the dry and hot Mediterranean summer). *S. strinatii* would be the superior competitor, able to confine *S. ambrosii* in the less suitable environment at both scales».

An experiment of *ex situ* artificial syntopy, carried out in a relatively xeric locality of the province of Siena, between specimens of *S. a. ambrosii* and *S. italicus* belonging to two populations respectively inhabiting a relatively xeric locality near La Spezia and a relatively mesic locality near Florence, allowed to demonstrate that *S. a. ambrosii* is clearly prevailing over *S. italicus* (FORTI et al., 2002b, 2005b; see also §§ 3.1 «Systematics, taxonomy and geographical distribution» and 5.1 «Habitats»)

6.3 Antipredatory adaptations

LANZA (1999c; free translation from German) writes: «BRODIE (1977, 1983; see also DUELLMAN & TRUEB, 1986) quotes for *Hydromantes shastae* Gorman et Camp, 1983, and *"Hydromantes genei"* (i.e. *Speleomantes* sp.) the following antipredator adaptations: tail undulation, body elevation, aposematic colouration and noxious skin secretions; however this author gives details only on the tail that is "elevated and undulated at about a 45° angle". The body elevation consists in the arching of the back. Within every *Speleomantes* species, *S. genei* excluded, there are many individuals with sufficiently vivid dorsal coloration to be defined as aposematic. The skin secretions are very irritating to the mucous membrane [cf. the severe reaction, including temporary blindness, suffered by a human after handling an adult *Hydromantes platycephalus* (Camp, 1916): HANSEN, 1990] and noxious; their toxicology has been studied by BENEDICENTI & POLLEDRO (1899a-b: *S. italicus* from the environs of Florence) and PHISALIX (1918 and 1922[i]: *S. strinatii* from the Alpes-Maritimes). The venomous skin glands are spread all over the dorsal parts and, according to my observations, are more crowded close to the eye and on the tail base; the tail base glands, studied by BRIZZI et al. (1991) in the Sardinian species, are not hedonic in nature and have been interpreted as playing "a role possibly involving defensive strategies or, alternatively, the production of pheromone-like substances which may help the animals to recognize each other". The tail undulation seems to direct the predator's attention to the very organ which produces the largest quantity of distasteful secretions». The defensive role of the tail base glans secretion has been later confirmed by BRIZZI et al. (1994, 2001).

According to PASTORELLI et al. (2002b), *Speleomantes* skin secretions are toxic also for human skin; they state that, during the handling of an adult *S. supramontis*, its tail base secretions mixed with urine reached accidentally the eyelid of one of the authors (P.L.), causing after a few seconds a rather painful stinging phlyctenular eruption which lasted about ten days; and it is worth noting that the venom effect was reduced by the prompt eyelid washing with fresh water. This is the first observed case of damage to human skin by tail base glands secretions of a *Speleomantes*, supporting BRIZZI's et al. (1991) hypothesis of their effective defensive function.

PASTORELLI et al. (2002b) first observed biting behaviour of the genus in some adult *S. italicus* from the cave «Grotta del Tritone» (near Bagno di Romagna, Savio Valley, province of Forlì-Cesena). What follows is an updated version of what have been reported in that work: «The observed behavioural sequence was the same in all the tested specimens. The animal, hanged from forceps or hands, rested immobile for a few seconds, then it tried to free itself with quickest coiling-uncoiling escape movements, sometimes while urinating or producing noxious skin secretions particularly from tail base region. In the meantime salamander often opened its mouth, sometimes biting its tail or the forceps. Before, while, or after biting, the animal often strictly coiled itself round the forceps. After some seconds the stressed animal returned to its initial position, remaining stationary or, rarely, repeating the sequence after a while. Biting as defensive behaviour is known for a number of plethodontid salamanders, such as *Aneides* Baird, 1849, *Desmognathus* Baird 1850, *Gyrinophilus* Cope, 1869, and *Plethodon* Tschudi, 1838 (BRODIE Jr. et al., 1989). […] *Desmognathus quadramaculatus* (Holbrook, 1840) use biting to repulse attacks of snakes such as *Thamnophis sirtalis* (BRODIE Jr. et al., 1989). *Speleomantes italicus* may take some advantage by biting behaviour against *Anguis fragilis* and *Natrix* snakes that are both quoted to prey on this salamander [see at the § 5.3 «Predators»]. Also adhesive nature of skin secretions of Cave Salamanders could be used against snakes, as quoted for *Plethodon* and *Ensatina* Gray, 1850 by ARNOLD (1982) […]. Only adult females displayed the biting behaviour. […] the hypothesis of a correlation between biting and nest defence in *Speleomantes* should be taken into account and verified, as it has been experimental demonstrated in some American plethodontids (BACHMANN 1984; HOM et al. 1990). Body coiling has been also observed in several plethodontid salamanders genera, such as *Aneides, Batrachoseps* Bonaparte, 1841, *Desmognathus, Ensatina, Gyrinophilus, Hydromantes* Gistel, 1848, *Plethodon, Pseudotriton* Tschudi, 1838, and *Bolitoglossa* Duméril, Bibron, and Duméril, 1854 (GARCÍA-PARÍS & DEBAN 1995). In *Hydromantes platycephalus*, which is closely related to *Speleomantes*, this generalized escape strategy, associated with tucking limbs close to the body, results in a peculiar rolling antipredator escape behaviour, similarly to those displayed by the anuran genus *Oreophrynella* Boulenger, 1895; this may represent a convergence between two distantly related taxa that both occur on rocky slopes (GARCÍA-PARÍS & DEBAN, 1995). A similar antipredator behaviour was also observed in *S. italicus.* Indeed, this species displayed limb tucking when coiling as a consequence of disturbance, and sometimes dropped down from the cave walls [which, under this point of view, could be assimilated to steep rocky slopes] to the floor; thus, the occurrence of rolling escape or falling escape strategies of the genus should be verified. In *S. italicus* we also observed coiling, abundant skin secretions in tail base region, immobility […] and escape by rapid snake-like or coiling-uncoiling movements».

LANZA (1999c; translated from German) wrote: «Immobility, another antipredation response I observed in the genus, should increase the likelihood that a predator will not distinguish the salamander from its environment; it occurs in *Hydromantes platycephalus* as well (Hansen, 1990)».

It's not even unlikely that the peculiar strong scent emitted by *S. imperialis* as a consequence of handling (STEFANI 1969) could play a role of advertisement for predators that can percept it (see also § 6.4 «Communication»). Recently FAVELLI et al. (2006) first observed the occurrence of tail autotomy (a phenomenon well known in plethodontids: cf. WAKE & DRESNER, 1967) in two specimens (a ♀ and a juvenile) of *S. i. sarrabusensis* from Sette Fratelli mountain (Cagliari). They wrote: «These two specimens, stressed by manipulation due to measuring, after twisting their bodies numerous times lost their tails using the hand of the operator as a fulcrum without loosing even a drop of blood». As in other salamanders which display tail autotomy, also in *Speleomantes* the breakage of the tail occurs intervertebrally; and the tail keeps on moving for a short time after the detachment (Marco Favelli and Stefano Bovero, pers. comm. to C. Pastorelli). Preliminary tests conducted by two of us (P. L. & C. P.) to assess the occurrence of tail autotomy in two other *Speleomantes* species gave always negative responses. Particularly we tested, by hanging them from forceps, 24 *S. a. ambrosii* (12 ♀♀, 2 ♂♂ and 10 juveniles from Pignone, La Spezia) and 6 *S. italicus* (4 ♀♀ and 2 ♂♂ from Verghereto, Forlì-Cesena). Also, as regards to *S. italicus*, we handled hundreds of individuals, from different localities in northern Apennines, in order to take measurements, and we never observed tail autotomy.

In several stressed *S. italicus* very small juveniles, P.Laghi & C. Pastorelli observed a sort of thanatosis, which lasted from two hours to about a day (cf. PASTORELLI et al., 2006).

6.4 Communication

LANZA (1999c; updated and free translation from German) writes «No data exists on this topic, but almost surely chemoreception plays an important role, aside from food search, in intraspecific and interspecific communication, as "many aspects of salamander behaviour, including courtship and territoriality, appear mediated through pheromones. Chemical signals are known to contain information on species, sex, reproductive condition, and familiarity in several species of plethodontid salamanders [...] In courtship, pheromones are thought to play an important role in mate attraction and recognition, persuasion of the female to mate by the male, and coordination of movements of the sexes for successful spermatophore transfer [...]" (OVASKA, 1989). BRIZZI et al. (1991) stated that tail base glands of the Sardinian *Speleomantes* could play a role possibly involving the production of pheromone-like substances which may help the animals to recognize each other. The pheromones involved may originate from specialized glands usually present only in males, or general epidermal odors may be used (OVASKA, 1989). The olfact is very developed (THIREAU, 1977; UVA et al., 1979; UVA and DEPLANO,1983) and chemoreception is improved by the nasolabial groove (BROWN, 1968): the liquid contacting the base of the nasolabial groove rapidly passes upward to the nostril by capillarity and then, by ciliary action into the nasal chamber, over the chemoreceptors of Jacobson's organ and down through the internal naris into the pharynx». According to ZANETTI & SALVIDIO (2006) who observed «nose-tap» behaviour in *S. strinatii* males under controlled conditions, «The data suggest that intraspecific chemical communication is present in *Speleomantes*, and that males are apparently able to recognise a substrate marked by a conspecific, and seem attracted by it». Also the *Speleomantes*' male vent glands, a small gland cluster occurring just in the posterior angle of cloaca, should release courtship pheromones (BRIZZI et al., 2004). According to PIEROTTI (2002), *Speleomantes* are territorial animals, able to use pheromones as territorial markers, for orientation and conspecifics recognition (sex recognition, as well as «dear enemy» recognition). Actually these statements are not supported by experimental data, and must be considered as arbitrary inferences, suggested by the occurrence of such behaviour in some American plethodontids, especially *Plethodon* (cf. MADISON, 1969; JAEGER & GERGITS, 1979; JAEGER, 1981; JAEGER et al., 1986; OVASKA & DAVIS, 1992; GILLETTE et al., 2000).

Regarding the *Speleomantes* inhabiting a cave close to the Castello di Medusa (near Samugheo, province of Oristano) LANZA (1991) writes: «The peculiar, strong and pervasive scent given off by this species when handled (STEFANI, 1969), owing to the high number of specimens I was forced to touch, rapidly spread in the cave, without however causing any apparent warning response in the colony» (See also § 6.3 «Antipredatory adaptations»).

7. REPRODUCTION AND DEVELOPMENT

7.1 Sexual dimorphism

According to LANZA et al. (1995: 62, updated version; see also LANZA, 1999c) «The best external characters for distinguishing the sex of adult *Speleomantes* are the hedonic chin gland and the enlarged premaxillary teeth, both occurring only in the male, and the cloacal morphology.

The chin or mental gland was discovered, probably in *S. italicus*, by WIEDERSHEIM who inappropriately named it "Submaxillar-Drüse" (1875: 179-180 and footnote 1; see also 1876: 9-10 and pl. I Fig. 2); afterwards it was studied by LESSONA (1883: 134, Fig. 21), FISCHER (1892: 6-7), NOBLE (1927: 14, Fig. 6), SEIFERT (1932) and especially by LANZA (1959: *S. strinatii, S. ambrosii, S. italicus, S. flavus*), BORGIOLI (1977: *S. italicus*), BRIZZI et al. (1991: all the *Speleomantes* species), and TESTA-RIVA et al. (1993: *S. genei*), who described its structure and ultrastructure. The mental "gland", actually a cluster of about 100-230 glands according to LANZA (1959: see above), is a subtriangular to elliptical, flat or feebly concave bulge of the anterior intermandibular area, not exceeding 5.5 mm in width and 4.2 mm in length [see Fig. 5]. It is more or less well-developed in any season and is sometimes already detectable in specimens with a body length of 40 mm (cf. also PASTORELLI et al., 2001: *S. italicus*); however the mental gland, whose development is directly correlated to the degree of testes maturity, varies individually so that occasionally it is not yet evident in larger specimens or, rarely, even in specimens with a body length of 48 mm.

The hedonic gland cluster occurring in the dorsal skin of the tail base of certain American plethodontids is lacking in the genus *Speleomantes* (BRIZZI et al., 1991).

Also the enlarged functional premaxillary teeth, usually two on each side, appear first in males with a body length over 40 mm»; their function is described in the § 7.3 «Mating behaviour».

In *S. flavus* LANZA et al. (1995) and LANZA (1999c, 1999d) found two males with a body length of 42 and 44 mm without chin gland, and two other males with a body length of 48 and 52 mm in which it was hardly detectable. In *S. supramontis,* according to LANZA et al. (1995) and LANZA (1999c, 1999h) the chin gland and lengthened premaxillary teeth may seldom be rather well-developed in specimens with a body length of 45 mm, but the same characters are exceptionally badly-developed still in individuals with a body length up to 55 (59) mm. In *S. imperialis* the male secondary sexual characters are usually already present in animals with a body length of 50 mm, but the chin gland may occasionally be absent in males with a body length of 55 mm (LANZA et al., 1995; LANZA,1999c, 1999f). In *S. genei* the male secondary sexual characters are usually already present in animals with a body length of 42-44 mm, but occasionally only a poorly developed chin gland occurs in specimens with a body lenght up to 61 mm (LANZA et al., 1995; LANZA, 1999c, 1999e).

Usually in the males the anterior ⅔ of the cloacal inner surface begins to show a feeble papillosity before the development of the chin gland and enlarged premaxillary teeth; in the female the cloacal inner surface is instead folded (for more details see LANZA et al., 1995: 44).

The snout is more projecting in the males and its ventral surface is usually more or less concave, while it is flat in the females (LANZA 1999c).

«According to BEDRIAGA (1897), in the females the anterior end of the cloacal slit is closer to the posterior attachment of the hind limbs than in the males. This has been confirmed by AELLEN (1958) who found the following percentages in 30 adult and subadult specimens of *S. strinatii* from southeastern France (distance between posterior hindlimb attachment and anterior end of cloacal slit x 100 : body length): 8 males 5.32(5.9)6.53%; 22 females 1.58(3.3)3.90%. These differences appear to be excessive if compared with the data by LANZA et al. (1995), based on 22 specimens from the provinces of Imperia, Savona and La Spezia: 11 males 3.33(4.91)6.04%; 11 females 3.17(4.24)5.17%. Also the personal elaboration of some measurements given by BOLOGNA & BONZANO (1975) shows only a modest average difference between the two sexes (8 males and 7 females from the province of Imperia). Consequently this character is not reliable for distinguishing sex» (LANZA et al., 1995:63).

The females, which may reach a larger size than the males (cf. also SALVIDIO & BRUCE, 2004), differ significantly from the latter ones also in a number of body ratios; adult females for instance, have relatively shorter legs and a longer trunk, so that their fingers and toes do not overlap when appressed (further details in LANZA et al., 1995 and LANZA, 1999c-h).

Concerning the size, LANZA et al. (1995) and LANZA (1999c-h) found that females average larger and reach a larger size than males [preserved adults; tl=total length, in mm; bl=body length, in mm (from snout tip to the anterior end of the cloacal slit)]: ***S. strinatii*** (including ***S. ambrosii***) ♂♂ tl=78(96.28)116 (n=149), bl=40(53.31)64 (n=167); ♀♀ tl=76(100.34)128 (n=130); bl=41(55.93)68 (=156); ***S. italicus*** ♂♂ tl=76(93.54)112 (n=55), bl=40(52.20)63 (n=58); ♀♀ tl=77(95.68)120 (n=38), bl=40(56.23)67 (n=42); ***S. flavus*** ♂♂ tl=91(110.25)127 (n=12), bl=48(60.00)70 (n=14); ♀♀ tl=84(114.75)146 (n=24), bl=50(63.92)80 (n=26); ***S. supramontis*** ♂♂ tl=87(109.17)135 (n=29), bl=52(60.47)75 (n=38); ♀♀ tl=89(113.53)133, bl=47(63.60)76 (n=55); ***S. imperialis*** ♂♂ tl=88(112.21)133 (n=57), bl=50(60.85)72 (n=66); ♀♀ tl=86(111.29)150 (n=44), bl=50(62.16)78 (n=61); ***S. genei*** ♂♂ tl=75(94.14)115 (n=49), bl=43(52.58)61 (n=55); ♀♀ tl=75(96.23)124 (n=42), bl=40(52.00)68 (n=50).

In 36 *S. strinatii* from the Bisagno Valley (province of Genoa, Liguria) SALVIDIO (1993a-b) found that females averaged larger and reached a larger size than males [bl= ♂♂ 50(58)68 mm, ♀♀ 58(64)74 mm; these data are not perfectly comparable to those by LANZA et al. (1995), LANZA (1999c-h) and PASTORELLI et al. (2001), as SALVIDIO (1993a-b) measured the body length from snout tip to the posterior end of the cloacal slit].

Analyzing morphometric data coming from 198 captures of *S. italicus* from the province of Forlì-Cesena, PASTORELLI et al. (2001) found that females body length (snout tip - anterior end of the cloacal slit) varied from 42 to 70 mm, while that of males ranged between 42 and 63 mm.

Also in the other members of the tribe Bolitoglossini the sexual size dimorphism is female biased (BRUCE, 2000).

Fig. 5. *S. italicus* mental gland. ♂ (head in ventral view) from the cave «Grotta del Tritone», 43°53'52''N – 11°58'06''E, 810 m a.s.l., Bagno di Romagna, Forlì-Cesena. The enlarged premaxillary teeth appears as two reflecting bulgings of the upper lip border. Photo by P. Laghi & C. Pastorelli.

7.2 Gametogenesis

According to LANZA (1999c: 119-121; updated and free translation from German), «The spermatogenesis of *S. italicus* has been extensively studied in the field by TERNI (1908, 1910, 1911) in specimens from the environs of Fiesole (near Florence) and Valdicastello (near Pietrasanta, on the Apuan Alps, province of Lucca), as well as, to a lesser extent, by CEI (1942b: *S. italicus* from Fiesole and the Monti della Calvana, near Florence), GALGANO [(1959 [i] and 1960 [i] *S. italicus* from Cardoso (near Stazzema, Apuan Alps, province of Lucca) and Fiesole] and UVA et al. (1973: *S. strinatii* from Savignone and Monte Fasce, near Genoa, and the environs of La Spezia); some data may be found also in GALGANO (1942, 1943, 1952, 1952a, b), LANZA (1951) and GORMAN (1956). In natural conditions a spermatogenetic stasis occurs during the cold months, when the testis contains only mature spermatozoa, protogonia (here corresponding to Witschi's "freien Spermatogonien" ("free spermatogonia") and the "primary spermatogonia" of the English and American authors), spermatogonia (= secondary spermatogonia) and pachytene spermatocytes; the spermatozoa leave the lobules during the winter but overall in the spring and are completely lacking in the testis during part of the summer; however, in spite of the statement by UVA et al. (1973), the spermaducts contain spermatozoa all year round (TERNI, 1911; LANZA, 1959; GALGANO, 1960) and, as observed by LANZA (1951), these latter, as in other urodeles, may be discharged with the urine independently from the spermatophore formation. Up to now *Speleomantes* is the only European amphibian in which the pachytene spermatocytes do not degenerate during the cold season; another of its peculiarities is represented by the extremely long spermatogenetic cycle as there is about a 20 (TERNI, 1911) or 28 to 29 (GALGANO, 1959) month span between protogonia and mature sperm cells; as the sperm discharge is annual, it is obvious that 2-3 subsequent cycles partially overlap each other in the course of the year. The differences between TERNI's and GALGANO's data might be ascribed to different environmental conditions. TERNI (1911) observed in specimens from Pietrasanta, not far from the sea, that some spermatogenetic phases were about a month in advance compared with those of the animals from Fiesole, a rather "continental" locality, and CEI (1942b) found a difference of about 15 days between specimens respectively collected near Fiesole (m 300 a.s.l.) and on the Monti della Calvana (more than 700 in a.s.l). Also, CEI's (1942b) experiments with animals reared in a hothouse show that spermatogenesis is temperature dependent and, according to LANZA's (1951) classification, "potentially continuous" as the winter stasis may be removed by high temperatures.

The occurence all year round of spermaductal spermatozoa and of well-developed secondary sexual characters allow hypothesizing the combination of a seasonal spermatogenesis with an aseasonal mating activity (LANZA, 1959).

Also ovogenesis, according to Cei's scanty observations, seems to be temperature dependent.

CEI's (1942b) and LANZA's (1951) statement that the photoperiod, due to the habits of *Speleomantes*, is probably scarcely or not at all influential on spermatogenesis, is to be checked.

The sperm cell has been studied by BALLOWITZ (1906: in an unspecified continental species) and TERNI (1911: *S. ita1icus*). Preliminary ultrastructural observations on that of *S. strinatii* (from Grotta del Bandito, near Roaschia, in the province of Cuneo, Piedmont; pers. comm. from Franco Andreone, 12.XI.2003) have been published by TRIPEPI et al. (1989). Sperm cells of *S. italicus, S. genei, S. imperialis* and *S. supramontis* have been recently described by SELMI et al. (2000), according to which their morphology is uniform and without any substantial differences in respect of those of the American plethodontids. The spermatozoa of *Speleomantes* are extremely long: 650-700 µm (WIEDERSHEIM, 1875), 750 µm (TERNI, 1911), 850 µm (TRIPEPI et al., 1989), 600-800 µm (SELMI et al., 2000).

TERNI (1909), among about 200 testes histologically studied, found two ovocytes, each with a diameter of ca. 0.8 mm, within a testicular lobule of a *S. italicus* collected on August at Valdicastello».

7.3 Mating behaviour

LANZA (1999c: 132-135; updated and enlarged free translation from German) writes: «The mating behaviour of the genus is scarcely known. BEDRIAGA (1897) obtained spermatophores, laid on the ground, from some captive *Speleomantes* sp. in October. Courtship was first observed by MERTENS (1923), probably in *S. supramontis* (or *S. imperialis*). "On April 10, 1923, a few minutes after eleven in the morning, I noticed that my brighter colored beast was meddling with the larger (almost 100 mm long) but somewhat duller one. The first I took from the beginning to be a male, the latter was to all appearance a female. They lay hidden among moss most of the time; only the head and the end of the tail (which kept up peculiar waving and writhing movements, perhaps tactile) visible. The male began to rub with his head first the tail and then the head of the other animal. When, a few minutes later, she crept out of her hiding place, the male climbed on her back, his head lying over the head of the female. He embraced the female with his arms right back of her armpits; body and tail were closely appressed to hers; both beasts then began to wave their tails in a lively fashion. The female had the energy to crawl forward; the male on her back was carried along so for a short distance. After about 3-4 minutes the male released the female; then it came back again. Then he sought the back of the female again, and this time embraced the neck in front of the arms. The peculiar snaky tail movements of the beasts, especially of the female, were seen again. […] This time also the male did not remain long on the female. As she crept up on the glass wall of the tank, the male followed and tried to climb on her there, in which he succeeded. The female could not cling to the wet glass with the male on her back, and it fell with her burden to the floor, where she broke loose from the male, and, apparently frightened, swiftly sought her accustomed hiding place, a narrow hollow under a flat stone. The male crept back on the glass wall, where he stayed quietly. This Liebespiel lasted not longer than 15 minutes. Further mating attempts, as well as deposition of spermatophores were not observed». SERRA (1968[i]) has confirmed in *S. genei* what MERTENS (1923) observed in the courtship probably of *S. supramontis* (or *S. imperialis*).

As BEDRIAGA (1897) had obtained spermatophores in October and had observed mating in April, MERTENS (1923) concluded that *Speleomantes* perhaps mates twice a year but at the same time he did not exclude the possibility of an aseasonal mating (but see also at the chapter 8 «Population dynamics»). NOBLE & BRADY (1930: unspecified continental and Sardinian species, respectively quoted as *Hydromantes italicus* and *H. genei*) studied the courtship of a series of plethodontid salamanders in a dark room using a red light for illumination. They write: "the general pattern of courtship is essentially the same in all these species even though some are aquatic and some are terrestrial. In all species, so far as determined, there is a series of preliminary rubbing movements during which the male applies his lips, cheeks, mental gland, or side of body to the snout of the female. This arouses the female's interest in the male. In the second phase of the courtship, the female follow the male [not in *Speleomantes*! See later] […]

another distinctive position noted [at the height of the courtship] especially in *Stereochilus* and *Hydromantes*, is the forcing of the mental gland tightly over the nostrils of the female while the male mantains a position directly over her back […] We obtained the spermatophore of *Hydromantes genei*. This was deposited on top of a damp flower pot. It resembled the spermatophores of *Eurycea* but was much larger and had less gelatinous material forming the base. Further, we have many records of courtship activity on the part of the males of this species. We have observed them astride females for extended periods, pressing their mental pads over the nostrils of the female [cf. NOBLE, 1931: 385, Fig. A]. But we have never seen the females follow the males as in the case with other plethodontids. Whether this was due to the failure of the females to exhibit sexual activity or whether this performance is not a part of the *Hydromantes* courtship pattern, we are at present unable to say". The courtship of *S. supramontis* has been described also by REHBERG (1960; translated from German): "While previously I've never had the chance to observe the mating of the animals, I catched them during courtship on 10.I.1960, at 10 p.m., with a temperature of +12 °C. The terrarium having been just cleaned, this may have had a stimulating effect. The switch-on of the cover light did not disturb the male, and in fact he continued his efforts towards the female. He was lying on the female's back with the head bent downwards so that the chin hedonic gland was resting on his partner. Their heads remained pressed against each other without the sideward movements characteristic, e.g., of *Aneides* and *Ensatina* courtship. With his fore- and hindlimbs the male tried to get hold at female's neck and flanks, while his tail performed snake-like movements. The female crawled around on the ground carrying the male and trying to disembarrass herself of him, having possibly been disturbed by the switch-on of the light. When, after 15 minutes, the male was rejected, he immediately tried to mount the female again. However she stepped aside and the male abandoned his efforts. The courtship was observed again the next evening. This time also the female showed more interest in. She performed snake-like tail movements as the male and kept her eyes retracted in the orbits without offering any resistance. I moved back so as not to disturb the animals. Since I failed to found any spermatophore in the terrarium, it remained doubtful whether fertilization had occurred".

Some other data on the courtship have been given by DURAND (1970, 1973; translated from French): "When he approaches the female, the latter reacts with tail movements; the courtship follows with axillary clasping as described by MERTENS [1923] in *Hydromantes genei*. On June 1966 and August 1967, I had the chance to observe what may have been the beginning of a courtship in *Hydromantes italicus gormani*. The bright coloured male, stays with his tail lightly raised in front of the female which keeps flattened on the ground. He caresses her flanks with the snout. At this moment might intervene the mental gland. Anyway the precise courtship modalities are poorly known as the light, necessary to the observer, notably disturb the animals".

According to ORGAN (1961) and ARNOLD (1972, 1976, 1977), the male plethodontids use their enlarged and protruding premaxillary teeth to scarify the female skin so that the edonic secretions of their chin gland may enter the blood system, in short performing a true aphrodisiac vaccination to rouse his partner (see also LANZA et al., 1995: 23)».

A sequence of colour photos of *Speleomantes* courtship, snapped by Salvatore Spano, were published in LEONARDI (2001) [the first four photos published refer to *S. genei* subsp. A from the environs of Domusnovas, various days of IV.2001; the last two photos refer to *S. imperialis sarrabusensis* from the forest of Minniminni, Sàrrabus, at the end of III.2001 (S. Spano, *in litt.*)] (Fig. 21). *Speleomantes* courtship during the so-called «vaccination» phase has been observed and photographed by PASTORELLI et al. (2001) in *S. italicus* overtaken on 19.V.1999 in the cave «Buca delle Fate di Badia Prataglia» (cadastral number 984 T/AR, 43°48'25"N-11°52'35"E, 1175 m a.s.l., near Badia Prataglia, province of Arezzo) (Fig. 6).

Fig. 6. *S. italicus*. Pair in courtship (♂ above) from the cave «Buca delle Fate di Badia Prataglia». Photo by P. Laghi & C. Pastorelli.

7.4 Oviparity, ovoviviparity and parental cares

LANZA (1999c: 117-119; updated and free translation from German) writes: «It is very demoralizing to realize that often our "knowledge" on the eco-ethology of a lot of taxa must be compared to a clay-footed colossus, being based almost completely or exclusively on a combination of mistakes, inaccuracies, misinterpretations, hypotheses raised to truths, bad uncritical copying, and even fiction, all of which is difficult, or impossible to disentangle. A particular instructive example is offered by the data concerning the reproductive biology of the genus *Speleomantes* for which I have taken into consideration only the few first-hand and reliable papers, while a part of the second-hand ones -dealing with either the continental or Sardinian species- are simply quoted, usually without any comment: CAMERANO (1885), BOULENGER (1910), WERNER (1912), SCHREIBER (1912), VANDONI (1914), DUNN (1926), NOBLE (1927; 1931), OPPENHEIMER & PINCUSSEN (1930), LANZA (1946; 1986), NELSEN (1953), VANDEN EECKHOUDT (1954), GORMAN (1956), SCORTECCI (1957), ELKAN (1958a, b), GHIDINI & ORSINI CAPOCACCIA (1959), REEDER (1964), FREYTAG (1967, 1970,1971), SIMONETTA (1968), CAPOCACCIA (1968; 1971), POZZI (1968; 1978), VILTER & DURAND (1970A), SERRA (1972B), CAVAZZUTI (1974; according to his absurd statements, the eggs, abandoned in subterranean streams, are flushed outdoors where they hatch; the "completely developed" animals than go back to the same place where oviposition occurred ?!), BRICOUX (1975), EWALD (1977: insemination occurs by juxtaposition of partners' cloacae ?!), ARNOLD & BURTON (1978; 1979; 1985), GRAFITTI (1980), ODELL (1981), MATZ (1983a-b), GROSSE (1983), BANI (1984), BALLASINA (1984a-d), OBST et al. (1984; 1988), ENGELMANN et al. (1985), SUTTO & PAOLI (1985), NUSSBAUM (1985), BOGLIANI & BARBIERI (1986; 1988) DELSOL (1986), PUDDU & VIARENGO (1988), CAPULA (1989), CASU (1989: "eggs laid amidst the sand" ?!), FERRI (1996), GATTELLI [2001: "the female lays small clutches of eggs inside holes digged by herself" (?!), a wrong statement, occurring also in POGGIANI & DIONISI, 2003], ACEMAV COLL. et al. (2003: 319; it's false that "The egg clusters adhere to the lower face of rocks or to rock crevices").

No field data exist on the egg laying place and time of the continental species. DURAND (1967a-b; 1970; 1973) collected *S. strinatii* in a cave near Peille (Alpes-Maritimes) and raised them in a terrarium (2). About three months later, during the night of 6 November 1966, he recorded the oviposition of a specimen (DURAND, 1970): "hidden among the stones and moss of the terrarium, a big female of *Hydromantes italicus strinatii* laid her egg mass directly on the clay" [see Fig. 7]. Later on DURAND (1967b: a female of *S. strinatii* from Sospel, Alpes-Maritimes; 1970 and 1973: *S. strinatii* from the Alpes-Maritimes and *S. italicus* and/or *S.ambrosii* from the Apuan Alps) obtained 13 more ovipositions staggered between February and September. However, notwithstanding the absence of any direct evidence, one may infer that also in nature the continental *Speleomantes* lay their eggs underground, presumably in holes safe from dangerous environmental extremes. The evidence given by DURAND as well as the presence in *Speleomantes* of a spermatheca (FISCHER, 1892; BOISSEAU & JOLY, 1973, maybe in the continental species; SERRA, 1968[i]: *S. genei* from near

(2) DURAND (1970, 1973; also *in litt.* 29.V.1986) reared his animals, collected on the Alpes-Maritimes (SE France), in the province of Genova and on the Apuan Alps, in the natural cave of the Laboratoire Souterrain du C. N. R. S. (Moulis, Ariège, France) at a temperature of about 12 °C and a relative humidity of 95% or more; the terraria had a clay bottom strewn with big stones and moss.

Iglesias; SERRA, 1972a[i]: *S. flavus, S. imperialis* from Villasalto and Nurri, *S. genei* from near Iglesias; SEVER et al., 1990: *S. strinatii*; cf. LANZA, 1946 and 1959), seems also to justify that egg-laying may occur all, or almost all, year round (but see also under the chapter 8 «Population dynamics»). Recently PAPINUTO (2005) was able to observe in the wild the behaviour of a *S. genei* brooding female and its hatchlings; the eight newborns hatched on 31.VIII.2005, about four and half months after the founding of the brooding female, occurred on 11.IV in a mine gallery near Domusnovas (province of Cagliari).

Up to 1966, when STEFANI & SERRA described the first egg mass of a *Speleomantes*, it was thought that it was live-bearing, as supposed since 1885 by CAMERANO (1885) and seemingly demonstrated by the finding in terrarium of some very small specimens assumed to be newborns (BERG, 1896; PROCTER, 1920 and 1921; CEI (1942a).

In the course of several years, BERG (1893) reared 123 specimens of *S. strinatii* from Genoa and *S. italicus* from Florence in a very humid terrarium rich in hiding-places, many plants, and the bottom covered with a thick earth layer; temperature ranged between 6 and 20 °C respectively in winter and summer. Berg (1896[i]: *S. italicus* from Florence and/or *S. strinatii* from Genoa; cf. also LANZA, 1999c) reports on finding his first "clearly newborn", 36 mm long, on 28 March 1984, followed 18 days later by three more, and then a fifth specimen, 38 mm long, on 8 July of the same year; *the author ruled out any possibility that these specimens were hatched from eggs laid "in" the moist earth*. PROCTER (1920, 1921: unspecified species) exhibited and remarked on a specimen, 30 mm long, born on 8 May 1920. Cei (1942a[i]: *S. italicus* from the environs of Fiesole, near Florence) gave a short description of the outer and internal morphology of a "newborn" 30 mm long found on 9 March 1941 in a terrarium containing some adult females, at a temperature a bit higher than the environmental one. As true "newborns" are only 22-23 mm long (DURAND, 1967a; 1970; 1973) the above-mentioned animals, notwithstanding BERG's (1896) opposing opinion, were almost surely already present incognito within the materials put in the terrarium (leaves, moss, humus etc.) or born by eggs which had escaped notice. This hypothesis is supported also by some ROSSI's and LANZA's data; ROSSI (1894[i], 1895[i]: *S. italicus* from the environs of Florence), in May, observed no sign of embryonation in any of the eggs found in the oviducts, even in their terminal parts, of two animals; an egg was also probably present in the oviduct of a *S. italicus* collected in September on the Calvana Mountains, near Florence by LANZA (1946) […]. I never found any embryos, fetuses or juveniles in hundreds of continental and Sardinian *Speleomantes* dissected during more than forty years; in a female *S. supramontis* died in captivity on 14 April, REHBERG (1960[i]) found 5 eggs in the left oviduct and 7 in the right one; they had a diameter of 5.5 mm.

Nevertheless the exceptional occurrence of the ovoviviparity, with females which might retain their eggs in the oviduct and give birth to fully transformed young (cf. also NOBLE, 1931: 31), cannot be completely excluded, also according to the opinion of ENGELMANN et al. (1985: 112)».

As expected, the sure occurrence of ovoviviparity (aplacental viviparity) in the genus has been verified by LANZA & LEO (2000, 2001) in *S. imperialis sarrabusensis*, a taxon living in an arid, granitic, caveless area of the southeasternmost Sardinia (Sàrrabus). They wrote: «Some subadults and adults, collected on 1.XII.1998, were placed in small plastic boxes provided with two layers of wet, white kitchen paper tightly pressed against their bottom (no hiding-place possible!); each box, containing 6-8 animals, was kept at 10-15 °C and cleaned at first every 3-4 days, later every 7-10 days, as soon as the evacuations decreased. After ca. 2½ months a newborn was found, surely born between 10.II. and 20.II.1999 [the animal was 32 mm long when about one month old]. Although this case of viviparity has been observed in captivity, it must be considered as a natural event, as there is no doubt that the intraoviductal development of the embryo had already begun when its mother was captured». In any case also Salvatore Spano (*in litt.* 30.IV. 2001) observed other two cases of ovoviviparity in the same taxon.

It goes without saying that these last records give reliability back to the above-mentioned Berg's, Procter's, and Cei's records.

A female of *S. genei* around her egg clutch was found by some speleologists on 19 May 1966 in a cave in locality Corongiu de Mari, about 200 m a.s.l., near Iglesias; it stayed in a niche situated at the base of a crevice flanked by two «organ pipes», part of a rather small stalactic-stalagmitic complex; the eggs, ten, and their mother laid on a rocky substratum covered with moist mud (SERRA, 1968[i]). The eggs, each provided with one or two peduncules, had a diameter, after fixation in formalin, of 5.5 and 6.5 mm respectively without and with the envelope; the eggs had reached a more or less advanced neurula stage (STEFANI & SERRA, 1966). At the beginning of September, in a cave of the same locality RIVALTA (1969) found an animal with an egg stuck on a leg (out of about 50 specimens). According to PAPINUTO (2005), another brooding female with 10 eggs was discovered on 11.IV.2005 within a shot hole of a 13 m long abandoned mine gallery near Domusnovas (Cagliari; Sa Duchessa; locality Maremma; 425 m a.s.l.; air temperature and relative humidity close to the nest 16-18 °C and 60-70%, respectively). The brooding female and her clutch were monitored each 3 days for 148 days till the hatching of 8 neonates on 31.VIII.2005. The egg diameter changed from 5-6 mm (16.IV) to about 10 mm (18.VIII). The female sporadically moved away from the eggs as far as the shot hole opening (cf. MUTZ, 1998: *S. i. imperialis*); when coming back to the clutch she was used to hold it with an arm and to keep the clutch raised with her tail. It was also observed that for about a week the newborn salamanders stayed close to or even on their mother, leaving the «nest» about 2 weeks after hatching.

Egg depositing behaviour has been firstly treated by DURAND (1970, 1973). DURAND (1970; translated from French) writes: «A second observation deals with the behaviour of the female which remains curled around her eggs for about 10 months. This behaviour, occurring in other American Plethodontidae, seems to be basically protective as the eggs contain plenty of yolk. Curiously, the female, though showing an exemplary maternal instinct and not feeding (unless one feeds her), can eat some of her eggs. Though layed in number of 6 to 14, sometimes one finds out that only half of them develops as the other ones disappears viciously. It even occurred to me to catch the animal in the act. One may wonder whether this is a case of accidental cannibalism due to captivity or, as defined by BOZKOV (1968), of constrained cannibalism caused by food shortage, or rather of regular cannibalism as in the case of the American salamander *Cryptobranchus alleganiensis*, whose male eats regularly part of the eggs which it is watching. A more careful observation enabled me to ascertain that it is a case of selective cannibalism. In fact, the female eliminates the unfertilized or badly developing eggs which could go mouldy, what allows to save the remaining ones. The accidental cannibalism may be observed in same old females toward her or of others eggs. The protective behaviour ceases at the hatching and, if the newborns do not seem to be in danger, the female becomes indifferent to their destiny and eats the egg envelopes».

SALVIDIO et al. (1994) (cf. SALVIDIO, 1994; PASTORINO et al., 1997) obtained oviposition by captive *S. strinatii* from Savignone (near Genoa), in December of three different years. The three females laid respectively clutches of 9, 6 and 5 eggs, but after two months of parental care (see above) all the animals ate their own eggs. Three of them, separated by the mother, died because of fungal and bacterial attack, possibly as no more protected by the antimycotic/antibacterial properties of *Speleomantes* skin secretions. W. Wiggins (pers. comm. to B.L., 1990), rearing *Speleomantes genei* with other specimens of both sexes, observed that «After the eggs were layed the female showed very aggressive behaviour so I decided to separate it from the others». Although not yet studied in *Speleomantes*, the contributions of parental cares to the survivorship of the eggs (by reduction of predation, microbial and fungal infections, and rate of dessiccation) have been clearly established in some plethodontids, and nest defense by attendants is well known to occurs e.g. in *Plethodon* and *Desmognathus* (cf. FORESTER, 1983 and 1984; BACHMANN, 1984; AUSTIN, 2000).

In any case «the length of development, from oviposition to hatching, may be different from that observed by DURAND (about 10 months: 1970, 1973); Gerhard Roth (pers. comm., 1991) obtained hatchs in captivity, at 15-16 °C, after periods between 6-7 and 10-11 months, in *S. italicus* from near Stazzema on the Apuan Alps (province of Lucca)» (LANZA, 1999c).

MUTZ (1998) reports the first succesful captive breeding of *S. i. imperialis*. The animals were kept at temperatures not higher than 15 °C in summer and between 8-12 °C in winter, in small terraria kept in a semi-open refrigerator. Four animals hatched from a clutch of 6 eggs after 173-175 days (5-7.VII.1996) from the egg-laying (ca. 17.I.1996); they measured about 5-6 mm. The female guarded the clutch during the whole time, staying almost always at close contact with the eggs, moving away for a short time only when disturbed or to feed. After a brief period of underfeeding she ate two of her eggs. The hatched young remained at the nest place together with their mother about three weeks and consumed the remaining yolk. In this time, the female did not eat the egg envelopes, feeding on house crickets, which were as big as the young cave salamanders; but, although cannibalism has been proved for cave salamanders, the female distinguished between the crickets and her young.

Fig. 7. *S. strinatii.* ♀ from Maritime Alps, brooding her own egg clutch in captivity. An egg peduncule is clearly visible. Photo by J.-P. Durand, 6.XI.1966.

7.5 Development

LANZA (1999c: 122-124; free and enlarged translation from German) writes: «The newly laid egg is ivory white, spheric and relatively large, reaching with its envelope a diameter of 5-6 mm. Each female lays a clutch of 6-14 eggs connected to each other by a string formed by the egg envelope (DURAND, 1970; 1973; the eggs have been erroneously quoted as free by BALLASINA, 1984a-d); the envelope, studied also histochemically by VILTER & DURAND (1970a-b), consists of seven layers wrapping the embryo and the mucous fluid surrounding it.

The development of the continental *Speleomantes* is known only thanks to the studies by DURAND (1967a-b, 1970, 1973); about other data published on this topic see also the § 7.4 «Oviparity, ovoviviparity and parental cares».

DURAND (1973; translated from French) writes: "We had the opportunity to observe the embryonal development of the cave salamander at the noticeably constant temperature of 12 °C of the cave laboratory (cf. footnote 2 of § 7.4

«Oviparity, ovoviviparity and parental cares»). During the days following the oviposition, the holoblastic and unequal cleavage seems to run the normal course peculiar to amphibians. The morula, white and with its surface delicately reticulated by the cell divisions, is evident at the end of the first week after which the gastrulation begins. Gastrulation and neurulation take place during a long period lasting up to two and half months. The neurula is of the classic type with a neural plate whose margins thicken becoming the neural folds which fuse each other to form the central nervous system.

The most important organogenetic period, during which the eggs enlarge slightly, is between the 3rd and 4th months and corresponds to the head individualization and eye and gill buds development.

During the 5th month the egg envelopes become swollen by the capsular fluid and the cephalic pigment appears. Toward the 6th month the dorsal part of the body becomes pigmented, and the vitellus begins to be reabsorbed. Behind the eye the outer gills are well-developed and pink coloured by the circulating blood.

Towards the 7th month the animals move within the envelopes if strongly illuminated. The eye shows the white spot corresponding to the lens. The mouth and nostrils begin to differentiate. The head region is large and pigmented with brown. The pigmentation attenuates gradually towards the tail which is already very long. The forelimb includes the elbow-joint, a shovel-shaped hand and the buds of the 4 fingers. The hind limb includes a knee and an already 5-toed foot. The gills are by now digitate and reach their greatest development. The vitelline mass is still very large and crossed by vessels.

At the 8th month the egg reaches a diameter of 10 mm or more according to VILTER & DURAND, 1970a.

Towards the 9th month the animals are able to turn within the egg and to move the limbs and the tail. The outer egg envelope, thin and coriaceous, allows seeing a cephalo-caudal more and more intense pigmentation. All the organs are well-developed. The mouth is open allowing sight of the tongue. The nostrils, the eye with its eyelids, the limbs with their developing digits, the uro-genital region, the tail and the costal grooves can be clearly seen. The vitellus reduces and the egg reaches a diameter of 7.5 mm. This stage is outstanding because of the sharp limit existing between the blackish grey pigmentation of the body and the light yellow colour of the vitelline region crossed by the perivitelline vessels. At the end of the development the gills undergo a very strong reduction.

The egg envelopes become thinner and softer. The preceeding period of larval activity is followed by a noteworthy slow-down forerunning hatching which occurs towards the end of the 9th or beginning of the 10th month. At hatching the embryo tosses violently within the egg misshaping its envelope, while the limbs and the snout remain bulging. Soon these envelopes are pierced and the capsular fluid flows facilitating hatching. The larva retains at first the bent position it had within the egg. After a short time it spreads and detaches the limbs from its body. A few hours more and the animal is able to creep on its belly. The pigmentation is black but the residual vitellus, crossed by some vessels, appears as a lighter ventral fusiform spot. This spot extends towards the heart and the caudal regions by mean of a white groove reaching the cloaca. The eye and nostrils are very large while the gills are reduced to a tiny growth. The gular fold and head shape are as in the adult. The hand and foot are functional and their digit tips enlarge. The animal is 22-24 mm long.

The larval lifespan is comprised between hatching and the first intake of food. The day after hatching the animal is already able to climb on the terrarium walls. After a few days the young larvae, 26 mm long and still very dark, are able to raise their head, keep their balance, turn over if reversed on the back and move easily on the terrarium floor (see also chapter 8 «Population dynamics»).

BIANCALANI & GIANNECCHINI's (1985) figures of 1-1.5 cm concerning some *S. italicus* «a few days old» seen on 26.VII.1981 in a cave of the Monti della Calvana, near Florence, m 626 a.s.l., are wrong».

The smallest known *S. italicus,* almost surely a neonate 24 mm long (SVL= 17 mm, tail= 7 mm), was found on 18.IV.1999 by PASTORELLI et al. (2001) in a cave near Bagno di Romagna (about 800 m a.s.l., Savio Valley, province of Forlì-Cesena).

MUTZ (1998) states that his 4 freshly hatched juveniles of *S. imperialis* (see § 7.4 «Oviparity, ovoviviparity and parental cares») had the following size and weight:

Total length (mm)	Head length (mm)	Tail length (mm)	Weight (mg)
28.2	6.4	11.4	190
26.4	5.8	10.4	170
26.0	5.9	11.5	170
26.2	5.6	11.2	160

According to LANZA et al. (1995), total lengths of smallest known specimens of the other Sardinian species are as follows: *S. flavus* 34 mm (body 21+tail 13); *S. supramontis* 37 mm (body 21+tail 16, weight = 0.3 g) [but MERTENS (1923) quotes a specimen, very probably belonging to this species, 26 mm long]; *S. genei* 33 mm (body 23+tail 10 mm). However, in a mine near Domusnovas, on 31.VIII.2005, PAPINUTO (2005) found 8 newborn *S. genei* 20-25 mm long.

8. POPULATION DYNAMICS

The demography of *S. strinatii* has been studied both in a rocky area along a stream (Bisagno Valley, province of Genova; SALVIDIO 1993a-b; 1998, 2001, 2006) and in an artificial cavity near Besolagno (Scrivia Valley, province of Genova; SALVIDIO et al., 1994; SALVIDIO, 2001, 2006; SALVIDIO & PASTORINO, 2002). Analyzing polymodal body-size (and –weight) frequency distributions from samples of several years, they found that the population structure was composed of three body-size classes (what has been confirmed by PASTORELLI et al., 2001, in *S. italicus* from a cave near Bagno di Romagna, province of Forlì-Cesena, as well as by SALVIDIO et al., 2002 in *S. a. ambrosii* from three caves in the province of La Spezia). According to the examination of dissected salamanders these components were estimated to correspond to three definite age classes, the two smallest ones corresponding respectively to juveniles in their first and second year of life, the third one to a mixture of large immature third-year individuals (subadults) and breeding individuals in their fourth year or older. The correspondence between body size and age classes was estimated only for immatures, since in the mature plethodontids there is high overlap in body size between age classes (HOUCK, 1982; BRUCE, 1990). Inferring from DURAND's data (1967b), the smallest individuals, observed in December and ranging from 19 to 23 mm of snout-vent length (SVL), were retained as juveniles probably about three months old (SALVIDIO, 1993a). Males reach sexual maturity in their third year of life, at a body size of at least 50 mm SVL. Females are in average bigger (64 mm SVL) and heavier than males and can reach a larger maximum body size (up to 72 mm, against 67 mm SVL of males; see also under § 7.1 «Sexual dimorphism»); they become sexually mature probably one year later and at a larger body size than males (at least 58 mm SVL). On the basis of the number of yolk-filled oocytes observed in mature *S. strinatii* females SALVIDIO (1993a) estimated a mean clutch size of 13.80 ± 2.05 (n=5, range 12-17). According to the same author, females of *S. strinatii* should be able to deposit their first clutches of eggs at an age of 5 years, while the animals reared by DURAND (1970; 1973; see footnote 2 of § 7.4 «Oviparity, ovoviviparity and parental cares») reached sexual maturity between the 3rd and 4th year after hatching.

The sex ratio of both above-mentioned *S. strinatii* breeding populations did not deviate from a 1:1 ratio (SALVIDIO, 1993b; SALVIDIO et al., 1994), as has been also found by PASTORELLI et al. (2001) in *S. italicus*. SALVIDIO et al. (2002: *S. a. ambrosii*), states that «If females reach sexual maturity at about 58 mm in SVL, as in *S. strinatii* (SALVIDIO, 1993) [quoted as SALVIDIO, 1993a in chapter «Bibliography» of this paper], then the sex ratio of the adult population was not different from 1 [17 males/9 (*sic! read "19"*) females; χ^2=2.46, P>0.05]».

LANZA (1999h; translated from German) writes: «VOESENEK et al. (1987) measured 82 *S. supramontis* specimens "captured [in a cave near Dorgali] and housed elsewhere temporarily"; they found 41 (39+2 not measured) "not adult" specimens, 14 adult males and 35 (33+2 not measured) adult females respectively with a total length up to 80 mm (juveniles), between 61-70 and 131-140 mm (males) and between 61-70 and 121-130 mm (females); if they truly did not kill their animals I wonder how it was possible to sex specimens 80-90 mm long or less, as the external secondary sexual characters are recognizable only in larger animals; almost surely some of their females actually were males and consequently their statement that the "number of females was significantly larger than the number of males (χ^2=9.0; p<0.001)" is probably wrong».

Demographic data on *S. strinatii*, collected since 1988, showed small year to year fluctuations, suggesting that the dynamics of the population studied (i.e. recruitment, survival and growth rates) remained relatively constant over a nine-year period (SALVIDIO, 1996; 1998).

No data are available about *Speleomantes* life span which, according to SALVIDIO (1993a), is not detectable by means of body size analysis distribution, because of the wide overlap in SVL between different age classes of breeding individuals. MERTENS (1923) reports that some of the animals reared by SCHMALZ (1916[i]: *S. strinatii* from Genoa) since March 1915 outlived this latter dying during the winter 1921-1922 when more than 6 years old.» To date the oldest known *Speleomantes* is a specimen (probably belonging to a mainland species) reared at the Cincinnati Zoo (Ohio, U.S.A.); this animal was still alive as of 31 May 1990, at an age of more than 10 years and 7 months (SNIDER & BOWLER, 1992; Andrew T. Snider, pers. comm.).

LANZA (1999c; updated and free translation from German) writes: «Age, organic diseases and infections (viruses, bacteria, fungi) apart, death could be favoured or caused by parasitoses [see also under § 5.4 «Parasites»] [...]. Death caused by traumas has been checked as specimens are occasionally found crushed, perhaps accidentally, on paths, tracks or roads travelled by man or vehicles at night. Also the adjustment movements of the rock piles in which *Speleomantes* spend a large part of their life are probably to be taken into account; to these, more than to the predators, might be ascribed the rather common presence of a regenerated tail, as autotomy does not occur in the genus [but see § 6.3 «Antipredatory adaptations»]. In some situations, such as along streams, death by drifting and/or drowning may occur; after heavy rains in the town of San Marino, on the pavement of some streets flanked by gardens retained by large dry-stone walls, have been found corpses of *S. italicus* washed through the drainage holes in the walls».

SALVIDIO (1997), collecting in the course of seven years 555 records of *S. strinatii* from near Genoa, found in 27 cases some kind of external wound or anatomical malformation. Only tail injuries, constituting 85% (23/27) of all traumatas observed, were taken into further consideration in the data analysis. «The observed frequency of individuals with clearly recognizable regenerating tail (e.g. short length and rounded tip, clear pigmentation) varied from 3.6 to 10.3% in juveniles, and from 0 to 4.9% in adults. Juveniles showed statistical more tail injuries than adults (χ^2=4.17, df=1, P<0.05). The overall frequency of injuried individuals varied from 2.5 to 7.5% across years averaging 4.1%. No directional trends in the proportion of individuals with regenerating tails were observed (Spearman rank correlation coefficient r_S=0.37, n=6, P>0.20). Thus, the proportion of tail-injuried salamanders seemed to remain constant, indicating that the agents causing tail loss in *S. strinatii* did not vary their intensity during the seven-year study period» (see § 6.3 for tail autotomy).

About death by drowning see § 6.2 «Activity, habitat use and displacement», for cannibalism § 6.1 «Feeding behaviour».

In May, MERTENS (1923) received a juvenile 26 mm long probably belonging to *S. supramontis*; he writes: «On October 22 the young *Spelerpes* had already a length of 41 mm, on February 10 one of 48 mm, and at the beginning of April, although apparently scarcely a year old, it reaches 54 mm».

Dealing with the juveniles obtained by him in captivity (see above §§ 7.4 «Oviparity, ovoviviparity and parental cares» and 7.5 «Development»), DURAND (1973; translated from French) writes: «Within 15 days they grow 2 mm reaching a total length of 28 mm. The gills are no longer visible. From this moment only a short time will elapse before the complete reabsorption of the vitellus and trasformation of the larvae into juveniles similar to those met with in the field during the spring. This transformation is accomplished at the age of one and a half months, when the young animal begins to eat prey suitable to its size and its pattern becomes richer in chromatophores, giving it its specific colouration. Towards the age of 5 months the juveniles are 29 to 38 mm long and the following year 46 to 50 mm long; the third year the reared animals reach a size of 80-89 mm and will become adults in a short time».

According to SALVIDIO (1993a), juvenile growth rates of *S. strinatii* range from 10 to 13 mm/yr, while those of juvenile *S. a. ambrosii* average 15 mm in their first year of life (SALVIDIO et al., 2002); such rates are similar to those reported for plethodontids inhabiting the American temperate regions (HOUCK, 1982, HAIRSTON, 1983, SEMLITSCH & WEST, 1983, BRUCE, 1988, 1990).

According to MUTZ's (1998) observations on *S. i. imperialis* (see above §§ 7.4 «Oviparity, ovoviviparity, and parental cares» and 7.5 «Development»), when aged about 6 months his captive juveniles had a mean total length and a mean weight respectively of 42.5 mm and 470 mg, showing a growth of 15.8 mm and 300 mg from the hatching [it is worth of mention that Mutz wrongly considers as total lengths the figures given by SALVIDIO (1993a) for the snout-vent length of his *S. strinatii* juveniles]. Length and weight growths were slightly lower in the cooler winter months; a weight decrease was observed during the first three weeks, when the young did not still prey but consumed the remaining yolk.

SALVIDIO (in press), who studied population dynamics and regulation in *S. strinatii*, found that competition for space, food, mates or territories may be important in the regulation of the population growth rate, and «minimum winter temperatures […] may affect survival of eggs, juveniles and possibly brooding females».

9. CONSERVATION

9.1 Abundance

LANZA (1999c-h; updated and free translation from German) writes: «*S. ambrosii* (including *S. strinatii*), considered by some people to be a more or less rare animal deserving protection (see f.i. MORISI, 1983a and CORBETT, 1989), actually is -like its congeners- one of the more common southern European terrestrial vertebrates, at least in most of its range and particularly in the areas which, rich in underground vacuities, offer suitable refuges during the dry and/or warm periods; even MORISI (1983b) found it abundant in some caves of the province of Cuneo. Among the Authors who regard the animal as common are FISCHER (1887), BERG (1893: "extraordinarily common" near Genoa), ANONYMOUS (1960: Cave "Tana dei Carbonari", province of Imperia; 1962: Cave "Grotta dell'Orso", province of Cuneo), TORCHIO (1963: cave on the left side of Sciusa River, province of Savona), PASTORINO & PEDEMONTE (1974: "impressive summer colonization" in some artificial cavities near Savignone, province of Genoa), RAFFAELLI (1983: 33 specimens in a tract 200 m long flanking a semi-dry stream of the Nice region, between 800 and 1000 m a.s.l., in September 1982, at night), SAUER (1989: near Genoa and La Spezia), and CORTESOGNO & BALLETTO (1989); these latter, in a woody area of the Alpe di Rezzo, m 1220-1250 a.s.l., province of Imperia, found a maximum concentration of 10 specimens x 100 m^2, but regard, quite rightly, this value as presumably lower than the actual one. On the walls of some caves, such as the Caverna Ossifera di Cassana (near Cassana, La Spezia) *S. ambrosii*, can be found as many as 50-60 specimens in a few m^2. […] What has been written about *S. strinatii* and *S. ambrosii* applies perfectly to *S. italicus*, which in most of its range appears to be extremely common: see for example BERG (1893: "extraordinarily common" in the environs of Florence) and CALANDRI & GRIPPA (1979) who observed a very large number of animals in the first tract of the 4th opening of the cave "Antro del Corchia" on the Apuan Alps (Mt Corchia, province of Lucca) [cf. also PIEROTTI, 2002]. According to my experience the species seems to be less abundant or even relatively uncommon only in the province of Pescara, i.e. in the southernmost portion of its range. […] *S. flavus* is a common species which, like the other *Speleomantes*, can be found in large numbers either in caves (FURREDDU, 1964; FURREDDU & MAXIA, 1964) or under stones and, with an overcast sky or at night, even outside, provided that the environmental conditions are favourable [see also § 6.2 "Activity, habitat use and displacement"]. […] *S. supramontis* has been quoted as abundant both in caves (FIACCAVENTO, 1969; ANONYMOUS, 1974; MUCEDDA, 1981; LORU, 1984; MASA, 1986; VOESENEK et al., 1987; LANZA, 1991) and outdoors (ANONYMOUS, 1986; VOESENEK et al., 1987; B.L. personal observations). VOESENEK et al. (1987), who carried out their research in a woody area near the Gulf of Orosei write: "the test site, at an altitude of 800 metres, had an area of 300 m^2 and 5° gradient […]. The "total method" was used. The density found can be extrapolated to approximately 300 animals/ha" [The "total method" is "a method in which every individual within a site is captured if necessary with local habitat destruction" (VOESENEK et al. 1987)]. The same authors also obtained a population size of 98 ± 7 salamanders in a cave near Dorgali. A very large number of *S. supramontis* specimens was observed on 3.V.1983 on the bottom of a small pothole, about 7 m deep, in the bare karstic zone of Scala 'e Pradu, on the Supramonte di Oliena, m 1225 a.s.l. (LANZA, 1991). […] Also *S. imperialis* can usually be found in abundance, according to the season, either in caverns or outdoors. Apropos of the karst area of

Samugheo and Asuni, municipalities in the province of Oristano, LANZA (1991) writes: "*Speleomantes imperialis* sometimes swarms in some of the caverns of the above-mentioned area reaching a greater concentration than ever observed in all the European Plethodontidae range. On 9.VIII.1988, in the first 10-12 meters of the cave "Grotta degli Spelerpes", there were at least 500 specimens of different ages, so thronged that in some places it would have been possible to collect them in handfuls". [...] *S. genei* is very common almost everywhere (cf. for instance RIVALTA, 1969, and ANONYMOUS, 1982); up to now it seems to be relatively uncommon only in the zone between Carbonia, Barbusi, and Mt Tasua, inhabited by its "subsp. B"». FERRETTI et al. (2002) found 71 and 144 active specimens of *S. a. ambrosii* (respectively on August 2001 and September 2002) in an artificial cave in the environs of La Spezia. In a single sampling session FAVELLI et al. (2006) were able to catch 52 specimens (18 ♂♂, 18 ♀♀, and 16 juveniles) of *S. i. sarrabusensis* in some artificial caves on Sette Fratelli mountain (Cagliari).

Actually, such qualitatives (or, at most, semi-quantitatives) data are not enough to deal with *Speleomantes* abundance and conservation, especially if one consider that they are not always referred to areal units and/or statistically processed [except for those from VOESENEK et al. (1987) and CORTESOGNO & BALLETTO (1989)], thus not directly comparable. Furthermore, according to ZUG et al. [2001; see also LANZA (2003), quoting BURTON & LIKENS (1975)] «high densities of resident populations are not uncommon for small amphibians and reptiles» and this is especially true for plethodontids, as BURTON & LIKENS (1975a) found that in eastern North America the biomasses of four species pooled together [*Plethodon cinereus* (Green, 1818) reaching alone 27,200 specimens/ha] exceed those of birds and mammals inhabiting the same area! In addition density values can vary considerably between populations and are affected by a number of factors, such as natural history traits of the species, climatic parameters, availability of food, shelters and breeding places, predation pressure, competition for food and space, a.s.o.. According to ZUG et al. (2001) «High densities may also be a response to the patchy distribution of resources». This is likely to be the case, for *Speleomantes,* of those caves that provide plenty of food ensuring contemporarily steady environmental conditions [see at § 6.2 «Activity, habitat use and displacement»], what could explain the «crowding» of cave salamanders that have been often observed in these habitats [according to FORTI et al., (2005a) the high densities observed could be also be determined by reproductive behaviour causing them to associate in high density at the beginning of the summer]. Even SALVIDIO & PASTORINO (2001; translated from Italian) suggest that: «the high abundance of cave salamanders in the subterranean environment could be more apparent than real». In conclusion, the high density values recorded in some places are not necessarily representative of the actual abundance of *Speleomantes* neither in the neighbouring areas nor, let alone, in its whole range.

Some quantitative data on cave salamander's population size, abundance and density have been provided by recent researches. Abundance and biomass of a *S. strinatii* population from near Genoa (Bisagno Valley) were investigated by

SALVIDIO (1998) using temporary removal methods on a rocky surface area of 190 m^2; during a four years period population size varied from 105 to 192 salamanders (mean=155), while population density varied from 0.6 to 1.0 individuals/m^2 of rock face (mean=0.8 individuals/m^2). Population biomass (expressed as wet weight) also varied from 0.98 g/m^2 to 1.54 g/m^2 of rock face, with an average value of 1.25 g/m^2. Salamanders older than 3 years accounted for about 70% of the total biomass; juveniles in their first and second year represented about 30% of the total population biomass, but more than half of the population by number (SALVIDIO, 1998). Later on, sampling in the same locality of 190 m^2, SALVIDIO (2001) obtained population size values ranging from 89.81 to 133.15 [juveniles (range): 29.66-72.78; adults (range): 31.03-74.87]. Temporary removal methods were also used by SALVIDIO (2001; cf. also SALVIDIO & PASTORINO, 2001) to estimate the abundance of *S. strinatii* on a sampled area of 120 m^2 in a tunnel near Besolagno (province of Genoa); during a four years period estimated population size ranged from 84.40 to 133.94 salamanders (juveniles ranging from 50.91 to 56.38, and adults from 28.00 to 81.98). Census data from temporary removals were obtained by CIMMARUTA et al. (1999) for a population of *S. strinatii* from Pietra di Vasca Mountain (Genoa): an overall number of 220 adult specimens was estimated as inhabiting the cave. According to SALVIDIO (2001), removal methods proved to be more efficient if sampling occurs in simple-structured, constant environments such as caves, than in relatively complex and variable ones (i.e. rock faces), since in the former habitat a higher proportion of the salamander population is exposed to capture.

SALVIDIO et al. (2002) estimated a population size of 79 *S. a. ambrosii* by means of temporary removal methods, in the cave Grotta di Cassana (near Cassana, province of La Spezia) (cf. the above mentioned quotation by LANZA 1999c: 106).

LAGHI et al. (2005) individually recognized *S. italicus* in a natural cave near Bagno di Romagna (province of Forlì-Cesena) by means of photographs of the dorsal pattern; during a period of 24 consecutive months they were able to recognize 243 different individuals [118 adults (60 males and 58 females) and 125 juveniles] collected within an area of 300 m^2. The extrapolated density is 0.8 individuals/m^2. During a four-night sampling in a site of the Most Serene Republic of S. Marino, CASALI et al. (2002a) were able to sight 128 specimens of *S. italicus* on a study area of about 600 m^2. SPILINGA et al. (2006), who studied ecology of *S. italicus* in a natural cave on Monte Tezio (province of Perugia) for one year, were able to observe an overall number of 88 individuals (16 ♂♂, 21 ♀♀, 2 subadults, and 37 juveniles).

9.2 Threats and conservation guidelines

According to LANZA (1999c, e, f, h; updated and free translation from German): «The range of *Speleomantes ambrosii* (including *S. strinatii*) is subjected to the manifold and well-known negative environmental changes affecting the more or less densely populated Mediterranean regions: pollution, deforestation, fires, impoverishment of the surface waters [cf. FERRI, 1996], introduction of alien species, etc. Nevertheless the species is not presently endangered thanks to its relatively large range and above all to its peculiar biology which, among other things, is characterized by a type of reproduction not linked to water (cf. LANZA & VANNI, 1987 and 1991. AELLEN & STRINATI's (1975; 1976) statement that caves have often been the only refuge for *Speleomantes* after deforestation is completely wrong as almost any type of natural or artificial subterranean cavity system represents a suitable habitat for it (crevices, interstices among rock debris or roots, dry walls, etc.). Also *S. supramontis* is not endangered as it is common and has a rather wide range, and the same applies to *S. imperialis* [the fears by SCHWARZER et al. (1984) and others are totally unwarranted], and *S. genei* [contrary to the customary, unjustified, alarming rumors, such as the journalistic one by ANONYMOUS (1991), the species does not deserve protection except for the environs of Carbonia]» (see under § 9.1 "Abundance").

A relevant ecological feature of *Speleomantes* is that species ranges are small. In particular, those of the four Sardinian species and of *S. ambrosii* are the smallest of all European Urodela species; only *Salamandra lanzai* Nascetti, Andreone, Capula et Bullini, 1988 has a range slightly smaller than that of the other two continental *Speleomantes* species, and only *Euproctus montanus* (Savi, 1838) and *E. platycephalus* (Gravenhorst, 1829) have ranges comparable in size with those of *S. italicus* and *S. strinatii* respectively (deducted by the maps published by S.H.I., 1996 and GASC et al., 1997).

When the conservation status of the Italian amphibians is treated through a quantitative and comprehensive approach (i.e. taking into account several variables, such as: range size and fragmentation, altitudinal distribution, life history traits and longevity, habits, habitat breadth, adaptability to altered environments, endemicity, taxonomic uniqueness, and insularity) *Speleomantes* turn out to be among the most endangered species, with high conservation priority (cf. ANDREONE & LUISELLI, 2000; SINDACO, 2000).

According to LANZA (1999d; translated from German): «Since the end of the last century Monte Albo as well as many other Sardinian expanses underwent serious deforestation that transformed wide regions covered by primary holm-oak (*Quercus ilex*) woods or maquis into half-naked rocky stretches. However, such a drastic environmental alteration did not affect the cave salamanders which, thanks to their peculiar biology, survived and, especially in the limestone territories, continued proliferating even in the most degraded areas. So, despite its relatively limited range, *S. flavus* is not to be considered an endangered species». On the other hand no data are available on the real density of *Speleomantes* on Monte Albo before its deforestation and, as a general rule, any heavy habitat alteration turn out to bring about damage, more or less serious, to the local populations. Numerous studies have demonstrated that logging can have negative effects on amphibians as regards the distribution, richness and abundance of species [SCOCCIANTI (2001), who quotes BURY (1983), POUGH et al. (1987), RAYMOND & HARDY (1991), PETRANKA et al. (1993), WALDICK (1997) and HERBECK & LARSEN (1999).

Dealing with *S. italicus*, LANZA (1999g; translated from German) writes: «It is worth saying that sometimes man has greatly improved the life conditions of this species as well as that of its congeners, especially in the areas which, because of their lithological nature (f.i. sandstones and ophiolytes), are not so fissured and rich in underground cavities as the karstic ones. An illuminating example is provided by the town of Fiesole, just north of Florence, and its two flanking sandstone hills, the Colle di San Francesco (m 345) and Monte Ceceri (m 414). Here, since Etruscan times man created habitats extremely favourable to the species in three different ways: field terracings reinforced by thick dry-stone walls, various types of underground cavities in the present archaeological site and, above all, enormous amounts of rock debris by the extensive exploitation of the «pietra serena» quarries. It should be noted that, as shown by period photographs, in the first quarter of this century at least the southern slope of Monte Ceceri, now covered by a thick secondary mixed wood, had been completely denuded by the mining activity». However, quarrying is among the most harmful human activities, that seriously damage both the hypogean and epigean ecosystems by means of direct destruction (cf. CHAPMAN, 1993, WATSON et al., 1997 and LANGTON & BURTON, 1997), and can contribute greatly to a decline of many species. Accordingly, SCOCCIANTI (2001: 106), dealing with the Apuan Alps marble quarries, writes «between species of amphibians that are at high risk in this sites, there is also *Speleomantes ambrosii*, due to the serious pollution of the groundwater and in particular to the obstruction of most of the natural rock crevices caused by the enormous quantity of marble dust that is dispersed in the area where quarrying is carried on». The same applies to the rare *S. genei* subsp. B, now threatened by mining in its small range.

The protection of cave salamanders' habitat is actually closely linked to the safeguard of the whole hypogean environment that, according to CHAPMAN (1993) and WATSON et al. (1997) is threatened by a number of factors, such as mining and quarrying, major land or hydrologic disturbance (by forestry, quarrying, land clearance, construction, agricultural activities, waste disposal or other land fill, and other developmental activities), groundwater pollution (by sewage, domestics, farm or industrial wastes), manifold human utilisations of caves, a.s.o..

A serious threat for any biocoenosis is represented by the introduction of alien species. «As indicated in the Document edited by the *Istituto Nazionale per la Fauna Selvatica* (AA. VV., 1997) rediscussed regarding herpetological species in the document edited by the *Societas Herpetologica Italica* (S.H.I., 1998), the term "immission" is used to indicate the transfer or release, intentional or accidental, of a taxon. When it is a question of intentional immission the term translocation is also used» (SCOCCIANTI, 2001). Introductions of *Speleomantes* are known in the French Pyrenees and in northern Italy, and artificial synthopies were also carried out in Italy both *ex situ* and *in situ* (see § 3.1 «Systematics, taxonomy and geographical distribution»). LANZA (1999f; translated from German) writes: «According to ANONYMOUS (1976) and BERTOLINO (1979), many specimens of *"Hydromantes imperialis imperialis"* were introduced for protectionist purposes (!!) in the protected cave "Sa Rutta 'e Scusi" from some unspecified caves of the region (i.e. Gerrei); a correct knowledge of the biology of *Speleomantes* would have avoided this absolutely unwarranted genetic pollution of the very population inhabiting the type locality of the species». It can be stated that translocation experiments, or artificial syntophy assessed *in situ*, bring an high risk of genetic pollution and therefore their use should be avoided.

Also the collecting threatens *Speleomantes*; especially in those periods in which they gather in caves, anyone could be able to collect them in large numbers (see § 9.1 «Abundance»). To give an example SALVIDIO et al. (2002: *S. a. ambrosii*) state: «Grotta di Cassana was a favourable habitat for salamanders that were highly exposed to disturbance and collection, at least during their underground peaks of activity» and, as a consequence, «caves hosting large numbers of salamanders should be closed or monitored to avoid disturbance and overcollection». GRUPPO SPELEOLOGICO C.A.I. BOLZANETO (undated), studied activity and spacing of *S. a. ambrosii* in the cave «Caverna di Quaratica» (Riccò del Golfo, province of La Spezia) for two consecutive years; according to them (translated from Italian): «At the end of the year 1997 the activity [i.e. the research] had to be interrupted because […] almost all specimens of *Speleomantes italicus* [*sic!* Actually *S. a. ambrosii*] were collected by a German researcher (Mr. Gerhard Roth)». Actually this statement should be verified, as the same authors wrote: «Recently [i.e. after the collection by Roth] the colony of *Speleomantes italicus* inhabiting Caverna di Quadratica have been re-established and […] it was possible to record a considerable presence of specimens».

According to some authors (who don't carry any data to support their statements) *S. flavus* would be threatened by collection (mainly for scientific purposes, but also for trade, particularly if one consider that the collection of the species is not regulated by any Italian law), habitat reduction, and population fragmentation (cf. PUDDU & VIARENGO, 1988; CAPULA, 1998; ANDREONE & LUISELLI, 2000; CAPULA et al., 2005).

It is worth to be mentioned that *Speleomantes*, not included in the C.I.T.E.S., are listed both on Italian (CAPULA, 1998) and French (DE BEAUFORT, 1983) red lists of endangered animals, on Appendixes II and III of the Berne Convention (1979, Convention on the Conservation of European Wildlife and Natural Habitat), on Annexes II and IV of the EU Natural Habitats Directive (Directive 92/43/EEC), as well as on IUCN Red List of Threatened Species (see Table 6; cf ANDREONE & EDGAR, 2004a-c; ANDREONE, et al., 2004a-c; LECIS et al., 2004; FERRI, 2006). To these one may add the several regional laws for the protection of fauna and flora, a.s.o.

Furthermore, caves not yet employed by tourism are listed as habitats of comunitary interest on Appendix I of the EU Natural Habitats Directive.

Table 6. *Speleomantes* in C.I.T.E.S., the annexes of Berne Convention, EU Natural Habitats Directive (according FERRI, 2006) and in IUCN Red List of Threatened Species.

Species	C.I.T.E.S.	B II	B III	H II	H IV	IUCN
S. ambrosii	-	-	X	X	X	NT
S. flavus	-	X	-	X	X	NT
S. genei	-	X	-	X	X	VU
S. imperialis	-	X	-	X	X	NT
S. italicus	-	X	-	-	X	NT
S. strinatii	-	-	X	X	X	NT
S. supramontis	-	X	-	X	X	EN

C.I.T.E.S.= Washington Convention on International Trade in Endangered Species of Flora and Fauna.
B II=Appendix II of the Berne Convention.
B III=Appendix III of the Berne Convention.
H II= Annex II of the EU Natural Habitats Directive.
H IV= Annex IV of the EU Natural Habitats Directive.
IUCN Red List Categories: NT= Near Threatened, VU= Vulnerable, EN= Endangered.

10. RESEARCH PROSPECTS

Although morphology and genetics of the genus have been extensively studied, the knowledge of *Speleomantes*' natural history is still very far from being satisfactory. Indeed, if demography, food habits, activity, and habitat use are well-known for *S. strinatii* (and, at a lesser degree, for *S. italicus*), on the opposite virtually nothing is known on the eco-ethology and life histories of the Sardinian species, and even main natural history traits, such as reproduction, are poorly known. Also, further research on abundance and life history variations in *Speleomantes* populations are still needed to clarify the conservation status of each species.

The study of social behaviour is virtually unexplored in *Speleomantes*. Indeed this represents one of the most intriguing address for future researches, as manifold studies carried out on the American species of the family, proved that plethodontid salamanders exhibit a rich diversity of social behaviour and interactions, mediated by visual and chemical (pheromones) communication, including f.i. intraspecific spacing strategies, territorial defense, clutch defense, antipredator strategies, kin recognition, a.s.o. (reviewed by JAEGER & FORESTER, 1993).

Concerning *Speleomantes*' taxonomy, it will be of prime importance to carry out thorough research in localities not yet explored, as they could be inhabited by undescribed *taxa*; what applies mainly to Sardinia whose strongly-fragmented orography is particularly complex also from a geological point of view.

11. ADDENDUM

According to the last synthesis on amphibians by FROST et al. (2006), Plethodontidae include 374 species and 25 genera included in the following four subfamilies: Hemidactyliinae (*Hemidactylium*), Bolitoglossinae [*Batrachoseps, Bolitoglossa, Bradytriton, Chiropterotriton, Cryptotriton, Dendrotriton, Nototriton, Nyctanolis, Oedipina, Parvimolge, Pseudoeurycea* (including *Ixalotriton* and *Lineaotriton*), *Thorius*], Spelerpinae [*Eurycea* (including *Haideotriton*), *Gyrinophilus, Pseudotriton, Stereochilus*] e Plethodontinae (*Aneides, Desmognathus, Ensatina, Hydromantes, Karsenia, Phaeognathus, Plethodon, Speleomantes*).

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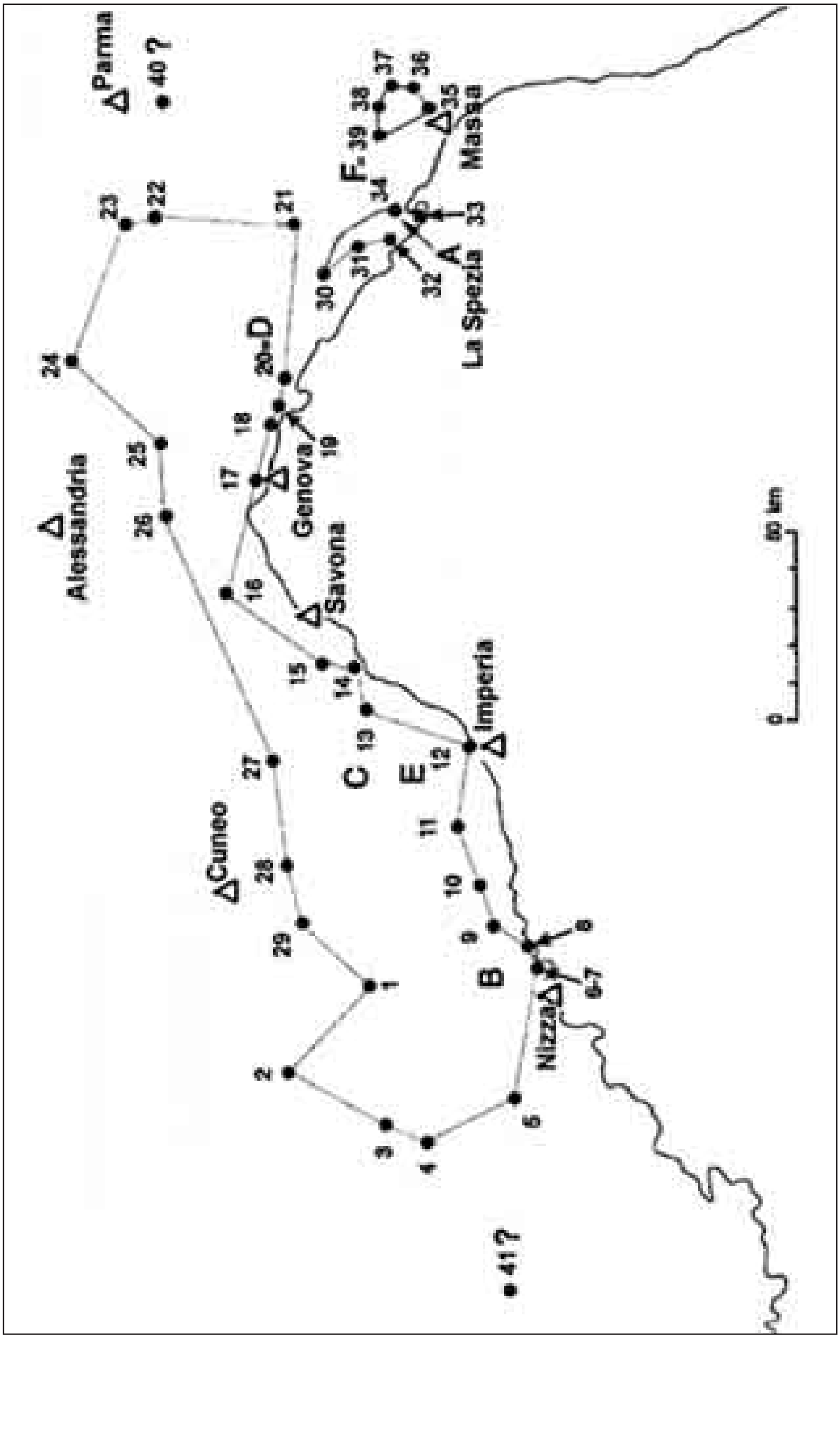


Map 1. Ranges of *S. strinatii* (1-29), *S. a. ambrosii* (30-34), and *S. ambrosii bianchii* (35-39).

DISTRIBUTIONAL MAPS AND SYNONYMS
(See also Fig. 1 and chapter 2 «Materials and methods»)

Speleomantes strinatii

Terrae typicae

B *Hydromantes italicus strinatii* Aellen, 1958, p. 156 (cave «Grotte d'Aspremont» = Balma d'Arena, about 1.3 km as the crow flies N - NE of Aspremont, Alpes - Maritimes, 690 m a.s.l.) (= *S. strinatii*).

See Fig. 9.

C *Hydromantes italicus argentatus* Stefani, 1969, p. 226 [cave «Grotte (misprint for "Grotta"; see STEFANI, 1969, p. 209) delle Ruccaie» = «Tana di Spettari», cadastral number 183 Li/SV, Liguria, province of Savona, commune of Toirano, Vallone del Vero in the Varatella Valley, 44°09'19" N – 08°10'11" E, 300 m a.s.l.] (= *S. strinatii*).

D *Hydromantes italicus ligusticus* Stefani, 1969, p. 228 (cave «Grotta Valdettaro», cadastral number 129 Li/GE, Liguria, province of Genoa, commune of Rapallo, locality Villa Valdettaro, 44°20'52" N – 09°13'20" E, 35 m a.s.l. (= *S. strinatii*).

E *Hydromantes italicus bonzanoi* Bruno and Bologna, 1973, p. 82 [cave «Tana Iª du Casà» = Tana 1 du Casà, cadastral number 573 Li/IM (not 537 as quoted by BRUNO & BOLOGNA, 1973), Liguria, province of Imperia, commune of Caravonica, locality San Bartolomeo Casà, 44°00'12" N – 07°56'41" E, 715 m a.s.l.] (=*S. strinatii*).

The range of *S. strinatii* may be bounded so far by the following localities:

France

1 Saint-Martin-de-Vésubie.

2 Sector «Haute-Tinée» of the Parc National du Mercantour.

3 Grotte du Chat, in the commune of Daluis.

4 Saint-Benoit, near Annot.

5 Aven du Manchot (= Aven des Manchotes) , upper La Malle Valley, in the region of Gourdon.

6 Mount Leuze, near Villafranche, Nice.

7 Grotte du Mont Bastide, close to the Col d'Eze.

8 Monaco.

9 Gouffre du Lion, near Castellar, Mentone.

Italy

10 Caves of the Mont Magliocca, near Seglia, Ventimiglia, province of Imperia.

11 Cave «Tana Longarua», cadastral number 322 Li/IM, 43°51'08''N – 07°42'39" E, on the Mount Caggio, Ceriana, San Remo, province of Imperia.

12 Imperia.

13 Cave «Cavernetta di San Pietrino», near Boissano, Toirano, province of Savona; perhaps a synonym of the «Grotta P2».

14 Artificial tunnel in a limestone quarry on the «Trabocchetto» hill, 95 m a.s.l., near Pietra Ligure, province of Savona (ONETO & OTTONELLO, 2006; P. Laghi & C. Pastorelli, personal observation on 22.III.2004; see Fig. 8).

15 Caves «Arma de 1'Aegua» (= Grotta dell'Acqua), cadastral number 29 Li/SV, 44°11'45"N – 08°19'15" E, locality San Antonino di Perti and «Arma do Buio», cadastral number 27 Li/SV, 44°11'43" N – 08°18'58'' E, locality Montesordo, near Finale Ligure, province of Savona.

16 Mount Beigua, ca. 9 km as the crow flies N of Varazze, province of Savona.

17 Genoa in some city gardens.

18 Nervi and caves near San Ilario, province of Genoa [Tanna do Santo (= Grotta di S. Ilario), cadastral number 63 Li/GE, 44°23'02''N – 09°02'54" E; Tanna do Scindichetto, cadastral number 169 Li/GE, 44°23'59" N – 09°03'45" E].

19 Ruta, ca. 2 km as the crow flies E of Camogli, province of Genoa.

20 Grotta Valdettaro, in the city of Rapallo, province of Genoa.

21 «Grotta della Cava del Canale delle Strette di Giaredo», ca. 500 m as the crow flies S of Codolo, Pontremoli, province of Massa Carrara.

22 Rocca di Bardi 44°38' N – 09°44' E, ca. 600 m a.s.l., municipality of Bardi, province of Parma.

23 cave «Grotta dei Cani» cadastral number 367 E/PC, 44°42'28'' N – 09°45'16" E, 5 km SE of Morfasso, 830 m a.s.l., municipality of Morfasso, province of Piacenza.

24 Sassi Neri, near Romagnese, province of Pavia and environs of the «Giardino di Pietra Corva», Pecorara, province of Piacenza.

25 Cave «Tan-na do Tobia» (= Grotta di Bric Castellazzo), near Isola del Cantone, Montessoro, province of Genoa.

26 Environs of the Laghi della Lavagnina, Casaleggio Boiro, province of Alessandria.

27 Cave «Tana della Rivoera», cadastral number 200 Pi/CN 44°18'17" N – 07°50'12" E, near Sant'Anna Collarea, Montaldo di Mondovì, province of Cuneo.

28 «Grotta Superiore del Camoscere», cadastral number 250 Pi/CN, and «Grotta del Camoscere», cadastral number 105 Pi/CN, near Chiusa di Pesio, province of Cuneo.

29 «Grotta del Bandito», cadastral number 1002 Pi/CN, 44°17'23" N – 07°25'44" E, near Roaschia, province of Cuneo.

Speleomantes ambrosii ambrosii

Terra typica

A *Hydromantes italicus ambrosii* Lanza, 1955, p. 152 [cave «Sprugola della Cornese» = «Sprugola La Canese», cadastral number 186 Li/SP, Liguria, province and commune of La Spezia, locality Fabiano, Sorgente Cornese, 44°05'15'' N – 09°47'54" E, 240 m a.s.l.].

See Fig. 12.

The range of *S. a. ambrosii* may be bounded so far by the following localities:

30 Passo del Bracco, ca, 9 km as the crow flies N-NW of Levanto, province of La Spezia.
31 Cave «Grotta di Cassana» (= «Caverna Ossifera di Cassana»), cadastral number 65 Li/SP, 44°12'37'' N – 09°41'32'' E, near Cassana, province of La Spezia.
32 Manarola, along the path to Corniglia, province of La Spezia.
33 Cave «Tana di Cadimare» cadastral number 251 Li/SP, 44°04'43'' N – 09°48'57'' E, near Cadimare, also between La Spezia and Fezzano and Fezzano and Portovenere, province of La Spezia.
34 La Spezia.

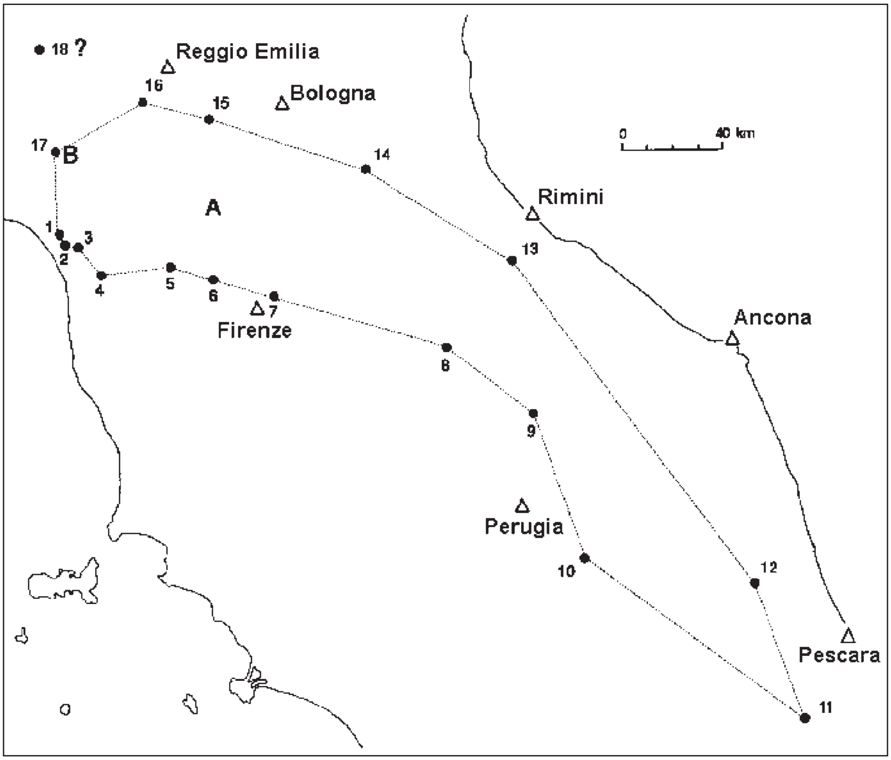
Speleomantes ambrosii bianchii

Terra typica
F *Speleomantes ambrosii bianchii* Lanza, Cimmaruta, Forti, Bullini et Nascetti, 2005 [cave «Tana della Bastiola», cadastral number 481 T/MS, 44°08'08'' N – 10°03'00'' E, on the N slope of Mt Bastione, 698 m a.s.l. and on the left side of the Rio Grande, about 1.2 km SSE of Pùlica (church) and 2.3 km E of Fosdinovo, 360 m a.s.l., province of Massa-Carrara, municipality of Fosdinovo, locality Rio Grande].
See Fig. 11.

The range of *S. ambrosii bianchii* may be bounded so far by the following localities:

35 Massa, along the banks of the Frigido River and town of Massa.
36 locality Pian della Fioba, above Antona, municipality of Massa, province of Massa-Carrara, 44°03'50'' N – 10°12'40'' E, 900 m a.s.l..
37 environs of Resceto, 44°05' N – 10°13' E, 436 m a.s.l., municipality of Massa, province of Massa-Carrara.
38 just N of Vinca, immediately W of Punta Natappiana, 800-1200 m a.s.l., municipality of Fivizzano, province of Massa-Carrara.
39 Caves near Pulica, Fosdinovo [«Tana della Bastiola», cadastral number 481 T/MS, 44°08'08'' N – 10°03'00'' E, and «Grotta del Ferdì» (= «Grotta del Paradisi»), cadastral number 831 T/MS; 44°08'02''5 N – 10°02'59'' E, ca. 1.6 km SSE of Pùlica (44°09'N – 10°03'E)] and Canale Pescioletta, near Marciaso, province of Massa Carrara.

Records to be confirmed:
40 unidentified species: *S. strinatii* or *S. italicus*? Mount Prinzera, ca. 6 km as the crow flies S-SW of Fornovo di Taro, province of Parma.
41 very doubtful record from an unspecified cave of the «Gorges du Verdon».



Map 2. Range of *S. italicus*.

Speleomantes italicus

Terrae typicae

A *Hydromantes italicus* Dunn, 1923, p. 40, *nomen novum* for *Geotriton fuscus* Bonaparte, 1837, p. 19, 1 (unnumbered) (not *Salamandra fusca* Laurenti, 1768, p. 42) [according to the Intern. Code Zool. Nom. 3rd ed., 1985, 75Bf, the *terra typica* is that of the neotype, designated by LANZA (1952, p. 335): «lungo il torrente Forra della Cava, affl. di sinistra della Limentra occ., tra Corniolo e San Pellegrino, non lungi dalla strada della Collina Pistoiese, a circa 650 m s.l.m.», i.e. between Corniolo and San Pellegrino al Cassero, ca. 650 m a.s.l., along the stream Forra della Cava, left tributary of the Torrente Limentra di Sambuca, not far from the road No. 64, commune of Sambuca Pistoiese, province of Pistoia, Tuscany].

B *Hydromantes italicus gormani* Lanza, 1952, p.339 [«Tana di Magnano» = cave Tana di Magnano, cadastral number 162 T/LU, 675 m a.s.l., 44°10'36''7 N –

10°23'17'' E, on the left side of the stream «Il Fiume», along the road Magnano-Corfino, just downstream of the Canigiano bridge, commune of Villa Collemandina, Province of Lucca, Tuscany] (= *Speleomantes italicus*).

The range of *S. italicus* may be bounded so far by the following checked localities:

1 Environs of Seravezza.

2 Cave «Buca di Maffei», cadastral number 172 T/LU, 43°58'01''5 N – 10°15'10'' E, near Capriglia, Pietrasanta, province of Lucca.

3 Valdicastello, near Pietrasanta, province of Lucca.

4 Cave «Buca Tana di Maggiano», cadastral number 827 T/LU, 43°51'31'' N – 10°24'09'' E, near Maggiano, province of Lucca.

5 Cave «Grotta Maona», cadastral number 215 T/PT, 43°54'05'' N – 10°46'42'' E, just N of Montecatini Terme, province of Pistoia.

6 Environs of Quarrata, ca. 11 km as the crow flies S-SE of Pistoia, on the NE slope of Monte Albano's ridge, province of Pistoia.

7 Southern slope of Monte Ceceri, close to Maiano, ca. 1.5 km as the crow flies SE of Fiesole, province of Florence.

8 Alpe della Luna, a few km N of Sansepolcro, province of Arezzo.

9 Caves «Grotta del Diavolo» and «Grotta Magnetica», cadastral number 236 U/PG, 43°21'23'' N – 12°34'41'' E, on the Monte Igino, near Gubbio, province of Perugia.

10 Cave «Grotta di Pian delle Rotte», cadastral number 80 U/PG, 42°50'01'' N – 12°47'53'' E, 875 m a.s.l., on the Monte Serano Sud, a few km N of Campello sul Clitumno, province of Perugia.

11 Cave «Grotta dei Cristiani», 42°15'41'' N – 13°52'36'' E, eastern slope of Monte la Queglia, close to Pescosansonesco, province of Pescara.

12 Cave «Grotta dei Porci», ca. 42°45'08'' N – 13°37'25'' E, close to the «Grotta di Sant'Angelo le Ripe», Salinello Valley, Civitella del Tronto, province of Teramo.

13 in a seminatural cave, close to Verucchio, 43°59'08.3'' N – 12°25'09.6'' E, 230 m a.s.l., municipality of Verucchio, province of Rimini (LANDI, 2000; P. Laghi & C. Pastorelli, personal observation on 01.III.2006).

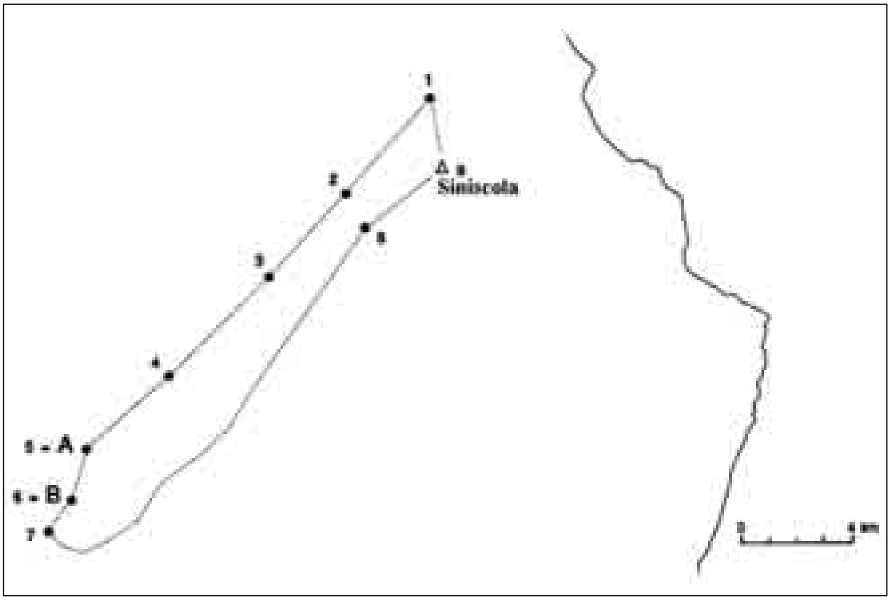
14 Locality «Ca' Carnè» (= «Casa Carnè», «Rifugio Carnè»), 44°13'37.3''N – 11°44'16.3''E (BASSI & FABBRI, 2006), and cave «Abisso Luigi Fantini» (= Abisso del Monte Rontana, Abisso del Pilato) on the Mount Rontana, cadastral number 121 E/RE, 44°13'22'' N – 11°44'32'' E, municipality of Brisighella, province of Ravenna.

15 Cave «Grotta della Tagliata», cadastral number 344 E/MO, 44°24'07'' N – 10°57'40'' E, Guiglia, province of Modena.

16 Cave «Grotta di Santa Maria Maddalena di Valestra», cadastral number 1 E/RE, 44°27'24'' N – 10°34'26'' E, about 900 m a.s.l., near Valestra, Carpineti, province of Reggio Emilia. See Fig. 14.

17 = B.

18 = unidentified species: *S. strinatii* or *S. italicus*? Mount Prinzera, ca. 6 km as the crow flies S-SW of Fornovo di Taro, province of Parma.



Map 3. Range of *S. flavus*.

Speleomantes flavus

Terra typica

A and **B** *Hydromantes genei flavus* Stefani, 1969, p.222 [«Grotte del (= caves of) Monte Albo», namely (see STEFANI, 1969, p. 209) caves «Tumba de Teneru», cadastral number 120 Sa/NU, 40°28’44” N – 09°31’39” E, or «Grotta di Nurai», cadastral number 111 Sa/NU, 40°28’18” N – 09°31’48” E, both in the commune of Lula, province of Nuoro, southwestern end of the Monte Albo range].

The range of *S. flavus* may so far be bounded by the following localities:

1 cave «Pozzo II di Posada», Monte Albo, province of Nuoro, unspotted locality of Mount Sasia.

2 northern slope ot Punta Cupetti, 530 - 570 m a.s.l., about 4.3 km as the crow flies W of the centre of Siniscola, province of Nuoro.

3 tableland immediately S of Punta Gurturgius, 900 m a.s.l., Monte Albo, province of Nuoro.

4 abyss «Sa Tumba de S'Aglioledda», ca. 900 m a.s.l., just S of Punta Romasino, Monte Albo, province of Nuoro.

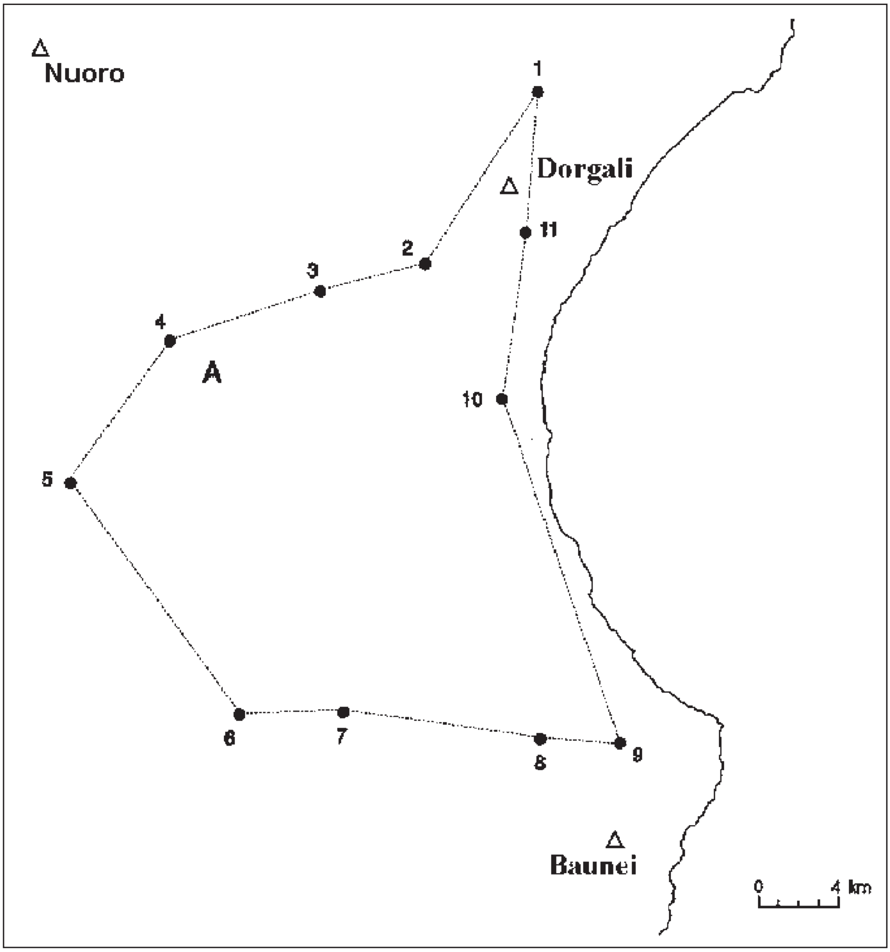
5 cave «Tumba de Teneru» (see *Terra typica* **A** and **B**).

6 cave «Grotta di Nurai» (see *Terra typica* **A** and **B**).

7 cave «Conca 'e Crapa», cadastral number 30 Sa/NU, 40°27'40" N – 09°31'18'' E, 1040 m a.s.l., Monte Albo, province of Nuoro. See Fig. 16.

8 close to the spring «Funtana Schiriddè», ca. 400 m a.s.l., about 3 km as the crow flies W-SW of the centre of Siniscola, Monte Albo, province of Nuoro.

9 cave «Grotta di Cane Gortoe», cadastral number 19 Sa/NU, 40°34'12" N – 09°41'35'' E, 40 m a.s.l., in the town of Siniscola, and locality Badde Ghiramonte, 40°35'00'' N – 09°41'38'' E, 50 – 60 m a.s.l., ca. 500 m as the crow flies N of the centre of Siniscola, province of Nuoro. See Fig. 15.



Map 4. Range of *S. supramontis*.

Speleomantes supramontis

Terra typica

A *Hydromantes supramontis* Lanza, Nascetti and Bullini, 1986, [small, nameless, natural karstic pothole, about 7 m deep, ca. 20 m S of the car park of Scala ‘e Pradu, at the top of the trail Oliena - Scala ‘e Pradu, ca. 1225 m a.s.l. (LANZA et al., 1986)].

See front cover photo, Fig. 3, and Fig. 17.

So far, the range of *S. supramontis* is bounded by the following localities:

1 cave «Grotta Pozzo n. 30», on the Monte Tuttavista, near Galtelli, province of Nuoro.

2 cave «Grotta Pisanu» (=Grotta Gurennoro and Grotta Urennore) cadastral number 215 Sa/NU, 40°17'54'' N – 09°33'03'' E, 142 m a.s.l., about 3 km as the crow flies W - NW of Dorgali, province of Nuoro.

3 cave «Grotta Cannagosula» (= Grotta del Guano), cadastral number 103 Sa/NU, 40°17'18" N – 09°30'28'' E, 300 m a.s.l., close to the spring «su Gologone», ca. 8 km as the crow flies E-NE of Oliena; also in the abyss «Voragine sa Icu», close to the preceding one, province of Nuoro.

4 mountains of Oliena and various outdoor localities and caves of the Supramonte of Oliena [type locality: «Sa Conca de Orgoi» (= Grotta Orgoi and Grotta di Cusidore), cadastral number 34 Sa/NU 40°15'33" N – 09°27°32'' E, 975 m a.s.l., on the Monte Cusidore; «Nurra de sas Palumbas, cadastral number 217 Sa/NU, 40°15'00" N – 09°26'14'' E, 1231 m a.s.l., N of Punta Corrasi; «Grotta di su Bentu», cadastral number 105 Sa/NU, 40°15'16" N – 09°29'12'' E, 200 m a.s.l., in the Lanaittu Valley, province of Nuoro]. See Fig. 4.

5 Orgosolo and a small cave on the Supramonte di Orgosolo, ca. 1360 m a.s.l., province of Nuoro.

6 cave «Grotta di su Mamucone I», cadastral number 304 Sa/NU, 40°05'33" N – 09°26'55'' E, 958 m a.s.l., about 5 km as the crow flies W of Urzulei.

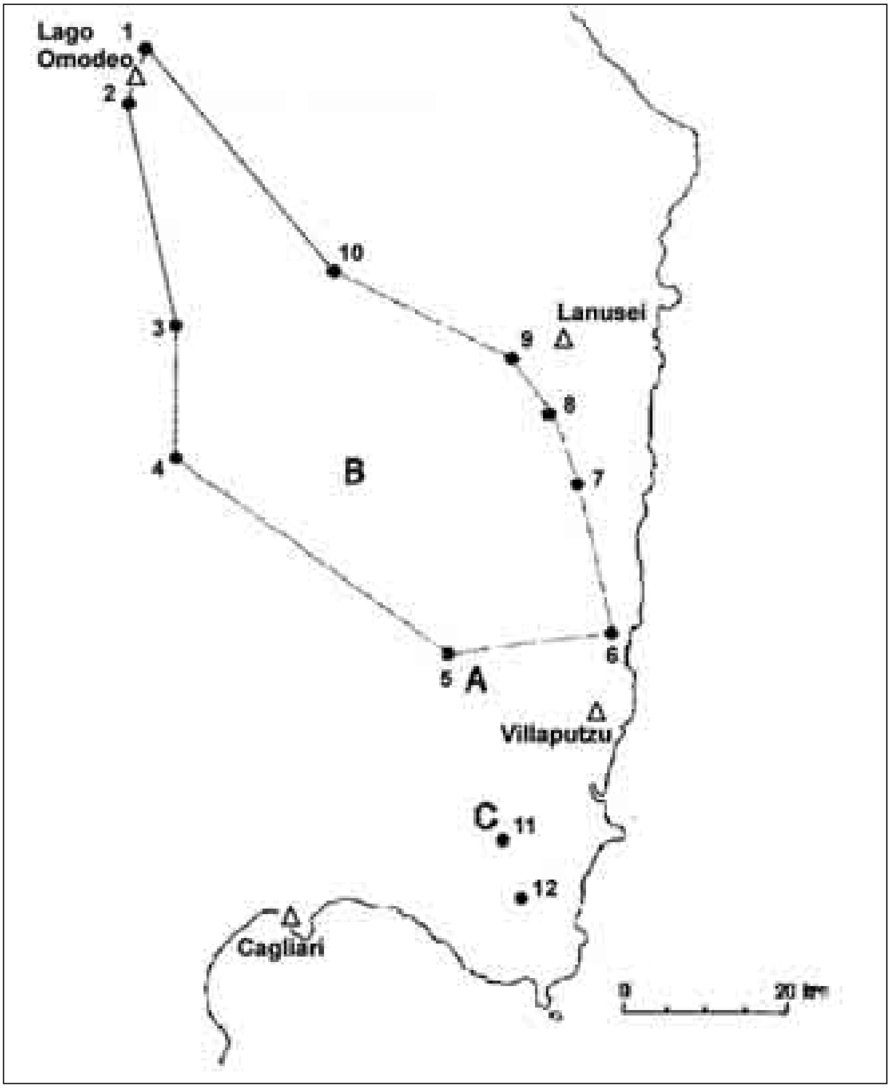
7 Urzulei, province of Nuoro.

8 cave «Grotta di Istirzili», cadastral number 50 Sa/NU, 40°04'46" N – 09°37'13'' E. 507 m a.s.l., about 7 km as the crow flies NW of Baunei and some close outdoor localities in the Bacu Erritzo and Bacu Stirsili valleys, province of Nuoro.

9 abyss «Voragine del Golgo» (= Su Sterru, S'Isterru 'e Golgo = Cratere Vecchio di San Pietro), cadastral number 63 Sa/NU, 40°04'56" N – 09°40'26'' E, 396 m a.s.l. (some specimens were collected at a depth of 290 m, i.e. at 106 m a.s.l.), about 6 km as the crow flies N of Baunei, province of Nuoro.

10 cave «Grotta di Toddeito» (= Grotta di Ziu Arzipreste or Grotta Nuova), 40°14'42"N – 09°37'02'' E, 166 m a.s.l., about 6 km as the crow flies S-SE of Dorgali, province of Nuoro.

11 cave «Grotta Prima di Iscala de su Anzu», cadastral number 213 Sa/NU, 40°19'00" N – 09°36'39'' E, 210 m a.s.l., about 4 km as the crow flies NE of Dorgali, province of Nuoro.



Map 5. Range of *S. i. imperialis* (1-10), and *S. imperialis sarrabusensis* (11-12).

Speleomantes imperialis imperialis

Terrae typicae

A *Hydromantes genei imperialis* Stefani, 1969, p. 220 [«Grotte di Villasalto, Gerrei (Sardegna sud-orientale)»; *terra typica restricta* on the basis of holotype label: cave «Sa Rutta'e Scusi», cadastral number 602 Sa/CA, 39°29'48" N – 09°24'17'' E, 525 m a.s.l., on the southern slope of Monte Pardu, commune of Villasalto, province of Cagliari].

B *Hydromantes genei funereus* Stefani, 1969, p. 222 [cave «Grotta di Asutta 'e Scracca», cadastral number 5 Sa/NU, 39°43'20" N – 09°14'44'' E, 490 m a.s.l., on the Monte Planomuro, Crabarida, commune of Nurri, province of Nuoro (see also STEFANI, 1969: 209)] (= *Speleomantes imperialis imperialis*).

The range of *S. i. imperialis* is so far bounded by the following localities:

1 about m 500 SE of Sèdilo, ca. 40°10' N – 08°55' E, not far from N end of Lago Omodeo, ca. 250 m a.s.l., municipality of Sèdilo, province of Oristano.

2 Tunnel in the Santa Chiara dam, on Lago Omodeo, ca. 40°03'05'' N – 08°52'10'' E, municipality of Ulà Tirso, province of Oristano (*leg*. Mauro Mucedda & Maria Luisa Bertelli, 06.XII.2001).

3 cave «Grotta dei Ragni», cadastral number 1854 Sa/OR, 39°53'32" N – 08°57'01'' E, 160 m a.s.l., near the Castello di Medusa, commune of Samugheo, province of Oristano.

4 close to the pond «Paùli Maiori», 573 m a.s.l., on the Giara di Gesturi, about 6 km NW of Barumini, commune of Genoni, province of Nuoro.

5 caves of Villasalto (see *Terra typica* **A**).

6 cave «Grutta de Giuanniccu Mene», cadastral number 735 Sa/CA, 39°31'29'' N – 09°36'10'' E, 7 m a.s.l., at the foot of Monte del Castello di Quirra, commune of Villaputzu, province of Cagliari. See Fig. 18.

7 caves «Pozzo (= pothole) di Monte Arbu» and «Voragine (= abyss) ot Monte Arbu», about 4 km NW of Tertenia, commune of Tertenia, province of Nuoro.

8 in front of a cave N of Jerzu.

9 cave «Grotta di Taquisara» (= «Grotta del Marmo»), cadastral number 86 Sa/NU, 39°51'09'' N – 09°27'32'' E, 860 m a.s.l.. See Fig. 19.

10 Aritzo.

Speleomantes imperialis sarrabusensis

Terra typica

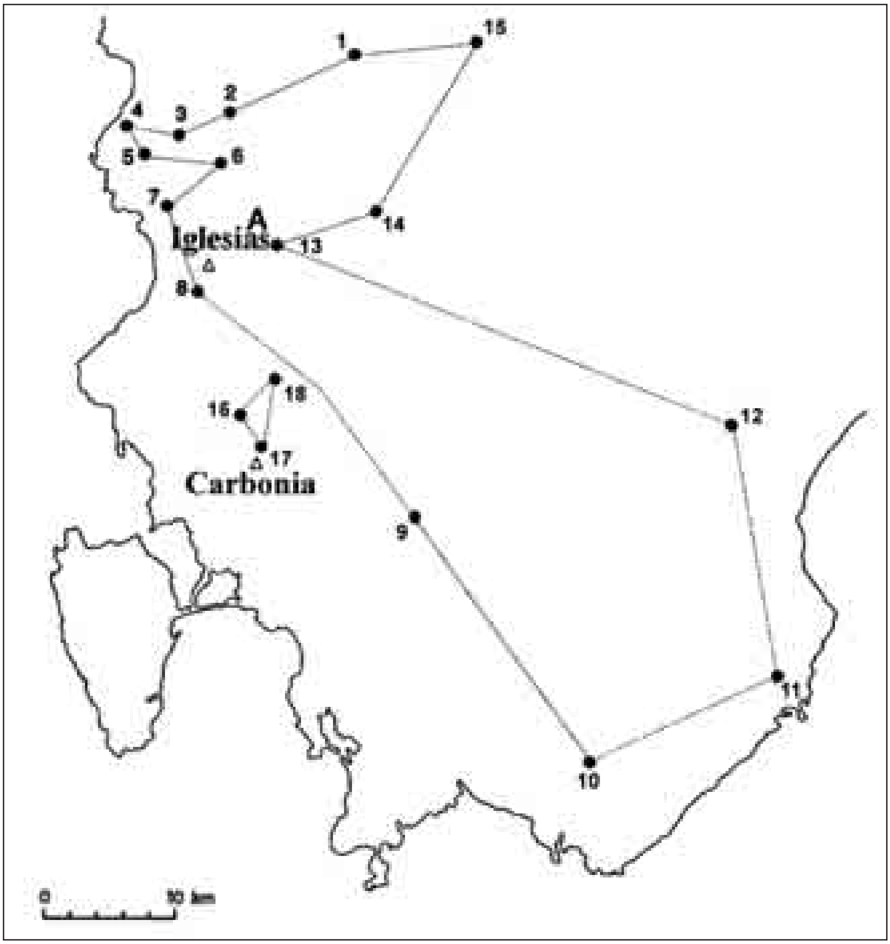
C *Speleomantes imperialis sarrabusensis,* Lanza B., Leo P., Forti G., Cimmaruta R., Caputo V., Nascetti G., 2001, p. 84 [hill «Bruncu de su Crabu», 39°15'20'' N – 09°06'18'' E, 240-260 m a.s.l., Sàrrabus, Monte dei Sette Fratelli's group, province of Cagliari, municipality of Quartuccio (LANZA et al., 2001b)].

See Fig. 20.

S. imperialis sarrabusensis has been so far collected in the following checked localities:

11 = C.

12 forest of Minniminni, 39°12’37’’ N – 09°29’17’’ E, 500-530 m a.s.l., Sàrrabus, Monte dei Sette Fratelli’s group, province of Cagliari, municipality of Castiadas (LANZA et al., 2001b). See Fig. 21



Map 6. Range of *S. genei* subsp. A (1-15), and *S. genei* subsp. B (16-18).

Speleomantes genei

Terra typica

A *Salamandra genei* Temminck & Schlegel, 1838, p. 115 [Sardinia (*terra typica restricta* by MERTENS & MÜLLER, 1928: «Berge bei Iglesias», i.e. mountains near Iglesias; SW Sardinia, province of Cagliari)].

***Speleomantes genei* subsp. A**

The range of *S. genei* subsp. A is so far bounded by the following localities:

1 Mount Linas, province of Cagliari (without any specification).

2 cave «Grotta di su Mannau», cadastral number 97 Sa/CA, 39°24'23" N – 08°29'39" E, 225 m a.s.l., about 3 km as the crow flies S of Fluminimaggiore, province of Cagliari.

3 cave «Pozzetto (= small pothole) n. 2 di Punta Sa Niva» cadastral number 1085 Sa/CA, 39°33'21" N – 08°27'23" E, 540 m a.s.l., about 5 Km as the crow flies E of Buggerru, commune of Fluminimaggiore, province of Cagliari.

4 Buggerru (municipality of Fluminimaggiore, province of Cagliari) (under stones in gardens).

5 cave «Grotta del Tre Composto», cadastral number 1589 Sa/CA, 39°22'48" N – 08°25'46" E, 190 m a.s.l., about 3 km as the crow flies SE of Buggerru, locality Gutturu 'e Sattu, commune of Iglesias, province of Cagliari.

6 cave «Grotta di Santa Maria Doloretta», cadastral number 557 Sa/CA, 39°22'08" N – 08°29'24" E, 540 m a.s.l., locality Genna Bogai, about 8 km as the crow flies E-SE of Buggerru, commune of Iglesias, province of Cagliari.

7 Mine gallery in locality Montecani, between Buggerru and Masua, about 9 km as the crow flies W-NW of Iglesias, ca. 445 m a.s.l., commune of Iglesias, province of Cagliari.

8 cave «Grotta di Fonnesu», cadastral number 1127 Sa/CA, 39°16'51" N – 08°28'33" E, about 2 km as the crow flies N of Gonnesa, on the Monte di San Giovanni, 285 m a.s.l., commune of Gonnesa, province of Cagliari.

9 western slope of the Conca is Ominis, on the left side of the stream «Riu di Monte Essu», about 2 km as the crow flies N of Villaperuccio, 150-190 m a.s.l., commune of Villaperuccio, province of Cagliari.

10 cave(s) in the environs of Domus de Maria, ca 5 km as the crow flies E-SE of Teulada, commune Domus de Maria, province of Cagliari.

11 Montesanto (unspotted locality) near Pula, commune of Pula, province of Cagliari.

12 caves in the environs of Santa Lucia, about 4 km as the crow flies NW of Capoterra, and San Leone (unspotted locality) in the environs of Capoterra, commune of Capoterra, province of Cagliari.

13 environs of Iglesias, province of Cagliari.

14 environs of Domusnovas, province of Cagliari. See Figs 22, 23.

15 environs of Villacidro, province of Cagliari.

***Speleomantes genei* subsp. B**

The range of *S. genei* subsp. B is so far bounded by the following localities:

16 cave «Grotta ‘e Conca is Ollastus», 39°12’07” N – 08°31’11’’ E, northern slope of the hill «Conca is Ollastus», left side of the Canale Peddori, about 1 km as the crow flies E-NE of Barbusi, ca. 320 m a.s.l., commune of Carbonia, province of Cagliari.

17 on the hill Serra de Mesu 39°11’32’’ N – 08°31’19’’ E near Carbonia, 1.5 km as the crow flies SE of Barbusi, province of Cagliari.

18 northern slope of Monte Tasua, 39°13’ N – 08°33’ E ca. 4 km as the crow flies NE of Barbusi, 250-300 m a.s.l., commune of Carbonia, province of Cagliari.

Fig. 8. *S. strinatii.* Adult ♂ from the «Finalese», locality «Trabocchetto», Pietra Ligure, Savona (see Map 1, loc. 14). Photo by P. Laghi & C. Pastorelli.

Fig. 9. *S. strinatii.* Left to right: two ♂♂ and three ♀♀ from the type locality of the species (see Map 1, loc. B). Photo by B. Lanza.

Fig. 10. *S. a. ambrosii.* ♀ from a cave in the karstic area of Sant'Antonio, Pignone, La Spezia (44°10'57.9''N – 09°43'15.7''E, 226 m a.s.l.). Photo by P. Laghi & C. Pastorelli.

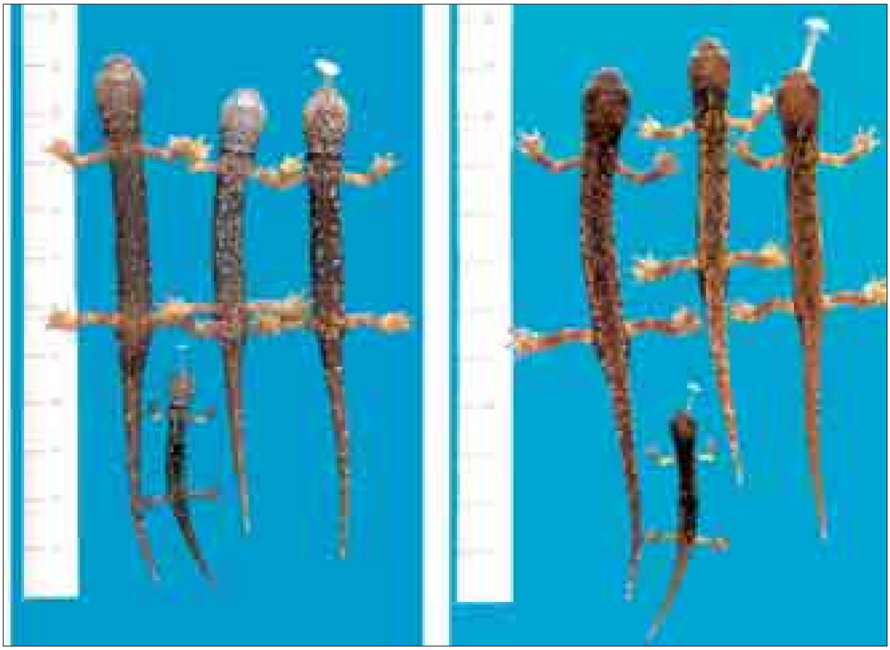


Fig. 11. *S. ambrosii bianchii*. Same individuals in ventral (left) and dorsal (right) view. Left to rigth: ♂ (holotype), juvenile, ♂, and ♀ from the type locality of the subspecies (see Map. 1, loc. F). Note the dark belly colour, typical of the continental species, the male mental glands, and the tongues partly protracted due to handling (anesthetized animals, submerged in waters (cf. Fig. 3 and § 3.3). Photo by Saulo Bambi, from LANZA et al., 2005.

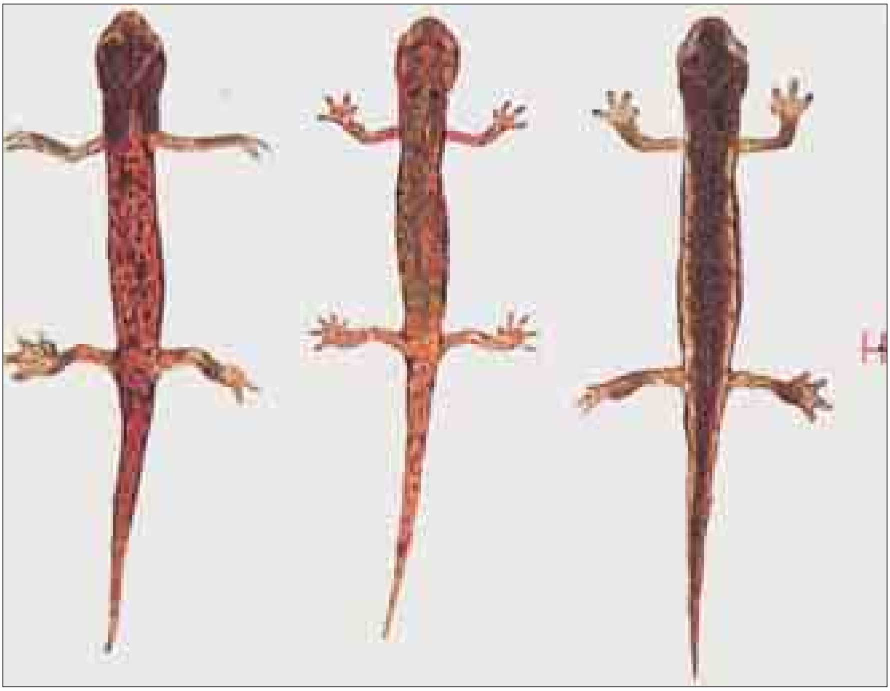


Fig. 12. Left to right: *S. italicus*, adult ♂ from Bibbiena, Arezzo; *S. italicus*, adult♀ whose genome is introgressed by genes of *S. a. bianchii* (from Vergemoli, Apuan Alps); *S. a. ambrosii*,♀ from type locality of the species (see Map 1, loc. A). Watercolour by B. Lanza, from LANZA, 1955.

Fig. 13. *S. italicus*. Adult ♀ from a nameless cave near «Passo del Muraglione», S. Godenzo, Florence (43°56’20.7’’N – 11°38’37.7’’E, 934 m a.s.l.). Photo by P. Laghi & C. Pastorelli.

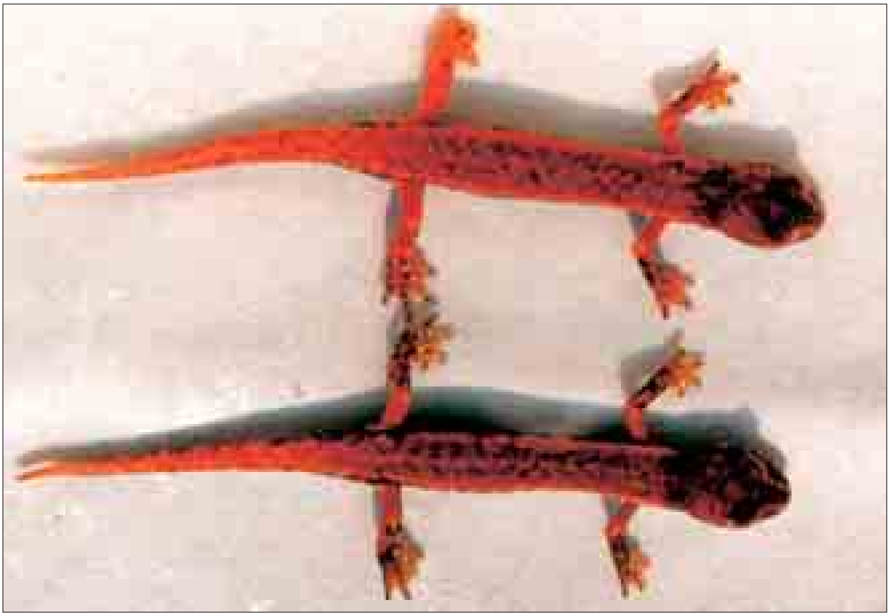


Fig. 14. *S. italicus.* Pattern of the reddish «*gormani*-type». Top to bottom: ♀ and ♂ from the cave «Grotta di S.Maria Maddalena di Valestra», (see Map 2, loc. 16). Photo by B. Lanza.

Fig. 15. *S. flavus.* ♀ from the locality «Badde Ghiramonte», Siniscola, Nuoro (see Map 3, loc. 9). Photo by P. Laghi & C. Pastorelli.

Fig. 16. *S. flavus.* Specimen from the cave «Conca 'e Crapa» (see Map 3, loc. 7). Photo by Stefano Vanni.

Fig. 17. *S. supramontis*. Adult ♀ from the type locality of the species (see Map 4, loc. A). The animal is attacked by a specimen of the leech *Batracobdella algira* (small black spot on the left axilla). Photo by P. Laghi & C. Pastorelli.

Fig. 18. *S. i. imperialis*. ♀ of the *«imperialis»* phenotype, from the northern slope of the Monte Castello di Quirra, Villaputzu, Cagliari, 200-260 m a.s.l. (near loc. 6 of Map 5). Photo by P. Laghi & C. Pastorelli.

Fig. 19. *S. i. imperialis.* Adult specimen of the *«funereus»* phenotype, from the environs of the cave «Grotta di Taquisara», Gairo Taquisara, Nuoro (see Map 5, loc. 9). Photo by P. Laghi & C. Pastorelli.

Fig. 20. Top to bottom: *S. imperialis sarrabusensis*, ♂, ♀, and juvenile from the type locality of the subspecies (see Map 5, loc. C); *S. i. imperialis*, ♂ and ♀ from the cave «Grotta VI Se Tomeu», cadastral number 220 Sa/NU, 39°39'33"N-09°29'36"E, 555 m a.s.l., Perdasdefogu, Nuoro. Photo by Saulo Bambi.

Fig. 21. *S. imperialis sarrabusensis*. Pair in courtship (♂ above) from the forest of Minniminni (see Map 5, loc. 12 and § 7.3). Photo by Salvatore Spano.

Fig. 22. *S. genei* subsp. A. Subadult specimen from the environs of the cave «Grotta San Giovanni», Domusnovas, Cagliari (see Map 6, loc. 14). Photo by P. Laghi & C. Pastorelli.

Fig. 23. *S. genei* subsp. A. Adult ♀ from the same locality of Fig. 22. Photo by P. Laghi & C. Pastorelli.

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