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On the distribution and chromatic differentiation of the Alpine Salamander *Salamandra atra* LAURENTI, 1768, between Val Lagarina and Val Sugana (Venetian Prealps): an updated review

(Urodela: Salamandridae)

Zur Verbreitung und Farbdifferenzierung des Alpensalamanders, *Salamandra atra* LAURENTI, 1768, zwischen Val Lagarina und Val Sugana (Venetianische Voralpen): Ein aktualisierter Überblick

(Urodela: Salamandridae)

LUCIO BONATO & KURT GROSSENBACHER

KURZFASSUNG

Publizierte und unpublizierte Daten zur Detail-Verbreitung und zur Farb-Differenzierung des Alpensalamanders (*Salamandra atra* LAURENTI, 1768) in den südlichen Voralpen zwischen Val Lagarina und Val Sugana werden zusammengetragen und kritisch betrachtet. Bekannt sind Populationen vom nordwestlichen Teil der Hochebene der Sette Comuni (Sieben Gemeinden) und von den Südhängen des Pasubio-Massivs, sehr wahrscheinlich gibt es Vorkommen aber auch im Gipfelbereich des letzteren sowie auf der Kette des Cornetto und im Carega-Massiv. Wenigstens zwei, wahrscheinlich allopatrische Typen von Populationen konnten aufgrund der Farbmerkmale unterschieden werden: solche mit ausgedehnt gefleckten Individuen (beschrieben als *S. atra aurorae*) auf der Hochebene der Sette Comuni, und solche mit schwach gefleckten, manchmal ganz schwarzen Individuen auf dem Pasubio-Massiv. Ein dritter Typ, bei dem völlige Schwarzfärbung häufiger auftritt, existiert möglicherweise auf Gebirgsmassiven im Südwesten.

ABSTRACT

Published and unpublished information was compiled and critically reviewed, in order to present an updated synthesis on the micro-distribution and the chromatic differentiation of the Alpine Salamander (*Salamandra atra* LAURENTI, 1768) in the Prealps between Val Lagarina and Val Sugana. Populations are known from the northwestern part of the Sette Comuni plateau and the southern slopes of the Pasubio massif. The Alpine Salamander is most likely present also at the top of the latter relief, on the Cornetto ridge and on the Carega massif. At least two types of populations, probably allopatric, could be distinguished on the basis of chromatic features: those of extensively patched individuals (described as *S. atra aurorae*), on the Sette Comuni plateau and those of poorly patched individuals, rarely completely black, on the Pasubio massif. A third type, in which entirely black individuals are more frequent, is supposed to exist on massifs in the south-west of the area.

KEY WORDS

Amphibia, Urodela, Salamandridae; *Salamandra atra*, *S. atra aurorae*, distribution, coloration, geographic differentiation, Venetian Prealps, Italy

INTRODUCTION

The occurrence of the Alpine Salamander *Salamandra atra* LAURENTI, 1768, is strictly limited to montane sites along the Alpine and Dinaric chains (S. H. I. 1996; GROSSENBACHER 1997). The actual distribution is still only roughly known, particularly in marginal regions such as the Southern Prealps. Here, recent investigations added new information but do not seem to have yet reached a satisfactory view of the distribution of the species (see: S. H. I. sez. Lombardia 2000 - for Lombardia; CALDONAZZI et al. in press - for the Trento Province; Gruppo Nisoria in press - for the Vicenza Province; Gruppo per la realizz. Progetto Atl. Erpet. Veneto 1996 - for all of Veneto; LAPINI et al. 1996 - for Friuli-Venezia Giulia).

Despite this situation, in the last two decades some findings and preliminary studies brought the first insights into an interesting case of geographic colour differ-

entiation within the species. This involved populations of the Venetian Prealps, particularly the Sette Comuni plateau and the Pasubio relief. At the end of the Nineteen-seventies, an unusual population characterised by largely yellow-patched individuals was discovered in a limited site on the Sette Comuni plateau (TREVISAN et al. 1981; TREVISAN 1982). Afterwards only few data were published on the distribution of this new form (see: GROSSENBACHER 1994). As a result, studies on the genetic differentiation were carried out on animals from a single site only until now (TREVISAN et al. 1984; JOGER 1986; OLIVIERI 1991; STEINFARTZ et al. 2000). More recently, another interesting population, characterised by a less extensively patched coloration, was discovered on the Pasubio massif (BONATO 2000), suggesting somehow complex relationships among the populations of Alpine Salamanders living in the region between of Val Lagarina (Adige Valley) and Val Sugana (Brenta Valley).

This paper is an update of our knowledge on the distribution and differentiation of *S. atra* in the above region, integrating the few published data and unpublished information. Our aim is to present a background (though a preliminary one) to further analysis of this interesting case of geographical differentiation and to any action plan for the conservation of these endemic forms.

STUDY AREA AND METHODS

Study area

Our survey was limited to the part of the Venetian Prealps between Val Lagarina (west) and Val Sugana (north and east). The region can be regarded as a natural geomorphological and biogeographical unit, being delimited by deep glacial valleys, that work as dispersal barriers for the Alpine Salamander today. Moreover, all available information suggests that an appreciable differentiation of these animals can be observed only inside this region.

The western part of the territory is occupied by steep massifs, often more than 2,000 m high, cut by several valleys and gradually degrading southwards to the Lessinian Hills and the Venetian Plain. From south-west to north-east the following major mountainous groups can be recognised: Lessini, Carega, Cornetto, Pasubio, Campomolon and Toraro, Becco di Filadonna.

The eastern part of the territory, instead, appears as a single large plateau (Sette Comuni plateau), about 1,000 m high but more elevated on the northernmost part; only few gorges open towards its core (Val d'Assa, Val Frenzela).

The western massifs and the eastern plateau are separated by a fluvio-glacial incision, running about north-south, represented by the deep Val d'Astico and the valley of the Centa stream. A rather narrow ridge, not more than 1,050 m high, seems to be the only potential bridge present for the dispersion of the Alpine Salamanders (BONATO 2000).

In the highest parts of the whole territory, the substrate is mainly dolomitic or calcareous, consequently the landscape is karstic; this feature characterises most of the Venetian Prealps and distinguishes them from the true Alps. Average temperatures of +10/+20 °C in July, -5/+5 °C in January, and precipitation intensity of 1,500-2,500 mm/year are registered (FLIRI 1975).

Methods

Information on the presence of Alpine Salamanders was gathered by different methods: planned field researches, carried out in the last years by the authors and occasionally by other persons; critical review of the available published data; requests for information directly addressed to persons often visiting montane sites for different purposes and considered reliable in reporting occasional encounters with these animals (e.g., botanists, entomologists and amateur naturalists).

Both published observations and other apparently reliable information were evaluated according to the reliability degree as we could judge.

Each record was mapped with a precision of one kilometre by assigning geographical coordinates according to the UTM system (relative to the zone 32T).

Toponyms and UTM coordinates were derived from the last edition of the Carta d'Italia published by the Istituto Geografico Militare (Firenze).

The individuals observed were assigned to the following chromatic types (fig. 1): body largely patched (P+) like in all *S. atra aurorae* TREVISAN, 1982 described from Bosco del Dosso (TREVISAN 1982; KLEWEN 1988; BONATO 1998); body poorly patched (P-), like in most individuals described from the southern slopes of Mt. Pasubio (BONATO 2000); body completely black (B), as is typical in *S. atra atra* according to all of the literature.

When permitted by the data available, we tried to assign each local population to one of the following chromatic types: (i) all individuals largely patched; (ii) most individuals poorly patched but some of them completely black; (iii) most or all individuals completely black.

RESULTS

The collected data on distribution and chromatic differentiation of the Alpine Salamander between Val Lagarina and Val Sugana are reported in table 1 and mapped in figure 2. They are summarised as follows for each apparently suitable mountain group:

* Sette Comuni plateau. This was the most intensely investigated area: since the beginning of the Nineteen-eighties (after the publication of the discovery of *S. atra aurorae*), many researchers visited the plateau, particularly north of Asiago. As a result, a relatively rich series of observations was gathered.

Alpine Salamanders are found along a stripe on the left of the Val d'Assa and north of the central basin, from Passo Vezzena to Gallio; populations were detected both in woody slopes exposed southwards and in shrubby elevations exploited in the past as meadows, from 1,200 to 1,800 m. Despite the research efforts, no individuals were found in other apparently suitable sites, such as the northernmost ridges, the eastern part of the plateau and the right side of Val d'Assa (just vis-à-vis of colonised slopes).

Only largely patched individuals seem to be present, their habitus agreeing with that of the typical *S. atra aurorae*. Rather old findings of completely black individuals reported in the literature (see: TREVISAN 1981; KLEWEN 1988) were not confirmed by recent surveys and have to be regarded as unreliable.

* Becco di Filadonna. No data .

* Campomolon and Toraro. No data.

* Pasubio. A population of poorly patched individuals, occasionally completely black, is found at least on the southern slopes and gorges, between 1,500 and 1,900 m.

Apparently black individuals were seen on the upper plateau of this relief, from 1,800 to 2,000 m; these observations, however, are variable in reliability and until now our researches failed to confirm them.

* Cornetto. An undocumented observation of an apparently black individual was reported from a steep slope, above 1,500 m.

* Carega. A completely black individual was reported to have been collected on the upper part of the massif, but unfortunately the preserved material cannot be identified with certainty.

* Lessini. No data.

DISCUSSION

Distribution

As already suggested by GROSSENBACHER (1994), the range of the endemic *S. atra aurorae* turned out to be wider than previously known from the literature. Populations chromatically referable to this taxon appeared to be distributed in the north-western part of the Sette Comuni plateau, at least on a stripe about 15 km long and few km wide. However, whether the distribution is continuous or scattered is hard to argue. The geomorphological and environmental features of the neighbouring

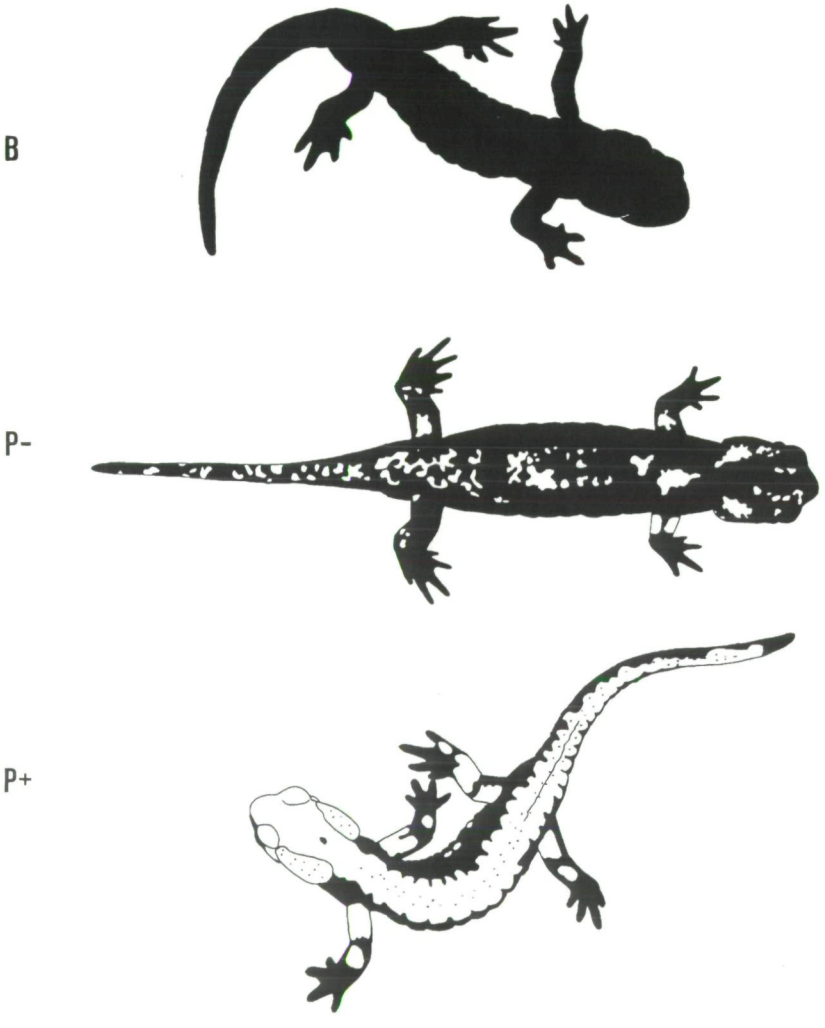


Fig. 1: Individual chromatic types recognised in the Alpine Salamander (*Salamandra atra*) in the area between Val Lagarina and Val Sugana (Venetian Prealps): P+ = largely patched; P- = poorly patched; B = completely black.

Abb. 1: Individuelle Zeichnungstypen des Alpensalamanders (*Salamandra atra*) im Gebiet zwischen Val Lagarina und Val Sugana (Venetianische Voralpen). P+ = ausgedehnt gefleckt; P- = schwach gefleckt; B = völlig schwarz.

Table 1 (opposite page): Available data on the distribution and chromatic differentiation of the Alpine Salamander (*Salamandra atra*) in the area between Val Lagarina and Val Sugana (Venetian Prealps). For criteria adopted and definition of chromatic types see text (Methods). Abbreviations in the column 'Habitat': *A - Abies, F - Fagus, L - Larix, P - Picea.*

Tab. 1 (gegenüberliegende Seite): Verfügbare Daten zur Verbreitung und Farbdifferenzierung des Alpensalamanders (*Salamandra atra*) im Gebiet zwischen Val Lagarina und Val Sugana (Venetianische Voralpen). Zu den angewandten Kriterien und zur Erklärung der Färbungstypen siehe Text (Methods). Abkürzungen in der Spalte 'Habitat': *A - Abies, F - Fagus, L - Larix, P - Picea.*

UTM Grid / UTM Raster	Site / Fundort	Elevation a.s.l. (m) Seehöhe (m)	Date(s) / Datum/Daten	Author(s) / Autor/en	1st published by / Erstpublikation	Reliability / Verläßlichkeit	Specimens / Exemplare	Type of colour-pattern / Zeichnungstyp	Habitat
663-5065	M. Carega: Cengia di Pertica	1,400-1,600	ca 1982	G. OSELLA	OSELLA (1985)	high / hoch	1	B	rocky, grassy, bushy / felsig, begrast, bebuscht
666-5077	M. Pasubio: Col Santo (near/nahe Rifugio Lancia)	1,800	?	?	BRUNO (1973)	low / gering	?	B?	?
669-5068	Monte Cornetto	1,500-1,800 ?	ca 1986	A. DE TOMASI	unpubl.	low / gering	1	B?	rocky, grassy / felsig, begrast
669-5075	M. Pasubio: Malga Buse Bisorte	1,800-1,900	ca 1981	S. SCORTEGAGNA	unpubl.	high / hoch	1	B?	rocky, grassy; meadows felsig, begrast; Wiesen
671-5071	M. Pasubio: Val Fontana d'Oro	1,550	VI-1994 VII-1999	A. FABRIS L. BONATO	BONATO (2000)	high / hoch	4	P-	rocky, grassy / felsig, begrast
671-5072	M. Pasubio: M. Forni Alti	1,600-1,700	VII-1999	L. BONATO	BONATO (2000)	high / hoch	9	P-, B	rocky, grassy / felsig, begrast
684-5092	Valle Sparavieri	1,400	VI-1993	A. NOELLERT	unpubl.	high / hoch	3	P+	coniferous forest (*P*), dense, ± grassy Nadelwald (*P*), dicht, ± begrast
685-5091	Bosco del Dosso (just/unmittelbar E Val Remaloch)	1,250-1,500	several / div. 1978 / 1996	P. TREVISAN and others / etc.	TREVISAN (1982)	high / hoch	> 10	P+	mixed forest (*P, A, F*), clear, grassy Mischwald (*P, A, F*), licht, begrast
685-5092	Bosco del Dosso (just/unmittelbar E Val d'Anime)	1,400-1,500	several / div. 1978 / 1996	R. KLEWEN L. BONATO	KLEWEN (1988)	high / hoch	> 10	P+	mixed forest (*P, A, F*), clear, grassy Mischwald (*P, A, F*), licht, begrast
686-5091	Bosco del Dosso	1,350-1,500	several / div. 1978 / 1998	P. TREVISAN and others / etc.	TREVISAN (1982)	high / hoch	> 100	P+	mixed forest (*P, A, F*), clear, grassy Mischwald (*P, A, F*), licht, begrast
686-5092	Vaio di Pian del Morto	1,500-1,600	several / div. 1978 / 1997	P. TREVISAN and others / etc.	TREVISAN (1982)	high / hoch	> 20	P+	coniferous forest (*P, A*), clear, grassy Nadelwald (*P, A*), licht, begrast
688-5091	Malga Koebele	1,300	ca 1987	G. GUEX	unpubl.	high / hoch	?	P+	mixed forest (*P, F*), dense Mischwald (*P, F*), dicht
688-5093	Val Renzola	1,450	several / div. VI-1987 / 1989	M. FRANZEN, S. NICOLAI etc.	FRANZEN & NICOLAI (1987)	high / hoch	> 2	P+	mixed forest (*P, F*), clear Mischwald (*P, F*), licht
690-5090	Monte Meatta	1,800	VII-1990	W. MISSLER	unpubl.	high / hoch	1	P+	?
693-5090	Val Galmarara (near/nahe Malga Galmararetta)	1,400-1,450	VIII-1994	M. BIONDO, M. WINISTOERFER	unpubl.	high / hoch	1	P+	coniferous forest (*P*), dense, ± grassy; meadows / Nadelwald (*P*), dicht, ± begrast; Wiesen
694-5090	Monte Zebio (near/nahe Casara Zebio Pastorie)	1,700-1,800	several / div. VIII-1994 / IX-1998	M. PAGANIN, S. SCORTEGAGNA	unpubl.	high / hoch	3	P+	rocky, bushy, grassy, ± wooded (*P*); meadows / felsig, bebuscht, begrast, ± bewaldet (P); Wiesen
695-5090	Val di Nos	1,300-1,400	several / div. VI-1995 / VI-1998	K. GROSSENBACHER	unpubl.	high / hoch	> 5	P+	mixed forest (*P, L, F*), clear, grassy Mischwald (*P, L, F*), licht, begrast
696-5086	Zebbo-Basso	1,200	VI-1995, 1999	B. PERTILE, P. RIGONI	unpubl.	high / hoch	2	P+	coniferous forest (*P*), dense, ± grassy; meadows / Nadelwald (*P*), dicht, ± begrast; Wiesen
696-5090	Val di Nos	1,300-1,400	several / div. VI-1995 / VI-1998	K. GROSSENBACHER	unpubl.	high / hoch	> 5	P+	mixed forest (*P, L, F*), clear, grassy Mischwald (*P, L, F*), licht, begrast

areas suggest that the actual range could be even larger. Nevertheless, *S. atra aurorae* remains a very local endemic form, a vulnerable one in a conservation perspective.

Further populations of Alpine Salamanders were found to have colonised other montane areas south-west of the Sette Comuni plateau, but only within a distance not exceeding 30 km. While all populations known from the Sette Comuni plateau can be easily referred to *S. atra aurorae*, all those discovered outside the plateau are clearly different in chromatic features from typical *aurorae*. However, insufficient information does not permit a satisfactory comprehension of their actual distribution, conservation status, phyletic relations and taxonomic position (BONATO 2000).

Outside the region considered in this review, the Alpine Salamander appears to be more widespread north of Val Sugana than in the other parts of the Venetian Prealps. Typically black populations are known from the Orobian Alps (S.H.I. sez. Lombardia 2000) through Adamello-Presanella (BRUNO 1973; BENNATI 1988), Gruppo di Brenta (BRUNO 1973, but not confirmed in CALDONAZZI et al. in press), Lagorai ridge and Cima d'Asta (CALDONAZZI et al. in press), Vette Feltrine and Dolomiti Bellunesi (LAPINI et al. 1998; TORMEN et al. 1998) to Friuli. A minimum distance of about 25 km can be estimated between *S. atra aurorae* and the nearest black population north of Val Sugana.

From the mountains just west of Val Lagarina (Bondone-Stivo and Altissimo-Baldo ridges) no populations are known. Nevertheless, more research is needed, because apparently suitable sites are available and there is an unpublished, rather reliable but not documented observation (M. Altissimo: la Polsa, 1,200-1,250 m, UTM coordinates 661-5050; May 1986; one individual found under stones, 14 cm long, completely black; P. LORENZI, pers. comm.).

East of Val Sugana, Alpine Salamanders seem to be absent from the Grappa massif, despite the fact that this area is environmentally similar to the Sette Comuni plateau. Less surprising is the lack of data from the Cesen-Nevegal ridge where the elevation is rather low and the climate less suitable. Further east, the Cansiglio plateau and the M. Cavallo host well known populations of completely black Alpine Salamanders, although apparently limited to few sites (DOLCE 1988).

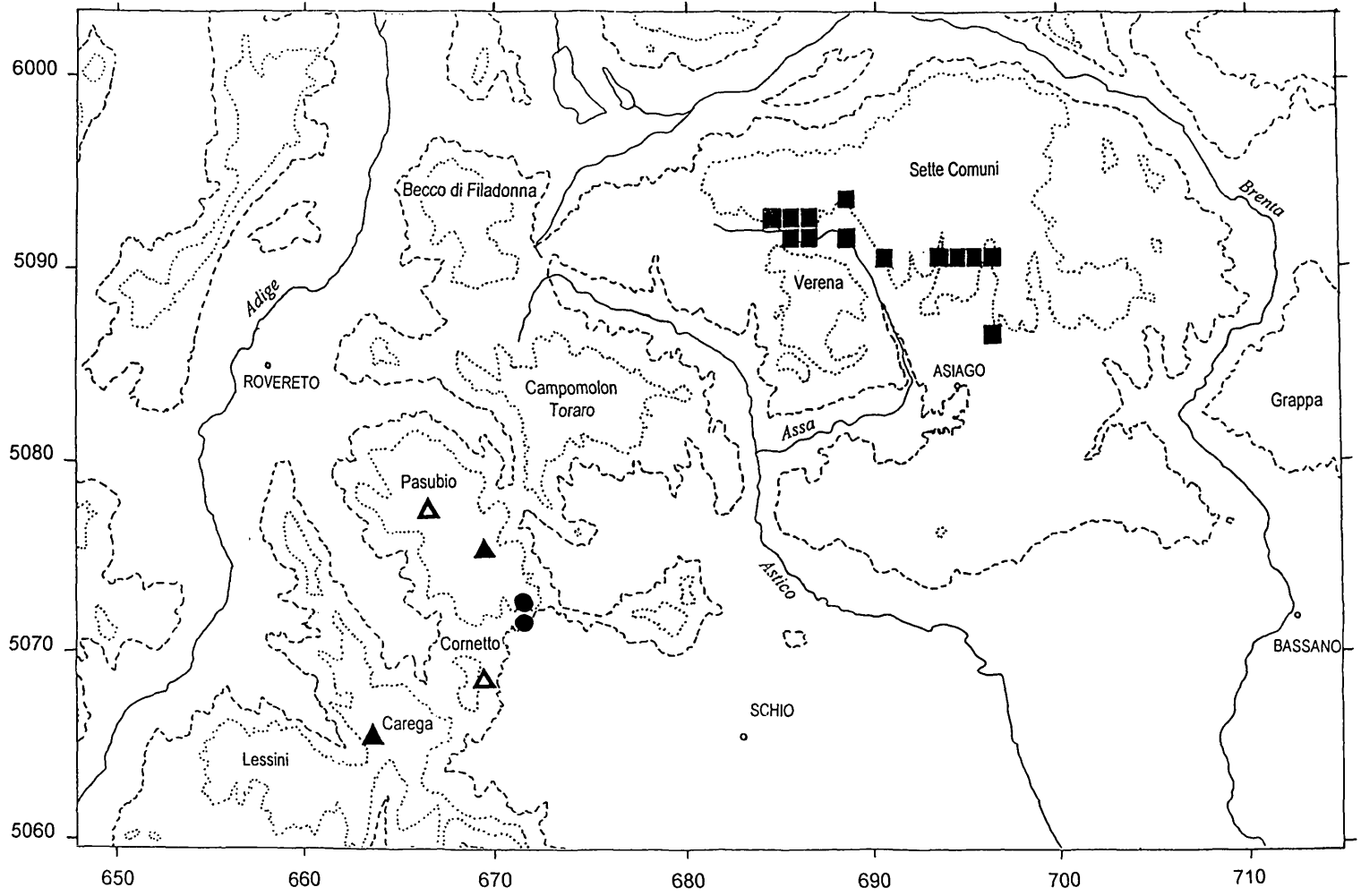
Ecological notes

Between Val Lagarina and Val Sugana, Alpine Salamanders live in a wide habitat range, from beech-woods to alpine prairies, from 1,200 to 2,000 m. Ecological conditions do not seem to differ from those reported for the nearest colonised Southern Prealps (DOLCE 1988; TORMEN et al. 1998; CALDONAZZI et al. in press).

In the considered region, the Alpine Salamander and the Fire Salamander *S. salamandra* (LINNAEUS, 1758), were never found syntopically. This may depend on the ecological differences between the two species and the environmental configuration of the territory. While the viviparous and microthermic Alpine Salamander can be found only in the karstic dry plateaus and ridges, never below 1,200 m, the ovoviviparous and mesothermic Fire Salamander is widely spread on the marginal hills, very rich in streams, mainly in the altitudinal range of 100-600 m and only occasionally up to 1,100 m (Gruppo Nisoria, in press). In the Sette Comuni plateau, Fire Salamanders can reach the southern edge of

Fig. 2 (opposite page): Distribution and chromatic differentiation of the Alpine Salamander (*Salamandra atra*) in the area between Val Lagarina and Val Sugana (Venetian Prealps), as suggested by the gathered data. For each square kilometre of the UTM coordinate system, the following information was mapped:
presence of the Alpine Salamander (● ▲ ■ = certain; Δ = suggested but to be confirmed);
chromatic type of local population (● = most individuals with largely patched coloration; ▲ Δ = most individuals with poorly patched coloration, yet some completely black; ■ = probably most individuals completely black).

Abb. 2 (gegenüberliegende Seite): Verbreitung und Farbdifferenzierung des Alpensalamanders (*Salamandra atra*) im Gebiet zwischen Val Lagarina und Val Sugana (Venetianische Voralpen) auf Grundlage der gesammelten Daten. Für jeden Quadratkilometer des UTM-Koordinatensystems wurden folgende Informationen dargestellt: Präsenz des Alpensalamanders (● ▲ ■ = sicherer Nachweis; Δ = vermutetes, zu bestätigendes Vorkommen); Färbungstyp in der Lokalpopulation (● = die meisten Individuen mit ausgedehnter heller Fleckung; ▲ Δ = die meisten Individuen mit spärlicher Fleckung, einige völlig schwarz; ■ = wahrscheinlich die meisten Individuen völlig schwarz).



the plateau and the bottom of the deeper valleys (P. RIGONI, pers. comm.). In the central basin, however, a small stable population of Fire Salamanders lives near Gallio, only few kilometres away from the nearest known population of Alpine Salamanders (Gruppo Nisoria, in press).

A similar pattern of spatial vicariance between the two species is known for other neighbouring prealpine regions, e.g., the Vette Feltrine, the Dolomiti Bellunesi (LAPINI et al. 1998) and the Cansiglio plateau (POMINI 1936; DOLCE 1988). Cases of syntopy are however reported from inner alpine regions (e.g., KLEWEN 1988).

Chromatic differentiation

According to the chromatic features of the body surface, the populations cluster into at least two groups, which are apparently allopatrically distributed:

* populations in which all individuals show patches (no exceptions have been documented so far), the total extension of which is - on the average - very large (P+). This type seems to be exclusive of the Sette Comuni plateau.

* populations in which most individuals show patches (some of them are completely black), the total extension of which is - on the average - rather limited (P-). This type seems to be typical at least in the Pasubio massif.

A third chromatic type, in which the patches are even less frequent or completely absent, is suggested but not proved to exist in the south-western mountains. The few reliable data reported from those sites refer to individuals described as completely black.

Unfortunately, an unresolved incongruency between different information sources forbids us to rely on a completely black specimen preserved in the Museum of Natural History of Verona (catalogue number: CE 1009). It is labelled as follows: "Salamandra atra Laurenti - loc. Mte Pasubio - 14/8/64 - det. Maucci - ex coll. Museo - sul sentiero che conduce al rifugio - leg. Raineri". Identical information is reported in the published catalogue of the collection (MAUCCI 1971); the site reported in BRUNO (1973) as "Col Santo presso il Rifugio V. Lancia, 1,800 m, sul M. Pasubio", although more precise, is very probably derived from the same material. But the presumed collector recently denied to have found such an animal (W. RAINERI, pers. comm.); moreover, a black individual collected in the early Nineteen-eighties on M. Carega was indicated to have been deposited in the same Museum (OSELLA 1985; G. OSELLA, pers. comm.), but recently no material labelled from that site could be found in the collection. As a conclusion, the present labelling is very probably erroneous.

The chromatic variations observed in the Alpine Salamanders between Val Lagarina and Val Sugana seem to be exclusive of this prealpine region. An interesting case of genetic differentiation underlies these phenotypical differences, as some preliminary studies already suggest (TREVISAN et al. 1984; JOGER 1986 - by means of protein electrophoresis; OLIVIERI 1991 - by means of allozyme analysis; STEINFARTZ et al. 2000 - by means of DNA sequencing). Moreover, the updated available information suggests that the phylogeographical pattern occurring here may be more complex than a simple *atra-aurorae* dichotomy (as it was thought previously) and so stimulates further studies.

The evolutionary history of these populations was obviously influenced by the climatic and environmental changes that occurred in the Venetian Prealps mainly in the last million years. This idea was already proposed on the basis of the theory of the "refuge massifs" (GROSSENBACHER 1994; LAPINI et al. 1996; LAPINI et al. 1998; BONATO 2000) and supported by estimates of divergence times recently obtained by a "molecular clock" model (STEINFARTZ et al. 2000). The distribution of glaciers during the recent ice-ages in the present region was described with great precision already several decades ago (PENCK & BRUECKNER 1909; TREVISAN 1939; CASTIGLIONI 1940) and was recently confirmed and given in more detail (CORÀ 1998). These paleogeographical models are expected to represent a good basis for the historical interpretation of the phylogeographical pattern.

Although not extensively studied, several other cases of biological differentiation were reported for this region: en-

demic forms of montane and barely mobile organisms, both plants (e.g., RAFFAELLI & BALDOIN 1997; PROSSER & SCORTEGAGNA 1998) and animals (review in BAGNOLI et al. 1997), are known to live only in few sites between Val Lagarina and Val Sugana. Until now, however, the case of the Alpine Salamander is the only one known among vertebrates.

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