

Rediscovery of *Salamandra algira* Bedriaga, 1883 from the Beni Snassen massif (Morocco) and phylogenetic relationships of North African *Salamandra*

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The genus *Salamandra* Laurenti, 1768 is distributed throughout most of continental Europe and is also present in Corsica, some parts of Turkey, Iran, Israel, Syria, Morocco, Algeria and, with less certainty, in Sicily and Tunisia (Arnold, 2002; Bons and Geniez, 1996; Degani, 1996; Klewen, 1991; Schleich et al., 1996; Thiesmeier, 2004; Thorn, 1968; Turrisi and Vaccaro, 1998). *Salamandra* has a very patchy distribution in North Africa, where it is restricted to a few humid or sub-humid forested regions in Morocco and Algeria (fig. 1; see also Donaire-Barroso and Bogaerts, 2003 and Thiesmeier, 2004). One such area is the Beni Snassen massif, situated in northeast Morocco (locality 5 in fig. 1). The presence of *Salamandra algira* Bedriaga, 1883 in this locality was reported for the first time by Melhhaoui and Chavanon (1989). After this first record, based on an observation made by a student of some larvae in Jbel Quartass, there have not been further records for the last 16 years in either its original locality or in other places of the Beni Snassen. As a result of this, this locality was not included in some publications (Schleich et al., 1996; Salvador, 1996). The Beni Snassen massif is very important from

a biogeographical point of view because it is separated from all other Moroccan localities of *S. algira* by the Moulouya river basin, a relatively arid plain that, according to some authors, might have acted as a geographical barrier to dispersal, promoting genetic divergence in some reptile and amphibian groups including *Salamandra* (Arano et al., 1998; Alvarez et al., 2000; Steinfartz et al., 2000; Paulo, 2001).

After several explorations to the region in different years and different seasons, in autumn 2004, six larvae and an a dead adult male specimen of *S. algira* were found in the Beni Snassen, at 1300 mts above sea level on the northern slope of a mountain near Quartass. The six larvae were found in a very shallow puddle formed besides a man-made fountain. The adult specimen was found on land near the fountain. The adult specimen has been deposited in the Museu de Ciències Naturals (Barcelona, Spain) <http://www.bcn.es/museuciencies>; with the following accession number MCNC 2005-0550. The adult specimen measures 190 mm of total length (124 mm from snout to vent and 66 mm from the vent to the tip of the tail). It was jet-black with yellow irregular spotting scattered all over the upper side of the body and presented very small red dots on the head, sides and legs (pictures are available from the authors upon request). It is now preserved in 70% alcohol and as a result of that its coloration has faded. It has large paratoids without black spotting. Larvae measured between 30-34 mm ($X = 32.5$) in total length and between 16-19 mm ($X = 17.83$) from snout to vent. The ecosys-

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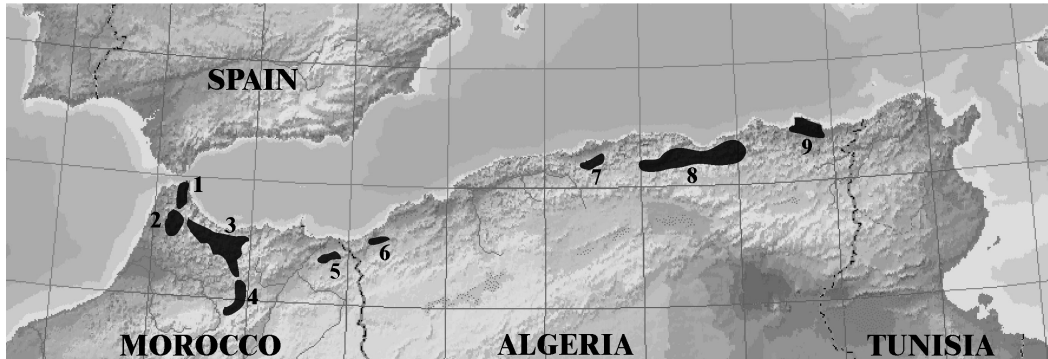


Figure 1. Map showing the distribution of all North African populations of *Salamandra algira* known to date. Numbers beside shadowed areas refer to geographical localities: 1. Tangitanian district (North Jebala), *S. a. tingitana*; 2. Western Rif mountains, *S. a. algira*; 3. Central Rif mountains, *S. a. algira*; 4. Middle Atlas, *S. a. algira*; 5. Beni Snassen massif, *S. a. algira*; 6. Rarh el Maden, *S. a. algira*; 7. Blida Atlas, *S. a. algira*; 8. Great and Small Kabylia, *S. a. algira*; 9. Edough peninsula, terra typica of *S. a. algira*.

tem where the animals were found consisted of a substrate of limestone karst, with abundance of crevices and relatively big cavities situated in a mixed forest of mature evergreen oak *Quercus ilex ballota*, *Pinus halepensis* and some scattered *Olea europaea*. The undergrowth was mainly a mixture of *Quercus coccifera*, *Cistus* sp. and *Pistacia* sp. *Salamandra algira* was found together in the same habitat with *Discoglossus pictus*, *Bufo mauritanicus* and *Bufo viridis*. Despite searching thoroughly, we could not find any macroinvertebrates in the water, one of the principal preys of *Salamandra* larvae (Baumgartner et al., 1999). Further studies on this population will be directed to try to clarify its diet (work in progress).

Although the single adult specimen found does not allow us to draw any definitive conclusions about the ecology and behaviour of this population, the habitat where it was found suggests *Salamandra algira* from the Beni Snassen might behave similar to other studied salamander populations from north Africa (Donaire-Barroso and Bogaerts, 2001, 2003; Donaire-Barroso et al., 2001) and use the high number of holes and crevices present in the limestone rocky substrate as refuge to stand the high temperatures and desiccation during the hottest summer months. Like in *S. algira* from other localities in north Africa (Donaire-Barroso and

Bogaerts, 2001, 2003; Donaire-Barroso et al., 2001), *S. s. longirostris* from southern Spain (pers. observ.), *S. infraimaculata* from Israel (Warburg, 1994) and other salamandrids from the Mediterranean basin as for instance *Lyiasalamandra helverseni* from the Aegean islands (Polymeni, 1994), activity in *S. algira* from the Beni Snassen is very dependent upon rainfall and therefore the annual activity period probably starts after summer, triggered by the first autumn rainfalls and probably extends through the winter (pers. observ.). *Salamandra* specimens from the Middle Atlas (Jbel Tazzeqa, Bou Iblane) and the Rif mountains (Moulay Abdesalam, Chefchaouen, Ketama) are usually found in relatively high numbers walking on the forest floor after heavy rains (pers. observ.; Bons and Geniez, 1996), while in drier conditions they were seen foraging usually at the entrance or very close inside limestone crevices or stone walls (pers. observ.), a pattern similar to that observed in *Chioglossa lusitanica* (Sequeira et al., 2001).

In order to investigate the phylogenetic relationships of the *S. algira* population from the Beni Snassen a tissue sample was obtained and used for the molecular analyses, which included many other representatives of both North African and Eurasian *Salamandra*. DNA extractions and PCR amplifications of the desired mitochondrial fragments were carried out according to methods described elsewhere (Caranza et al., 1999, 2000). Primers used in both amplifica-

Table 1. Details of material and sequences used in the present study. Numbers between brackets after locality names refer to localities shown in figure 1.

| Taxa | Locality | Accession Numbers | | | Codes |
|--|--------------------------------------|-------------------|------------|------------|----------|
| | | Cyt <i>b</i> | / 12SrRNA | D-loop | |
| <i>Salamandra algira algira-1</i> | Beni Snassen (Morocco) [5] | DQ221247 | / DQ221231 | / DQ221248 | E9035.1 |
| <i>Salamandra algira tingitana-1</i> | Djebel El Fahies (Morocco) [1] | AY247732 | / DQ221227 | | E1712.7 |
| <i>Salamandra algira tingitana -2</i> | Tagramt (Morocco) [1] | AY247733 | / DQ221228 | | E309.10 |
| <i>Salamandra algira algira-2</i> | Akshur near Talembot (Morocco) [3] | AY247734 | / DQ221229 | | E1712.9 |
| <i>Salamandra algira algira-3</i> | Chefchauen (Morocco) [3] | AY247735 | / DQ221230 | | E1712.14 |
| <i>Salamandra infraimmaculata orientalis</i> | W. of Adana (Turkey) | DQ221242 | / DQ221222 | | E3009.22 |
| <i>Salamandra salamandra longirostris</i> | Los Barrios (Spain) | DQ221243 | / DQ221223 | | E1712.37 |
| <i>Salamandra atra aurorae</i> | Bosque del Dozzo (Italy/Austria) | DQ221246 | / DQ221226 | | E3009.16 |
| <i>Salamandra lanzai</i> | Italy | DQ221244 | / DQ221224 | | E3009.23 |
| <i>Salamandra corsica</i> | Cascade des Anglais Corsica (France) | DQ221245 | / DQ221225 | | E3009.18 |
| <i>Salamandra salamandra almanzoris</i> | Sierra de Gredos (Spain) | DQ221239 | / DQ221219 | | E1712.17 |
| <i>Salamandra salamandra crespoides</i> | Sta. Lucia, Algarve (Portugal) | DQ221237 | / DQ221217 | | E1712.25 |
| <i>Salamandra salamandra morenica</i> | Villanueva del Rey (Spain) | DQ221238 | / DQ221218 | | E1712.40 |
| <i>Salamandra salamandra bernaerzi</i> | Valle del Rio Tendi (Spain) | DQ221240 | / DQ221220 | | E1712.20 |
| <i>Salamandra salamandra giglioli</i> | Serra de San Bruno (Italy) | DQ221241 | / DQ221221 | | E1712.34 |
| <i>Salamandra salamandra bejarae</i> | San Pablo de los Montes (Spain) | DQ221236 | / DQ221216 | | E1712.44 |
| <i>Salamandra salamandra gallaica</i> | Pto. Arrabida (Spain) | DQ221253 | / DQ221215 | | E7110.11 |
| <i>Salamandra Salamandra fastuosa</i> | Bagneres de Luchon (France) | DQ221234 | / DQ221214 | | E1712.27 |
| <i>Salamandra salamandra salamandra</i> | Ukraine | DQ221232 | / DQ221213 | | E7110.15 |
| <i>Salamandra salamandra terrestris</i> | Montseny (Spain) | AY222503 | / AY222459 | | E1712.49 |

tion and sequencing of three mitochondrial genes were cytochrome b1 and cytochrome b2 (Kocher et al., 1989) for the cytochrome b (cytb) gene, 12Sa and 12Sb (Kocher et al., 1989) for the 12S rRNA gene and D-loopF (5'-CAT TGT TGT GGC GAC ATA TTA TGC T-3') and D-loopR (5'-GTC TTA ATA ATC GTA AGT AAA TAG GGC-3') for a fragment of the control region (D-loop) homologous to the region comprised between nucleotides 16005 and 16379 of the *Lyciasalamandra atifi* mitochondrial genome (Genbank accession number NC_002756). Genbank accession numbers for the sequences used in this study are presented in table 1. Alignments were performed with ClustalX (Thompson et al., 1997) with default parameters (gap opening = 10; gap extension = 0.2). Phylogenetic analyses were carried out using the maximum likelihood (ML) method implemented in either PHYML (Guindon and Gascuel, 2003) or PAUP* 4.0b10 (Swofford, 1998), depending on the size of the dataset. The models of sequence evolution that fit the datasets better were calculated using MODELTEST (Posada and Crandall, 1998). These were the HKY+I+G for the combined dataset including the cytb and 12S sequences and the HKY+G for the dataset including the control region (D-loop) sequences only. ML analyses performed in PAUP* included heuristic searches involving tree bisection and reconnection (TBR) branch swapping with 100 random stepwise additions of taxa. Reliability of the phylogenetic trees was assessed by bootstrap analysis (Felsenstein, 1985), involving 1000 replications.

Three hundred and twenty base pairs (bp) of cytb and 370 bp of the 12S were sequenced for the *S. algira* from the Beni Snassen and compared with sequences from the recently described *S. a. tingitana* (Donaire-Barroso and Bogaerts, 2003) from the Tangitanian district (locality 1 in fig. 1), *S. a. algira* from the Central Rif region (locality 3 in fig. 1) and nearly all Eurasian species and subspecies of *Salamandra*. The result of the phylogenetic analysis combining the information from the cytb and 12S mitochondrial sequences is shown in fig. 2A and, contrary to what was suggested by Steinfartz et al. (2000), indicates North African *S. algira* is a relatively ancient monophyletic assemblage, sister to all the rest of Eurasian members of the genus *Salamandra*. The phylogeny also shows that *S. a. algira* is paraphyletic. Within Morocco, the rediscovered population from the Beni Snassen represents a very divergent lineage, sister to the rest of Moroccan populations. Genetic divergence values (uncorrected

p-distance) between the Beni Snassen population (locality 5 in fig. 1) and all other Moroccan populations analyzed (localities 1 and 3 in fig. 1) range between 7.2%-9% for the cytb fragment and 2.4-2.7% for the 12S. Divergence between *S. a. algira* from the Central Rif region (locality 3 in fig. 1) and the recently described *S. a. tingitana* (locality 1 in fig. 1) ranges between 4.6-5% for the cytb and is 1% for the 12S. Preliminary data using cytb partial sequences indicate that specimens from the Middle Atlas region (locality 4 in fig. 1) are very closely related to specimens from the Central Rif region (locality 3 in fig. 1) and therefore are also very distinct from the population from the Beni Snassen (data not shown). Divergence values among Moroccan samples fall within the range or are higher than the genetic divergence found among all recognized species of Eurasian *Salamandra* (4.3-7.5% for the cytb gene and 1-4% for the 12S) but a bit lower than that found for reptile species (Harris, 2002).

In order to analyze the phylogenetic relationships of *S. algira* from the Beni Snassen further, a phylogenetic tree was inferred using information from the mitochondrial control region (D-loop) from this population of *S. algira* from the Beni Snassen and two other sequences from specimens from the Central Rif region (locality 3 in fig. 1) and from the surroundings of the type locality of *S. algira* (Massif of Edough in northeast Algeria; locality 9 in fig. 1) not available in Genbank but included in Steinfartz et al. (2000). The only available D-loop sequence in Genbank from Steinfartz et al. (2000) (*S. corsica*) was also included in the analysis and *Lyciasalamandra atifi* was used to root the tree. The results of the phylogenetic analysis are presented in fig. 2B and clearly show that *S. a. algira* from the Beni Snassen is genetically distinct from the other two North African samples of *Salamandra* analyzed to date. Surprisingly, it is more closely related to *S. a. algira* from the type locality in Algeria than to the individual from the closer population of *S. a. algira* from the Central Rif region.

Phylogenetic relationships among Eurasian *Salamandra* are not very well resolved and some unsupported relationships such as the sister taxa relationships between *S. i. orientalis* and *S. s. longirostris* are probably artifactual (*S. Carranza*, work in progress). *Salamandra atra*, *S. lanzai* and *S. corsica* form a monophyletic group, although the bootstrap support is very low. All European Fire salamanders form a very well supported clade with internal relationships congruent with García-París et al. (2003). The phylogeny presented in fig. 1B combined with previous knowledge of the phylogenetic relationships within the family Salamandridae (Larson et al., 2003; Titus and Larson, 1995), genetic divergence between North African and Eurasian taxa (9.8% for the cytb) and the rate of molecular evolution calculated for exactly the same cytb region of *Pleurodeles* (1.95% per million years; see Carranza and Arnold, 2004), indicate the ancestor of *Salamandra* probably originated in Eurasia, from where it colonized North Africa approximately 5 Myr ago. This date coincides with the end of the Messinian Salinity Crisis (Duggen et al., 2003; Hsü, 1983; Hsü et al., 1977; Hsü et al., 1973; Krijgsman et al., 1999) and indicates *S. algira* most probably colonized North Africa via the land-bridge that connected the Iberian Peninsula with Morocco for more than 600,000 years (5.9-5.3 Mya), allowing many reptiles and amphibians and other non-volant groups to disperse overland from one continent to the other (Arntzen and García-París, 1995; Blondel and Aronson, 1999; Carranza and Arnold, 2004; García-París and Jockusch, 1999; Martínez-Solano, 2004; Martínez-Solano et al., 2004).

As shown in fig. 1, the distribution of the *S. algira* complex in North Africa is very fragmentary. As in *Neurergus strauchii*, it may be as a result of poor knowledge of its real distribution range, or it may be as a result of restriction to just few favourable places (Pasmans et al., in press). The phylogenies presented in fig. 2 suggest *S. algira* might have once been more widely distributed over the mountainous

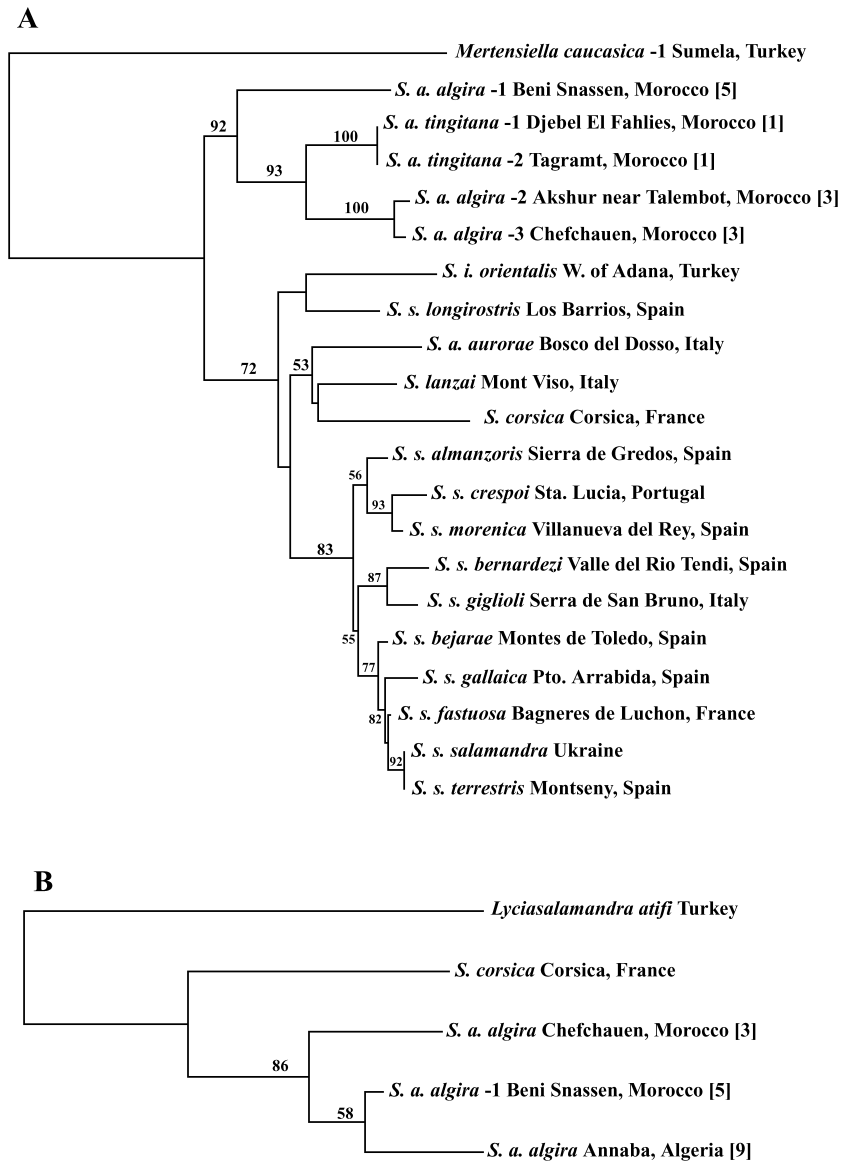


Figure 2. Phylogenetic relationships of *Salamandra*. A. ML tree (inferred using PHYML and the HKY+I+G model of sequence evolution) combining 320 b.p. of *cytb* and 370 b.p. of 12S mitochondrial sequences (690 b.p. with 159 variable positions). B. ML tree (inferred using PAUP* and the HKY+G model of sequence evolution) using 374 b.p. (78 variable positions) of mitochondrial DNA sequences from the control region (D-loop). Values by the nodes indicate bootstrap values above 50. Numbers between square brackets after locality names refer to locality numbers in fig. 1.

regions in northern Maghreb. However, the high genetic divergence between all populations analyzed to date (see above) indicate genetic isolation between these populations is relatively old and occurred approximately 5-3.6 Mya, during the Lower Pliocene. This pattern of high genetic divergence among relatively close populations of *Salamandra* is similar to the pattern observed in south Iberian *Salamandra* (*S. s. longirrostris* vs. *S. s. crespoi/morenica*) or *Lyciasalamandra*, where highly divergent lineages were found to have diverged between 6 to 8 Mya, when extensive uplifting of the Anatolia occurred in response to geological events in the area (Weisrock et al., 2001).

Genetic divergence among populations of *S. algira* is also supported by morphological differentiation. For instance, *S. a. tingitana* from locality 1 in fig. 1 (North Jebala in the Tangitanian district) was recently described as a different subspecies based on molecular, morphological and ecological characters. Among other features, *S. a. tingitana* is characterized by its relatively small total length, total absence of red coloration and tendency towards hypoliteism and even melanism (dark-brown instead of jet black coloration). Another unique feature of *S. a. tingitana* is its reproductive mode, which is largely viviparous instead of ovoviviparous like all other *S. algira* populations known to date (Bogaerts and Donaire-Barroso, 2003; Donaire-Barroso and Bogaerts, 2001, 2003; Donaire-Barroso et al., 2001). Although all these differences and the phylogeny presented in fig. 2A suggest *S. a. tingitana* could be considered a species, a taxonomic revision of North African *Salamandra* must await until morphological and molecular data from other Moroccan and Algerian isolated populations become available (Bogaerts and Donaire-Barroso, 2003; S. Caranza, work in progress).

The population from Annaba in northeast Algeria is especially interesting. This represents the type locality of *S. algira* and a preliminary analysis of the D-loop mitochondrial gene (see above) and morphological features (Bogaerts

and Donaire-Barroso, 2003) suggest it might also be distinct from all other North African populations of *S. algira* complex.

A morphological feature that seems to play an important role in differentiating among North African *S. algira* is the presence of red coloration mainly in the throat, head and tail in a high proportion of specimens of some particular populations (Bogaerts and Donaire-Barroso, 2003; Donaire-Barroso and Bogaerts, 2003). The presence of very small red dots on several parts of the head and body of the only adult specimen from the Beni Snassen found to date suggest that, as already predicted by Bogaerts and Donaire-Barroso (2003), this population might be related to the population from Rhar el Maden, near Remchi, NW Algeria (locality number 6 in fig. 1) situated less than 100 km to the east of the Beni Snassen. This Algerian population is characterized by the presence of conspicuous red coloration in different parts of the head and body (Doumerge, 1901). Red coloration is certainly absent from specimens from the type locality region (locality 9 in fig. 1), it is present in specimens from the Blida Atlas (locality 7 in fig. 1) and no data exists for the specimens from the Great and Small Kabylia (locality 8 in fig. 1; see Donaire-Barroso and Bogaerts, 2003). In Morocco, red coloration is present in the animals from the Central Rif Mountains and Middle Atlas (localities 3 and 4 in fig. 1) and is absent in specimens from the Tangitanian district and the northwestern Rif Mountains (localities 1 and 2 in fig. 1) (Donaire-Barroso and Bogaerts, 2003).

Salamandra algira from North Africa presents a fragmentary distribution restricted to mixed Mediterranean mountain forests in the proximity of relatively clean springs. These factors make them very sensitive to any alterations of their habitat, especially those linked to human activities that directly or indirectly produce aridification. It has been shown that such alterations might be driving some populations of *S. salamandra* from southern Spain into extinction (Buckley et al., 2004) and negatively

affecting Moroccan amphibian fauna (Franchimont and Saadaoui, 2001).

Although enough data is not yet available to assess the conservation status of the Beni Snassen population, the increased desertification of the general area that has occurred in recent years linked to the canalization of some natural springs and construction of fountains (preventing access to the limited water bodies by pregnant females) is probably affecting the population, and might explain why it has remained undiscovered since 1989. As a result of that, one of the conservation priorities will be to assess the distribution area of this population in the Beni Snassen and its breeding points in order to be able to preserve them from desiccation and alteration (work in progress).

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