NOTES ON *SALAMANDRA SALAMANDRA* ssp.

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1. THE BIRTH OF COMPLETELY METAMORPHOSED YOUNG

On 22-VII-1960 I caught some specimens of *Salamandra salamandra fastuosa* Schreiber between Lago Ercina and Lago Enol, ± 1000 m above Covadonga (Picos de Europa, Cantabrian Mountains, Spain). On 14-VIII-1961 from one of the salamanders two young were born (length 40 and 45 mm). Only one specimen showed traces of gills ± 1.5 mm long, both specimens were in all other characters completely metamorphosed, also the colour pattern resembled the typical *fastuosa*-pattern, i.e. longitudinal yellow stripes almost without interruption (see fig. 1). The 15th of August two more young were born, both with gills, the smallest specimen (35 mm) in the form of a normal larva (fig. 2) with gills of ± 4 mm and with a normal larval coloration. One day later a fifth young was born, also purely larval in form and colour. The last one was completely metamorphosed on 3-X-1961. Freytag mentions 2-3 months for the larval period, so the development of the young *fastuosa* which were not discernable from normal larvae, took only a relatively short time. No more than 5 young were born.

Fig. 1. Completely metamorphosed young of *Salamandra salamandra fastuosa*, after a photograph taken the day after birth. 40 mm.

(Drawing J. A. Mastro)

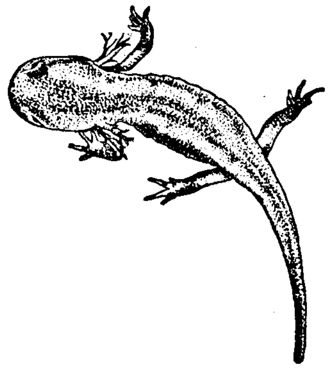

Fig. 2. More or less normal larva of *Salamandra salamandra fastuosa*, of the same litter as the specimen of fig. 1. 35 mm.

(after a photograph, drawing by J. A. Mastro)

In March 1967 the same female deposited ± 30 unfertilized eggs in the water of the paludarium. The difference between the small litter and the large number of eggs (in large specimens 70 or more larvae may be born) suggests a same kind of pregnancy as in *Salamandra atra*, in which only two completely metamorphosed young are born, which are fed before birth with the other eggs.

The birth of completely or almost completely metamorphosed *Salamandra salamandra* has been reported several times, mostly from specimens of the Spanish subspecies. Lantz, cited by WOLTERSTORFF (1928) mentions two cases from Mont de Bedat, Bagnères de Bigorre (one litter of 24 normal larvae and 4 metamorphosed young, one litter of 2 metamorphosed young). Wolterstorff himself added 4 more cases of "Vollmolchgebären", all in specimens from Oviedo. FREYTAG (1955) mentions a case from Coimbra. Mr. P. J. H. van Bree received once a collection of salamanders from Linares de Rio Frio (Province of Salamanca) among which some completely developed young probably born on the way. MERTENS (1956) mentions a case from Corsica (i.e. an animal from Corsica from which young were born in captivity). KLINGELHÖFFER mentions Voida as a place where the salamanders often get completely metamorphosed young. I have not been able to find Voida on the map, but as Klingelhöffer speaks of the subspecies *bernardezi*, originally described (by Wolterstorff) from Oviedo, I suppose that Voida is somewhere in the neighbourhood of Oviedo. So we find this phenomenon especially and probably even normally in the subspecies *fastuosa* (according to EISELT distributed from the central Pyrenees westward over the Cantabrian mountains, so Bagnères de Bigorre as well as Covadonga and Oviedo, and Voida – see above – belong to this range). The occurrence of this kind of birth in specimens from Coimbra, Salamanca and Corsica is probably not the rule. At least from Salamanca and Corsica many normal larvae are known as against from both places only one case of completely metamorphosed young. WOLTERSTORFF (1928) suggested that the much polluted water in the treeless surroundings of Oviedo would be the cause of the deviating birth. The absence of trees has probably nothing to do with it. It is true that EISELT (1958) shows that the range of *Salamandra salamandra* coincides roughly with the range of the beech tree (*Fagus silvatia* incl. *F. orientalis*, p. 124), but first there are more salamanders known from treeless regions bearing normal larvae (the extreme case is that of *Salamandra salamandra almanzoris* Müller & Hellmich, see also p. 33) and secondly the Covadonga area is not treeless, there are even beeches, which are lacking in the rest of Spain beyond the Pyrenees and the Cantabrian Mountains. More important seemed to be the pollution of the water. However, in Bagnères de Bigorre the water seems to be very good and the laguna's above Covadonga are extremely fresh and clear. In the beginning of August 1967 I went back there, especially to seek for larvae of the salamanders. In the night, during a drizzling rain (it is often raining or at least misty in this region) I quickly caught some adult though small specimens (125, 130 and 140 mm).

In Lago Enol I only saw some fish and hundreds of crayfis (*Austropotamobius pallipes* Lereboullet). Of course the crayfish could be a reason to avoid the larval state. Indeed I also did not find here larvae of *Alytes obstetricans* either, although lots of adult ones were living in the neighbourhood.

But also in a small pond close to the other laguna (Ercina), in which no crayfish live and in which I caught (and released after examination) hundreds of larvae of *Alytes obstetricans, Triturus alpestris cyreni* and *Triturus helveticus helveticus* no larvae of *Salamandra* could be found. Neither did I find them in a small brooklet, which as far as I could judge, was ideal for the development of larval salamanders. The only small salamander I caught (± 3.5 cm) was hidden on the land under stones, and completely metamorphosed.

So I do not think that the polluted water is the reason for the salamanders of Oviedo to skip their larval stage. Besides, the pollution is probably of recent origin, so it would be unthinkable that in such a short time an important adaptation could have been selected. That it is a hereditary character is suggested by the fact that the phenomenon also occurs in captivity, under circumstances in which other salamanders have produced normal larvae. On the other hand it is possible that the possession of this character (probably within the whole subspecies *fastuosa*) prevented the extinction of the population of Oviedo, after all the available water had been polluted. The answer to the question as to what circumstances did select the probably hereditary character of bearing gill-less, completely metamorphosed young probably cannot be deduced from the recent occurrence of the phenomenon. Considering, however, the analogous cases of births of completely developed young in the related *Salamandra atra*, and the fact that the ovoviviparous *Lacerta vivipara* and *Vipera berus* are the species which occur higher up to the north as well as higher up in the mountains than any other european reptile (the same applies to the ovoviviparous species around *Chamaeleo bitaeniatus* compared with the oviparous chameleons) we are led to the suggestion that this kind of birth is an adaptation to extremely cold circumstances, perhaps originated during the ice-ages. That the mutation occasionally occurs might be deduced from the rare occurrence in other subspecies. This leaves the question why this character did not originate in the eastern refugium (Balkan or Turkey). To which we may answer that perhaps the character *did* originate in an isolated mountain-dwelling population, but that because of other changes this form became specifically different from

Fig. 4a

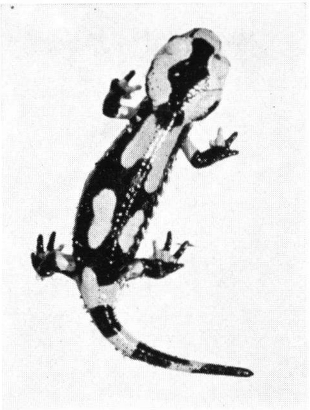

Fig. 4b

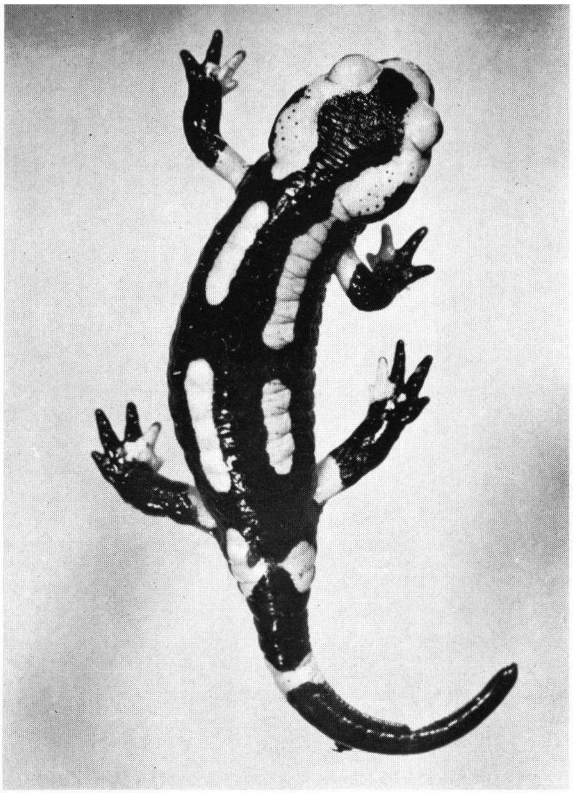

Fig. 4c

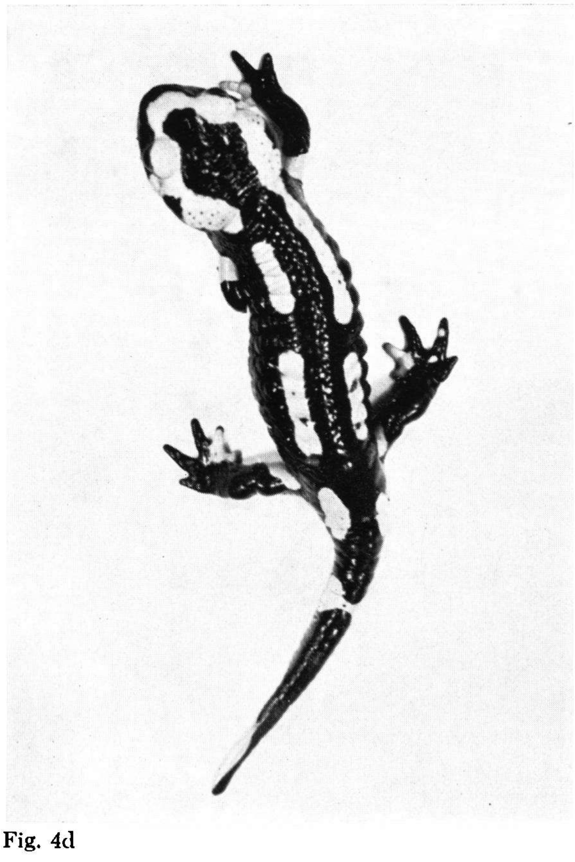

Fig. 4d

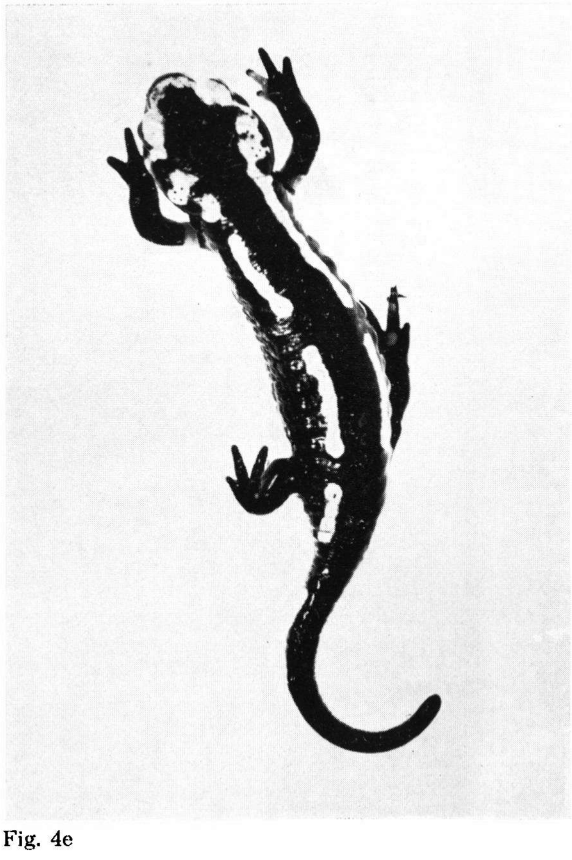

Fig. 4e

Fig. 4a-e. The development of the colour pattern in a specimen of *Salamandra salamandra terrestris* from Daoulas (Finisterre, France). Respectively IX.1965, 13.III.1966, 19.VIII.1966, 10.XI.1966, 14.IX.1967.

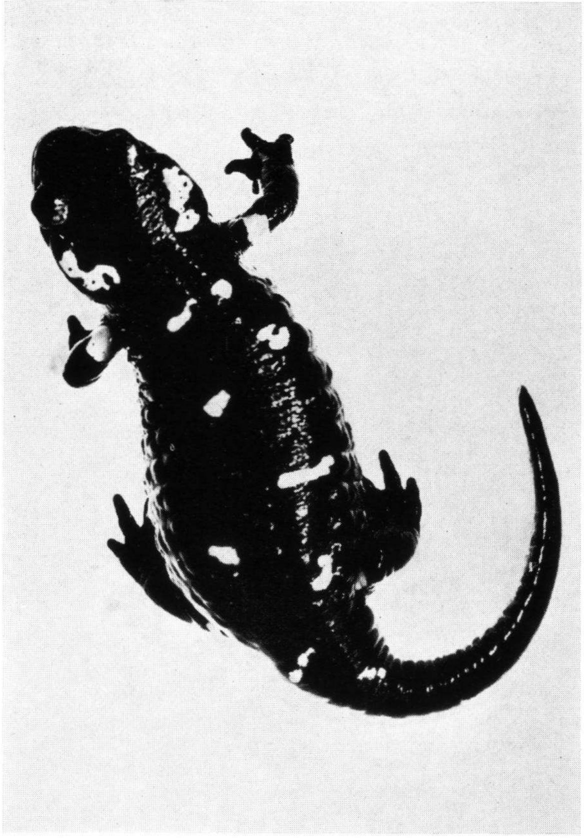

Fig. 5. Adult *Salamandra salamandra almanzoris,* caught as larva, raised in captivity. Note the small yellow spots compared with the young ones in fig. 3.

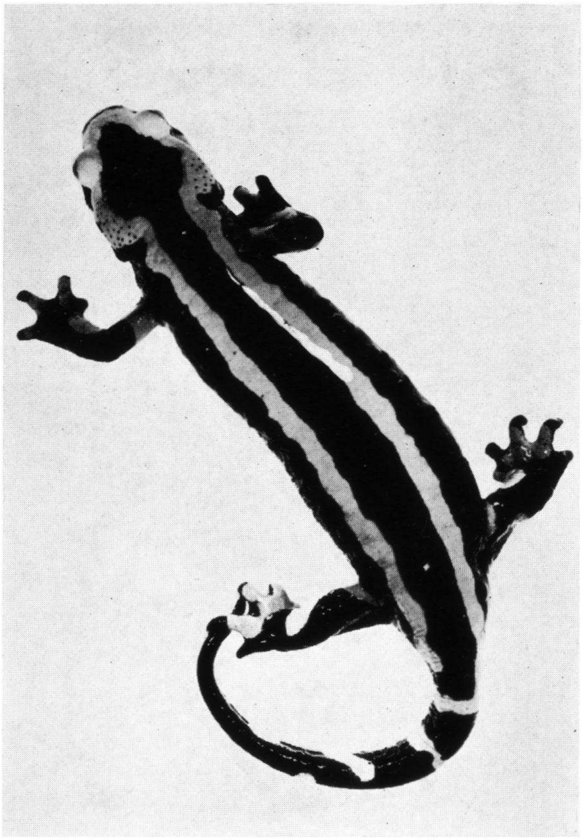

Fig. 6. *Salamandra salamandra terrestris* from Cantegrel, Dordogne, France, mother of the young ones in fig. 7.

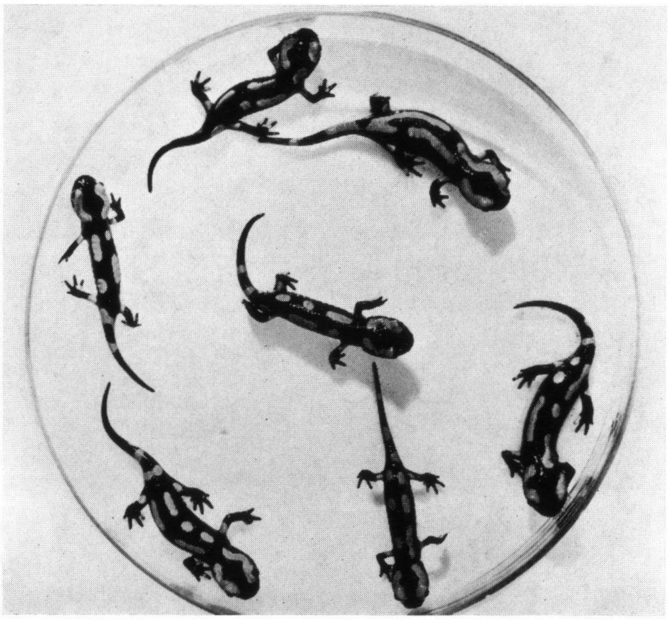

Fig. 7. Young *Salamandra salamandra terrestris,* born 5.X.1966 (mother, see fig. 6). Picture taken on 14.IX.1967.

for *probable* differences (indices differing less than three times and more than twice the sum of the mean errors: $2 < \varrho < 3$). This is done in table 2. If statistics have any sense in systematics I think they have to give indications as to the degree of kinship; the less significant the differences, the closer has to be the relationship.

Only two groups of regions do not have even probable differences (see table 2): the regions 2 and 4 and the regions 7 and 9 (for the meaning of the numbers see fig. 8). Especially the latter offers something of a problem, to which we may turn later on.

All in all the following conclusions may be drawn from the tables 1 and 2:

Region 1 is connected — with slight deviations, none of them significant — with 2.

The populations of regions 2 and 4 are closely related; apart from that the populations of 2 have most in common with those of 3.

Region 3 has most in common with 9, less with 5, still less with 2, 4 and 7.

Region 4 has most in common with 2, less with 3.

Region 5 has most in common with 3.

Region 6 is rather isolated in this survey, perhaps because no important material has been examined from France. As it is, most connection can be found with 5 (because of the colourpattern), less with 3.

Region 7 is closely connected with 9, less with 3, still less with 10.

Region 10 is most connected with 9.

Region 11 shows some relation with 9, 4 and 7.

Region 12 has most in common with 13.

Region 12a shows connection with 9 and 10.

Region 13 has most in common with 3, something with 12.

Region 14 has most in connection with 10.

Region 3 has clearly a central position, because apart from the direct connections with 9, 5, 2, 4 and 7, the only connections that can be pointed out for 13 and 8 are also with 3. In my opinion this means that the populations of 3, the Near East, have probably most in common with the ancestral salamanders before the ice-ages disturbed their continuous distribution.

The Balcans (2 and 4) remained probably in connection during the ice-ages with 3 and with each other. The Alps (1) most probably became populated from the Balcans (2).

So far I can agree with Eiselt that the salamanders of the regions 1, 2, 3 and 4 belong to the same subspecies: *Salamandra salamandra salamandra,* but as to the populations of Weser-Harz (5) and Mohnhausen (6) I have my doubts. Statistically 5 is clearly connected with 3 and not with one of the western regions. Of course it is a pity that Eiselt had not more material from France, but from the material available the only possible conclusion is that at least 5 was populated from the east. The colour pattern in itself is not enough evidence for a western origin.

Number of significant differences	0	1	2	3	4
region					
1	2	3, 4		7, 11	5, 9, 10
2	1, 3, 4, 5	9	12a	6, 7, 8, 10, 11	13
3	2, 4, 5, 7, 9	8, 13	6, 10, 12a	11, 12	14
4	2, 3, 5	9	7, 8, 11	10	12a
5	2, 3, 4	7, 9	6	10	1, 11, 12a
6			3, 5	2, 12	7
7	3, 9	5	4, 11, 12a	1, 2, 10	6, 14
8		3	4	2, 9	10,11
9	3, 7, 10	2, 4, 5, 12a	11, 14	8	1
10	9	12a, 14	3	2, 4, 5, 7, 11	1, 8
11			4, 7, 9	1, 2, 3, 10, 12, 13	5, 8, 12a
12			13	3, 6, 11	
12a		9, 10	2, 3, 7	14	4, 5, 11, 13
13		3	12	11	2, 12a
14		10	9	12a	3, 7

Table 1. *The number of significant differences ($\rho >$ 3) between the salamanders of the regions 1-14 (for the meaning of the numbers see fig. 8) as concluded from the diagrams of* EISELT. *For instance the salamanders of region 1 do not have significant differences compared with the salamanders of region 2, one significant difference when compared with the salamanders of regions 3 and 4, three when compared with regions 7 and 11, etc.*

Number of probable differences	0	1	2	3	4
region					
1				2	
2	4		3	1,5	
3		5,9	2, 4, 7		
4	2		3		5
5		3		2	4
6					
7	9		3		
8					
9	7	3	10		
10			9		
11					
12a					
13					
14					

Table 2. *Probable differences (2 $< p <$ 3) between regions which (in table 1) do not have significant differences. Concluded from the diagrams of* EISELT.

Mohnhausen (6) is still more of a problem as the only clear connection is with 5 (and less, because of the colourpattern, with 3), but significantly differing from 5 in two characters. Most probably this problem will only be solved when more is known of the French populations. According to EISELT the populations of Central Italy and Calabria belong to the same subspecies: *Salamandra salamandra giglioli.* ("Ob *S.s. giglioli* als Relikt einer sehr frühen Einwanderung (? noch gestreifter Formen) anzusprechen ist, oder ob postglazial von Balkanrefugium herkommende Tiere eine eigene Rasse gebildet haben, kann derzeit nicht entschieden werden.")

The populations of 7 and 8, Central Italy and Cala-

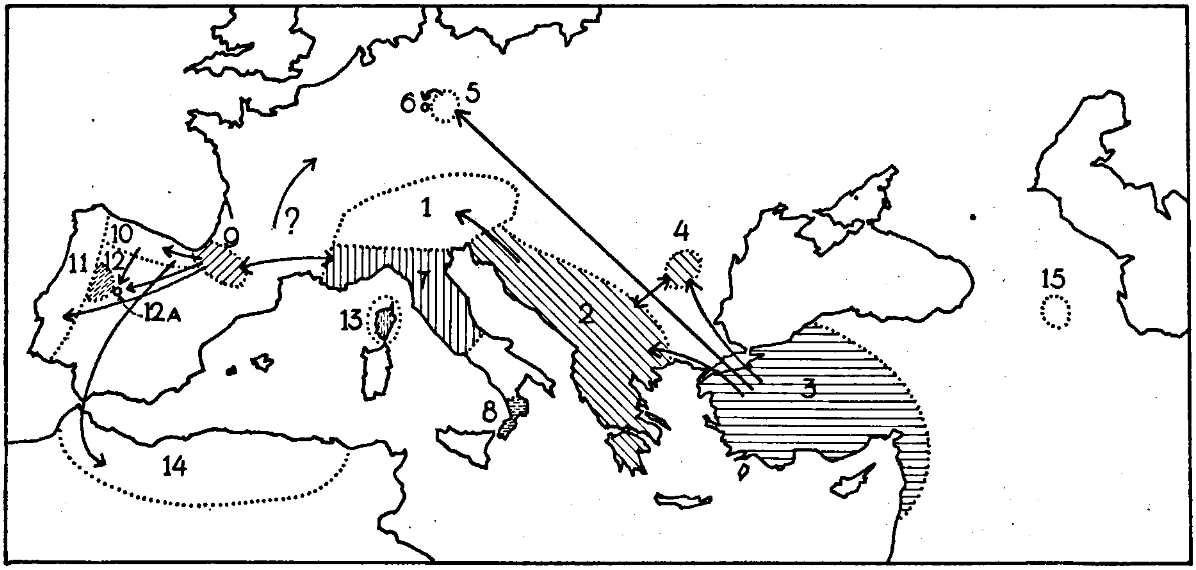

Fig. 8. Map with the regions mentioned in EISELT. 1. Alps, 2. Near East, 4. Rumania, 5. Weser-Harz, 6. Mohnhausen, 7. Central Italy, 8. Calabria, 9. Pyrenees, 10. Cantabrian Mountains, 11. Portugal, 12. Province of Salamanca, 12a. Sierra de Gredos, 13. Corsica, 14. N.W. Africa, 15. Kurdistan. Striped regions probably the remnants of the continuous distribution before the ice-ages. Hatched regions probably isolated already pre-glacially. Arrows indicate probable relations as concluded from the diagrams of EISELT.

bria, differ significantly in 6 characters. Considering that 7 shows so clearly a relation with 9 and slightly less with 3, whereas 8 independently shows some relation with 3, I think that the populations of 7 and 8 have to be regarded as originated from at least two different relict groups (the relict character indicated by the connection with 3). Although Eiselt mentions gradual shifts between 7 and 8 I think that even now we have sufficient reason to regard the extremes as separate subspecies. The one of Calabria has to be called *Salamandra salamandra giglioli*. It is improbable that the populations of 7 have come from the Balcans, because the populations of 7 and 2 are significantly different in 3 characters, whereas no significant or even probable differences exist between 7 and 9 (Western Pyrenees). According to this the populations of Central Italy and the Western Pyrenees have to be considered closely related. If they are separated by clearly different populations we might conclude that both are almost stagnant relicts from before the ice-ages. This relict-character follows also from the close relation between 3 and 9 and the slightly less close relation between 3 and 7. I think the most consistent course to follow is to decide that until a clear separation between Central Italy and the Western Pyrenees is proved, the populations of Central Italy (7) may be regarded as belonging to *Salamandra salamandra fastuosa*, together with the populations of the Western Pyrenees (9) and the Cantabrian Mountains (10).

As to the Spanish salamanders Eiselt proposed the following hypothesis: "Der nach dem endgültigen Einbruch der Strasse von Gibraltar im Süden der Pyrenäenhalbinsel zurückgebliebene Teil der nach Afrika gezogenen Gruppe bildete dort zu seiner Fleckung noch die Merkmale von *S.s. bejarae* aus und kam dann mit den gestreiften Tertiärrelikten in ihrem weit westlich gelegenen Refugium in Kontakt. Dabei entstand nahezu explosiv die Mannigfaltigkeit von *S.s. gallaica* und die zarteren gestreiften Altformen wurden nach Norden abgedrängt. Postglazial erweiterten dann letztere, als *S.s. terrestris* die Pyrenäen im Westen umgehend, ihr Verbreitungsgebiet über ganz Frankreich bis nach Mitteldeutschland. Sie erreichten den Aermelkanal erst nach dessen Einbruch (hätten sie die Eiszeit in Süddeutschland oder Nordfrankreich überdauert, wären sie wohl sicher bis nach England hineingelangt, denn besonders im aquatilen Larvenstadium hätte diese Wanderung nach Norden stromab sehr rasch vonstatten gehen müssen), versperrten *S.s. bejarae* den östlichen Umgehungsweg um die Pyrenäen und liessen in Kantabrien die ebenfalls gestreifte *S.s. fastuosa* zurück, die schliesslich die Besiedelung der Pyrenäen durchführte."

So Eiselt suggests the existence of two relict populations (or groups of populations) in Spain. Relict A, "bereits gefleckt gezeichnet" ("already" spotted), from which *S.s. algira* developed first and later on *S.s. bejarae*. After contact with relict B "zartere gestreifte Altformen" (more tender, striped ancestral forms) *S.s. gallaica* would develop. Remnants of relict B were then driven to the north, post-glacially developing into the subspecies *terrestris*. The subspecies *fastuosa* developed out of *terrestris*.

According to this hypothesis *S.s. algira* and *S.s. bejarae* would show a close relationship. Moreover *S.s. algira* would be irregularly spotted. In fact *S.s. algira* has most in common with *S.s. fastuosa* from region 10 (Cantabrian Mountains) and *S.s. algira* and *S.s. bejarae* are significantly different in 6 characters, moreover some specimens of *S.s. algira* show a tendency towards the arrangement of spots in parallel rows. Also *S.s. gallaica* would have to show connections with *S.s. bejarae*. Eiselt regarded them so closely related that in part of his diagrams he took the salamanders of Portugal and the Province of Salamanca together. However, as table 1 shows they are significantly different in three characters and also their affinities with other groups are different. As to the relict B, it is difficult to imagine a tender form, driven away by *S.s. gallaica*, then developing into the fairly successful *S.s. terrestris*, which in its turn would be vital enough to prevent *S.s. bejarae* from entering France eastward from the Pyrenees. Neither is it clear why relict B after having entered France westward from the Pyrenees would have completely disappeared in the Western Pyrenees, so that a branch from *S.s. terrestris* could develop there into *S.s. fastuosa*.

As we have seen already the *S.s. fastuosa* of the Western Pyrenees is closely related to the salamander of the Near East. I think the only possible explanation is that *S.s. fastuosa*, especially the populations of the Western Pyrenees, have to be regarded as preglacial relicts. In a map (EISELT, p. 125) of the vegetation zones is shown that during the last glacial period there is a continuous zone of mixt maritime forest from the south of France till southern Spain. This eastern refuge forest might well be populated with *fastuosa*-like salamanders. Probably before the end of the ice-age some salamanders of *fastuosa*-like form could reach North Africa. Post-glacially they might have populated Italy to the east, France to the north (*terrestris*), the Pyrenees to the northwest. As the populations of the Cantabrian Mountains –

though closely related to those of 9 — show also some deviations, this region was probably populated later on.

Compared with the neighbouring subspecies, S.*s. gallaica* has most in common (2 significant differences) with S.*s. fastuosa* from the Western Pyrenees (9); there is also some connection (3 significant differences) with S.*s. bejarae* from Salamanca. As S.*s. bejarae* probably is the more original form (to which points the relation with the isolated subspecies of Corsica), we may conclude that S.*s. gallaica* arose indeed out hybridization of *fastuosa*- and *bejarae*-like ancestors. The hybrid character may also be deduced from the large size, in fact the largest of all Spanish subspecies (according to Eiselt the greatest *fastuosa* — from Cantabria — is 180 mm, the greatest *bejarae* is also 180 mm, the greatest *almanzoris* is 170 mm and the greatest *gallaica* is 220 mm).

On the map mentioned above (EISELT, p. 125) Spain has also a large mixt maritime forest in the west. This might be the refugium for S.*s. bejarae*, the hybrid S.*s. gallaica* might have originated in the south of Spain where the eastern and western forests touched each other. Although the problem is not quite solved it is imaginable that S.*s. bejarae* was driven away from Portugal by the more vital hybrid S.*s. gallaica* and that S.*s. bejarae* found new territory in the rest of Spain when the climate changed after the ice-ages.

As the only clear connection (with two significant differences) of 12 is with 13 (Corsica) and as Corsica in its turn has most in common with the Near East (3), I conclude that 12 as well as 13 represent ancient relict groups, probably already isolated from the main group (just as Calabria) before the great disruption originated by the ice-ages.

The deviating population of the Sierra de Gredos (12a) probably derived from *fastuosa*-stock after the ice-ages.

Summing up I think the following points may be concluded from Eiselt's statistics:

1. The salamanders of the western Pyrenees, of Central Italy, the Balcans and the Near East are closely related. They probably constitute the more or less separated remnants of the species as it existed in continuous distribution before the ice-ages.

2. S.*s. bejarae*, S.*s. corsika*, S.*s. giglioli* (in the strict sense: only from Calabria) were probably already isolated before the ice-ages. Perhaps the same may be thought of S.*s. semenovi.*

3. Apart from S.*s. semenovi* Nesteroff (15) and S.*s. infraimmaculata* Martens (16), of which no statistical material exists (the former probably more valid than the latter) and S.*s. terrestris* Lacépède, (France and western Germany, the regions 5 and 6 — especially the former — only doubtful under this heading) of which only a confusing picture may be given, the following subspecies may be considered valid according to statistical evidence and/or geographical isolation (the numbers indicate the regions in which they live, see also the map, fig. 8):

S.*s. salamandra* (Linnaeus): 1, 2, 3, 4, perhaps 5, region 1 populated from 2 after the ice-ages.

S.*s. giglioli* Eiselt & Lanza: 8, pre-glacially isolated relict.

S.*s. fastuosa* Schreiber: 9, 10 and probably 7. The populations of 9 the most ancestral.

S.*s. gallaica* Seoane: 11, derived from *fastuosa*-stock, perhaps by hybridization with *bejarae.*

S.*s. bejarae* Wolterstorff: 12, perhaps the rest of Spain, apart from 9, 10, 12a and 11, pre-glacially isolated relict.

S.*s. almanzoris* Müller & Hellmich: 12a, derived from *fastuosa*-stock.

S.*s. algira* Bedriaga: derived from *fastuosa*-stock.

S.*s. corsika* Savi: 13, pre-glacially isolated relict.

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