



Proposal for a new taxonomic arrangement of *Ichthyosaura alpestris* (Laurenti, 1768) (Urodela, Salamandridae), an iconic species with a complex phylogenetic structure

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The Alpine Newt *Ichthyosaura alpestris*, for long considered as the unique species of its genus, harbours a very complex molecular structure and is composed through its vast area of distribution in Europe of four highly divergent and old lineages which warrant each the level of species. The taxonomic situation of the genus was for years largely darkened by a lack of clear morphological divergences between the different molecular lineages, a situation unique among European newts. On the other hand, some isolated populations described on a morphological basis only are phylogenetically nearly identical, which does not mean that they do not represent unique biological entities. We have elevated the four lineages to the species level by using existing nomina, considering that further taxonomic splitting should be done to as possible reflect the very complex molecular structure of the genus. We tentatively present short diagnosis of the taxa and their distribution. Many isolated populations, some of them paedogenetic, became extinct or on the verge of extinction, largely due to fish introductions in glacial lakes in the three southern European refuges. Alain Dubois was one of the first scientists to observe this dramatic situation in Prokosko Jezero in Bosnia, where lived a highly divergent population, now considered as extinct in the wild.

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INTRODUCTION

Alpine Newt is an iconic polytypic European aquatic newt described in 1768 by Laurenti, composed of several subspecies, one of them being discovered in Southern Italy by Dubois & Breuil (1983), and for most of them described on a morphological basis before molecular taxonomic revolution. Alain Dubois and Annemarie Ohler visited recently the lake where has been described *Proteus tritonius* by Laurenti at the type locality located in Etschero Monte (Ötscher), west of Mariazell, in Austria, to collect topotypes for sequencing (Ohler *et al.* 2018). The species has been described in the genus *Triton* Laurenti, 1768 (junior homonym of *Triton* Linnaeus, 1758), then transferred to *Triturus* Rafinesque, 1815, later to *Mesotriton* Bolkay, 1927, then *Ichthyosaura* Sonnini & Latreille, 1801. During all the 20th century, *Ichthyosaura alpestris* has been taxonomically divided in subspecies, the nominative one covering all Western and Central Europe, north of multiple subspecies described from the three Mediterranean post glacial refuges of Southern Europe (Iberic, Italian and Balkanic peninsulas). Recent molecular works (Sotiropoulos *et al.* 2001, 2007; Recuero *et al.* 2014) showed that the species is harbouring a complex phylogenetic structure, composed of three major clades harbouring at least four divergent lineages. One clade is distributed in the Western part (B-C) of the range, another in the Eastern part (D-E), and a 3rd relict one (A) in Serbia (Vlasina Lake), with some slight discrepancies in the results if taking in account mtDNA or nDNA genes, as it is often the rule in many cases in present molecular biology.

In 2009, Dubois & Raffaëlli have tried to translate these informations in a new taxonomy with 2 exerges (aggregate of subspecies) without formally naming species, because of a lack of species-series nomina for some taxa that should be recognized as subspecies and the lack of clear morphological diagnosis between the 2 major clades previously included in *I. a. alpestris*, especially in the Eastern Balkans. The clade A could be erected as a taxon only after its formal description. Here, we have tried to translate the different clades and our 2 exerges into species and subspecies through nomina available, that before necessary works that could conduct to further splitting. Many populations are on the verge of extinction or already extinct. Alain Dubois, for long captivated by these beautiful newts, told me as sad he was to observe the disappearance of one very divergent population in a lake in Bosnia (*I. a. reiseri* str. s.).

DISCUSSION

Molecular divergence in this genus, even if old (Miocene), has not been associated with distinctive morphological characters, a unique situation among European newts (Sotiropoulos *et al.* 2001). Instead, subclades C2 (Eastern Italy), C3 (Western and Central Europe), E2a (Northern Balkans), E2b (Romanian Carpathians) are nearly undiagnosable on a morphological basis, despite huge geographical distances between them, and all are considered nowadays as parts of the nominative form (Sotiropoulos *et al.* 2007). I have tried to find good diagnosable characters separating *Triturus alpestris carpathicus* Dely, 1959 (clade E2 of Sotiropoulos *et al.*), described from Sinaia (Romania), from populations of *T. a. alpestris* from western Europe, and could not find any solid ones, except slight details including the form of the

vomeropalatine teeth, some red pigment in females and relatively large head, but these characters largely enter in the intraspecific and intrapopulational variation (Raffaëlli 2013). Two subspecies described by Dely in 1959 from Hungary (*Triturus a. satoriensis*, *T. a. bukkiensis*) are not diagnosable from other central european populations and have been later synonymized with the nominative form. I further more could not find any good morphological characters separating some Balkanic newts (E2) and *alpestris* from France (C3) maintained in captivity. On the other hand, very isolated populations like the one from Prokosko Jezero (Bosnia, *T. a. reiseri*) or the one from Crno Jezero in Slovenia (*T. a. lacusnigri*) are highly divergent by morphometry or coloration, the latter, entering in the C2 subclade, having been synonymized with the nominative subspecies (Luznik *et al.* 2011).

Adequation between molecular and morphological divergences is more obvious in the Western populations (clades B-C), with morphometric characters existing in clades C1 from Spain (*cyreni*) and B from Italy (*apuana*, *inexpectata*). Results of combined mtDNA and nDNA dataset in the work of Recuero *et al.* (2014) went further than the one from Sotiropoulos *et al.* It clearly recovers 4 lineages with high statistical support, corresponding more or less to the four lineages recognized by Sotiropoulos *et al.*, if not taking in account their clade A from Serbia: 1) subspecies *I. a. veluchiensis* (clade D of Sotiropoulos *et al.*), 2) subspecies *I. a. apuana* + *I. a. inexpectata* (clade B), 3) subspecies *I. a. cyreni* + part of *I. a. alpestris* (western and central populations, including Northern Romania) (clade C), 4) the remaining populations, including part of subspecies *I. a. alpestris*, *I. a. montenegrina*, *I. a. reiseri* (clade E). In the works of Recuero *et al.*, clade A from Vlasina rather enters in the Balkanic clade (E).

Under the evolutionary species concept, a present trend is to elevate to the species level monophyletic subspecies or alternatively to synonymize them when they appear to be non monophyletic (Folt *et al.* 2016). Given the monophyly, old origin, parapatric distribution of most of the taxa previously included in *Ichthyosaura alpestris*, the high and complex genetic structure of the entire genus, and following the principle that each clade or lineage should ideally bear a taxonomic recognized status at a subspecies or species level, we propose to formally recognize four species inside *I. alpestris sensu lato*, by elevating Eastern clade (*I. reiseri*) to the species level with several subspecies, by maintaining *I. alpestris* for the Western clade, where is the type locality of Laurenti in Austria, by elevating a third one in Italy (*I. apuana*) and a fourth one from Southern Balkans (*I. veluchiensis*). This latter clade (D) is composed of several divergent populations which warrant at least subspecies level. These four subclades are distributed as follows: D1 (Mt Jablanica, Macedonia, Sara Mt, Serbia plus Albany), D2 (North of Pindus, Drakolimni, Tymphi Mts and Smolikas), D3 (Peloponnese), D4 (central Greece). Type locality of *I. veluchiensis* is Mount Veluchi (Tymphreste), which enters in the D4 clade. Radiation in *I. veluchiensis s. lato* recalls the one detected in *Lissotriton vulgaris* (Linnaeus, 1758) supraspecies in Southern Balkans, with the taxon *L. graecus* now recognized as a valid species composed of four lineages (Pabijan *et al.* 2014, 2017). The split of *I. veluchiensis* from other Balkanic populations (*I. reiseri*) is at least as old as the one between *Triturus marmoratus* and *T. pygmaeus* or between *T. carnifex* and *T. macedonicus* (Recuero *et al.* 2014). Further more, a very large genetic distance (Nei $D = 0.31$) has been detected between Peloponnese (D3) and central Greece (D4) populations (Sotiropoulos *et al.* 2008; Pysanets 2012: 151).

Further more, with subspecies alone recognized in the genus *Ichthyosaura*, no conservation status from IUCN is available for the different lineages when some of them are highly endangered if not extinct. Taxonomy can help to protect some populations of these beautiful newts, at least for a while, recalling that the following taxa, *I. a. reiseri*, *I. a. montenegrina*, *I. a. serdara*, *I. a. piperiana*, *I. a. lacusnigri*, some of them considered junior synonyms, are extinct today. *Ichthyosaura alpestris reiseri*, described by Werner in 1902 from a glacial lake at Prokosko Jezero, in the Vranica Mountains (Bosnia) on a morphological basis, has been observed by thousands by Alain Dubois who visited the lake in August 1978 (Dubois 1998). This population is now considered as extinct in the wild (EW) due to trout introductions. Some specimens of this taxon could be saved before fish introduction and raised by German keepers, then by the French Urodela Group (FUG). A conservation program has been launched in 2016 by the Zoo of Paris and the FUG who keep several dozens of specimens alive in terraria, with the collaboration of Bosnian scientists who check the situation of the population in the lake.

Isolated populations of *I. alpestris sensu lato* should not be ignored by the scientific community, as a phylogeny never gives us all the biological informations. Several of these populations, now extinct, could help us in better understanding the phylogenetic structure of this very attractive and endangered genus if taking in account its underestimated biodiversity. Dely (1959) described populations of *T. alpestris* from Bukk and Sator Mts in Hungary with slight morphological divergences, no more recognized, but which might represent isolated units which could be resurrected under an ideal future when all diagnosable populations could bear taxonomic status in a world where biodiversity should be understood as part of a worldwide paleohistoric jewel disappearing at an incredibly fast level.

Inside **URODELA**, as a counter-example, one can make here a parallel with *Calotriton asper* (Dugès, 1852), the Pyrenean Newt, very divergent morphologically, but harboring a low phylogenetical structure driving to a lack of recognized taxa. Many isolated populations in this widely distributed species surely warrant a taxonomic status. Names and descriptions exist for some populations and surely need to be resurrected while other wait to be named. Another good example of major discrepancy between phylogenetical and morphological understandings of what can be biological units are the Mexican neotenic *Ambystoma* Tschudi, 1838, which warrant taxonomic status if taking in account their very recent morphological adaptation to extreme aquatic habitat (as is the case for *I. a. reiseri* from Prokosko Jezero or *T. a. lacusnigri* from Crno Jezero), but with low molecular phylogenetics, showing extreme adaptive divergence. In this last case, as scientists as actors of protection agreed to give them an IUCN status, even if they are not phylogenetical entities *per se*.

TAXONOMIC IMPLICATIONS AND DIAGNOSIS

If taking in account the large diversity of *Ichthyosaura alpestris* s. l. and following the molecular works of Sotiropoulos *et al.* (2007), Luznik *et al.* (2011) and Recuero *et al.* (2014), we propose the following taxonomical arrangement to as better as possible reflect the complex structure of the genus, with recognition of four species.

Ichthyosaura alpestris (Laurenti, 1768)*Ichthyosaura alpestris alpestris* (Laurenti, 1768) (fig. 1)

This nomen applies to the western and central clades, including northern Romanian populations (Clades C2 and C3 of Sotiropoulos *et al.* 2007).

Protonym

Triton alpestris Laurenti, 1768.

Onymotope

Etschero Monte, Alps, Austria.

Vernacular names

English: Alpine Newt; French: Triton alpestre.

Description

♂ 8 cm, ♀ 12 cm. Male smaller than female. Head a little longer than broad, with a rounded snout. Stout body, trunk subquadrangular in male, more rounded in female. Vertebral groove in female. Tail length equal to or a little shorter than rest of body, pointed at extremity. Skin smooth in the aquatic phase, granular in the terrestrial phase. Male has a low middorsal crest which continues on the upper caudal keel, with light and dark vertical bars or a zigzag band. Dorsal parts greyish to blackish, bluish during aquatic phase with some marbled spots more pronounced and darker in female. White yellowish longitudinal band on the flanks in male beginning behind the eye, spotted in black and bordered under it by another band sky blue. Flanks are spotted with black in female without blue band. Ventral parts bright orange to red. Sometimes a few dark spots on the throat. Lower part of the tail orange with rounded dark spots.

Distribution

Western and central Europe. France from northern Finistère in the west to the east of the country, to Lyon and Massif central to the south, Benelux except in the Netherlands (rare), Germany to Denmark (threatened), Alps, and from northeastern Italy (Group C2) to Romania through Austria, northern Hungary, Czech Republic, southern Poland to extreme western Ukraine. Lacks in Danube valley. Rare in Hungary (several sites created), introduced in southern England and in southern France (Hérault, one site). One site in southwestern Finland (Turku), probably resulting of an introduction (Lemerrier, pers. com.). *Triturus alpestris lacusnigri* (Seliskar & Pehani, 1935) from Slovenia, considered as a junior synonym of *I. a. alpestris* (Luznik *et al.* 2011) might apply to the C2 clade but this population is considered now as extinct and further molecular works seem impossible.



Figure 1. *Ichthyosaura alpestris alpestris*. (a) Male. (b) Female. Czech Republik © Joachim Nerz.

Ichthyosaura alpestris cyreni (Wolterstorff, 1932) (fig. 2)

This nomen applies to the Iberian clade (C1).

Protonym

Triton alpestris subsp. *cyréni* Wolterstorff, 1932.

Idiognosis

Similar to *I. a. alpestris*, but broad and rounded head, trunk laterally compressed in males and stout, especially in females. Black spots on flanks poorly pronounced.

Onymotope

Lake Ercina, 1000 m, near Covadonga, Cantabrian Mts, northwestern Spain.

Vernacular name

English: Cantabrian Alpine Newt; French: Triton alpestre des Monts Cantabriques.

Distribution

Northwestern Spain along the Cantabrian Mts to western Pyrenees to the east. One population isolated in the Sierra de Guadarrama (Segovia, central Spain), probably resulting of an old introduction.



Figure 2. *Ichthyosaura alpestris cyreni*. (a) Male. (b) Female. Asturias, Spain © Lionel Serra.

Ichthyosaura apuana (Bonaparte, 1839)*Ichthyosaura apuana apuana* (Bonaparte, 1839) (**new combination**) (fig. 3)

This nomen applies to the Northern Italian clade (B).

Protonym

Triton apuanus Bonaparte, 1839.

Onymotope

Serravezza, Apuane Alps, northwestern Italy.

Vernacular name

English: Apennine Alpine Newt; French: Triton alpestre des Apennins.

Idiognosis

Similar to *I. a. alpestris*, but ♀ 10 cm. Belly bright red, throat heavily spotted of black. Dorsal parts in male blue azur, dorsal parts in female heavily marbled on a greenish ground. Black spots on the flanks generally very pronounced. Sometimes black spots on the ventral parts. Paedogenesis frequent.

Distribution

Northwestern and central Tuscany, Liguria to extrem southeastern France to the west, in Alpes-Maritimes and Alpes de Haute-Provence, where lives a paedogenetic population sharing characters from *I. alpestris* (Lauzet lake) (Raffaelli 1982).



Figure 3. *Ichthyosaura apuana apuana*. (a) Male. (b) Female. Po Plain, Italy © Lionel Serra.

Ichthyosaura apuana inexpectata (Dubois & Breuil, 1983) (**new combination**) (fig. 4)

This nomen applies to the Southern Italian clade (B).

Protonym

Triturus alpestris inexpectatus Dubois & Breuil, 1983.

Onymotope

Lago dei Due Uomini, 1077 m, Calabria (Southern Italy).

Vernacular name

English: Calabrian Alpine Newt; French: Triton alpestre de Calabre.

Idiagnosis

Similar to *I. a. apuana*, but dorsal coloration darker, less black spots on the throat. Series of small black spots on lower flanks. Neoteny frequent.

Distribution

Three lakes in Catena Costiera, Calabria, southern Italy (Lago dei Due Uomini, Lago Trifoglietti and Lago Laghicello, between 1077 and 1130 m). Highly endangered.



Figure 4. *Ichthyosaura apuana inexpectata*. (a) Male. (b) Paedogenetic female. (c) Female. Lago dei Due Uomini, Calabria, Italy © Lionel Serra.

Ichthyosaura reiseri (Werner, 1902)*Ichthyosaura reiseri reiseri* (Werner, 1902) (**new combination**) (fig. 5)

This nomen applies to the Prokosko Jezero population (E2).

Protonym

Molge alpestris var. *reiseri* Werner, 1902.

Onymotope and distribution

Prokosko Jezero near Fojnica, around 1650 m, Vranica Mts, Bosnia.

Vernacular name

English: Prokosko Lake Alpine Newt; French: Triton alpestre du lac Prokosko.

Idiognosis

Similar to *I. a. alpestris*, but head very wide, habitus robust, short trunk. Females heavily mottled on dorsal parts with black spots on the flanks rare or absent. Male dark blue, nearly black on the upper parts. Neoteny frequent. Highly endangered, if not extinct.



Figure 5. *Ichthyosaura reiseri reiseri*. (a) Male. (b) Female. In captivity. © Fred Braux. (c) Stamp illustrating *Ichthyosaura reiseri reiseri* from Prokosko Lake, extinct today in the wild.

Ichthyosaura reiseri carpathica (Dely, 1959) (**new combination**) (fig. 6)

This nomen applies to Northern, central Balkans and Romanian Carpathians (clades A, E2).

Protonym

Triturus alpestris carpathicus Dely, 1959.

Onymotope

Sinaia, Romania.

Vernacular name

English: Balkanic Alpine Newt; French: Triton alpestre des Balkans.

Idiognosis

Very variable, similar to *I. a. alpestris*, without clear morphologically divergent characters. Populations from Romanian Carpathians show often wide heads and sometimes slight red pigment.

Distribution

Romanian Carpathians, Northern and central Balkans, from Slovenia and northern Croatia to Serbia, including Vlasina Lake (clade A), and to Rodope Mts in Bulgaria and eastern Greece to the south-east.

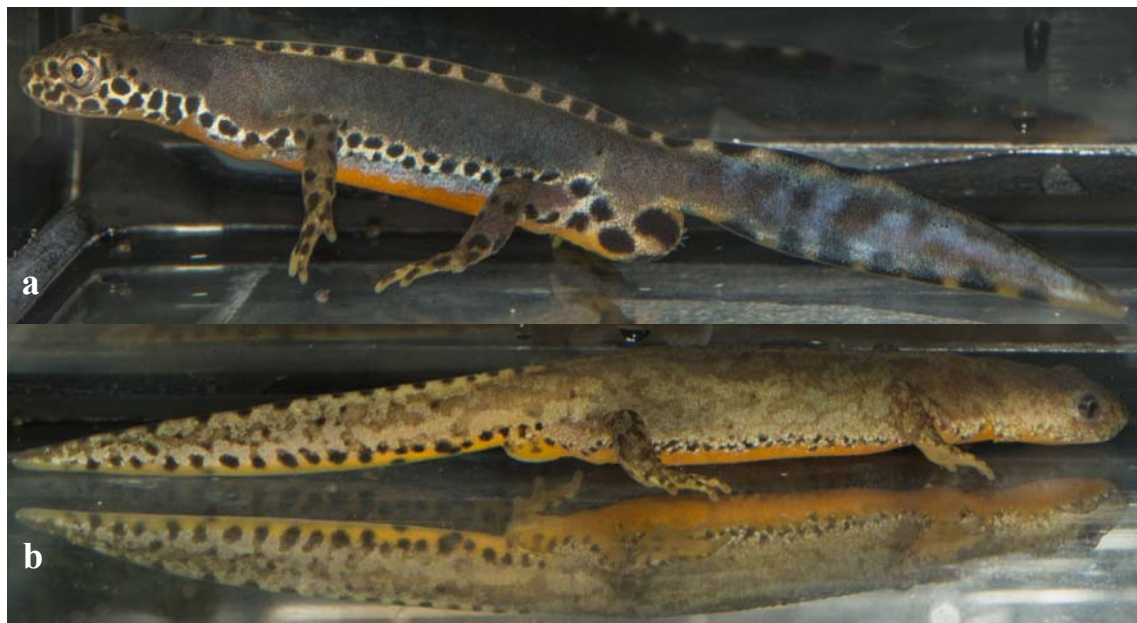


Figure 6. *Ichthyosaura reiseri carpathica*. (a) Male. (b) Female. Brasov, Romania. © Lionel Serra.

Ichthyosaura reiseri montenegrina (Radovanovic, 1951) (**new combination**) (fig. 7)

This nomen applies to paedogenetic populations from Montenegro (clade E1), including *Triturus alpestris piperianus* Radovanovic, 1961 and *Triturus alpestris serdarus* Radovanovic, 1961, considered as junior synonyms (Breuil & Guillaume 1985). The taxon *serdarus*, now considered as extinct, was nevertheless the most derived of the three isolated populations (Sotiropoulos *et al.* 2001, 2007).

Protonym

Triturus alpestris montenegrinus Radovanovic, 1951.

Onymotope

Bukumirsko Jezero, 1448 m, Montenegro. Highly endangered, if not extinct.

Vernacular name

English: Montenegrin Alpine Newt; French: Triton alpestre du Montenegro.

Idiognosis

Similar to some paedogenetic populations of *I. a. alpestris*, but trunk elongated, head wide. Neotenic.

Distribution

Kapetanovo Lake (1678 m), Brnicko Lake [Manito] (1773 m), Bukumirsko Lake, Zminicko Lake (1788 m), Montenegro. Non paedogenetic populations of uncertain status are present near the lakes in the Durmitor Park.



Figure 7. *Ichthyosaura reiseri montenegrina*. (a) Male. (b) Female. Durmitor Park, Montenegro, out of glacial lakes © Lionel Serra.

Ichthyosaura veluchiensis (Wolterstorff, 1935)

Ichthyosaura veluchiensis (Wolterstorff, 1935) (**new combination**) (fig. 8–9)

This nomen applies to four lineages, from which three unnamed (D1, D2, D3), with D4 harbouring the type locality of the species.

Protonym

Triturus alpestris veluchiensis Wolterstorff, 1935, substitute name for *Triturus alpestris graeca* Wolterstorff, 1935.

Onymotope

Veluchi Mt, 1870 m, Greece.

Vernacular name

English: Greek Alpine Newt; French: Triton alpestre hellénique.

Idiagnosis

Similar to *I. a. alpestris* but ♀ 12.5 cm, sometimes more, the largest taxon of the genus (Smolikas, Albanian populations). Some populations from central Greece are small. Short limbs. Dorsum pale blue in male, never dark blue, no blue and black mottling as in *I. a. alpestris* or *I. r. carpathica*. Upper lateral band yellow to white, lower band blue to silver blue. Bands sometimes spotted with black or brown pigment, often extending to ventral and gular areas. Dorsal parts of females often olive, often black spots on ventral parts of females. The head of adults is wider at high altitude. Smolikas population (D2) is one of the most differentiated morphologically (Breuil & Parent 1987, 1988; Sotiropoulos *et al.* 2008). D2 is often paedogenetic.

Distribution

Central Greece between 1280 and 2200 m, to Peloponnese to the south and southeastern Albany and Macedonia to the north. Four subclades detected. Endangered.



Figure 8. *Ichthyosaura veluchiensis*. Male. Mt Timfi (Pindus), Greece (D2 clade). © Radek Sejkora.



Figure 9. *Ichthyosaura veluchiensis*. Peloponnese (D3 clade). (a) Male. (b) Female. © Lionel Serra.

CONCLUSION

As an alternative, a more conservative taxonomy would leave only two species for the two major clades, *I. alpestris* with *apuana*, *inexpectata* and *cyreni* as subspecies, and *I. reiseri* containing the rest of the subspecies including *veluchiensis* and the relict clade A from Serbia. But with that option, the deep divergence of Italian (*apuana*, *inexpectata*) and Southern Balkan (*veluchiensis*) clades would not appear clearly, and the different lineages of *veluchiensis* would be ignored in the future, without status.

RÉSUMÉ

Le Triton alpestre *Ichthyosaura alpestris*, longtemps considéré comme l'unique espèce du genre, abrite une structure moléculaire très complexe et est composé à travers sa vaste aire de répartition de quatre lignées très divergentes et anciennes qui méritent chacune le niveau d'espèce. La situation taxonomique du genre a été pendant des années obscurcie par l'absence de divergence morphologique claire entre ces différentes lignées moléculaires, une situation unique au sein des Tritons européens. Par ailleurs, certaines populations isolées décrites sur une seule base morphologique sont phylogénétiquement presque identiques, ce qui ne veut pas dire qu'elles ne représentent pas des entités biologiques évolutives uniques. Nous avons relevé les quatre lignées au niveau de l'espèce, en utilisant des nomina existants, et en considérant que des divisions taxonomiques ultérieures devront encore être effectuées pour refléter au mieux la structure moléculaire complexe du genre. Nous présentons, quand cela a été possible,

une diagnose courte des différents taxons et leur distribution géographique. De nombreuses populations isolées, certaines d'entre elles pédogénétiques, sont désormais éteintes ou au bord de l'extinction, à cause notamment de l'introduction de poissons dans des lacs glaciaires des trois refuges du sud de l'Europe. Alain Dubois a été l'un des premiers scientifiques à observer et s'alarmer de cette situation dramatique au Prokosko Jezero en Bosnie, où habitait une population très divergente, considérée comme éteinte dans la nature.

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