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THE PROBLEM OF THE REFUGIA OF CERTAIN PREGLACIAL AND GLACIAL RELICT POPULATIONS FROM THE CALCIPHILOUS FLORA OF THE APUSENI MOUNTAINS (ROMANIA)

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Abstract: The aim of the present paper is the unitary interpretation of the hypotheses and of certain concrete results, which speak for the existence of refugia that preserve preglacial and glacial relict populations from the Apuseni Mountains, with special regard to the calcareous massifs as potential refugial areas.

Introduction

The exact localization of the refugial areas and the assessment of the impact they had on the present-day distribution and diversity of the species have a phytohistorical importance and at the same time implications in the nature conservation activities. Unfortunately, our current knowledge of their existence in the Carpathians is based almost exclusively on hypotheses.

This paper is intended as a synthesis of the valuable hypotheses contributed by the traditional phytogeography, which must constitute the basis of future, modern, and more complex studies, that will address the multitudinous questions raised with regard to the phytohistory of the Apuseni Mountains and of the Carpathians in general.

The term 'refugia' used in this paper refers to two meanings, namely: *glacial refugia* (territories on which vestiges of the warm-temperate climate flora of the end of the Tertiary, respectively of the interglacials, survived during the glaciation) and *interglacial refugia* (of the orophyte tundra and alpine pasture elements which, during the interglacials, contracted their range towards the north, leaving behind the mountain populations, some of which have a relict character).

The southern thermophilous elements of the Tertiary and of the interglacials are generally called *preglacial thermophilous relicts*, since a finer approximation is practically impossible. The elements of the interglacial refugia are known under the denomination of *glacial relicts*.

Discussions

In the attempts of localizing the glacial refugia, the picture offered by the macro- and microfossils tends to exaggerate the role of the anemophilous and wetland species. Thus, it is known that peat and coal originate from peatland and waterside plants. The Miocene and Pliocene vegetal macrofossils originate from the waterside vegetation of those times or from waterlogged forests, while the mountain vegetation left fossil traces only accidentally, due to the lack of conditions for fossilization [12].

Of special interest in this respect is the identification of the orophyte *Pyrola* cf. *secunda* by R. Givulescu in the diatomitic shales of Chiuzbaia, near Baia Mare [39].

As for that, numerous phytogeographic considerations [10,14,59] and cytotaxonomic [35,45], but also molecular [42] studies speak in favour of the preglacial origin of the mountain flora. According to these studies, the temperate flora existed and kept developing and diversifying as early as the Tertiary subtropical flora, but concentrated in the mountains, without leaving too many fossil traces [59]. Thus we have to consider a larger number of (especially orophyte) relicts than those accepted in the traditional phytohistory.

The pollen spectra, conclusive in evidencing the Tardiglacial and Holocene forest successions, bring little information regarding the topography of the glacial refugia. Thus, firstly, they are evidences of the woody landscape, and less of the herbaceous vegetation, particularly if we refer to the intrazonal communities.

Likewise, due to the insular aspect of the refugia, their vegetation has great chances of being underrepresented or missing from the pollen spectra.

Added to this is the fact that from among the plants of the Tertiary and of the interglacials, the entomophilous ones had a low pollen production, and as a consequence, the pollen remains are rare and rather selective [43].

More important is, however, the fact that the fossil evidences are less informative regarding the morphological or taxonomical particularities of the species, and they do not always allow the possibility of correctly establishing the evolutive directions, or the distribution area of the infrataxa. The data of the molecular phylogeography are much more conclusive in this respect.

Thus, besides supplementary evidences in favour of the existence of certain previously recognized glacial refugia and postglacial colonization routes, the studies on the variability of the chloroplastidial DNA succeeded in topographically identifying new refugia on the basis of the increased genetic diversity of their populations, as compared to the probable descending populations [23].

The decrease in genetic diversity of the populations, directly proportional to the distance from the refugia, is a consequence of the severe genetic bottlenecks suffered by them during the repeated interglacial or interstadial expansions towards north. Moreover, in the new territories the genetic diversity acquired during an interglacial is considered to be lost during the following glacial period, while in the glacial refugia it has accumulated in the course of several climatic oscillations. Consequently, it is possible that the populations of the refugial areas have preserved all the genetic variability a species has witnessed during the course of time, extinct or not in other populations, whence the importance of localizing the refugia for the conservation activities [23].

While this type of data suggests that the number of the refugia has been underestimated on the basis of the fossil evidences, we must emphasize that at molecular level there are also fundamental problems, such as those concerning the interpretation of the results. Thus, the increased variability of certain populations may indicate refugial areas, but at the same time also contact zones between the different recolonization routes [40], while a particular genetic constellation may be the result of hybridization with very close species, as it has been suspected in the case of the Crimean beech populations [23].

Topographically speaking, the refugia are areas in which – for different reasons – the climatic conditions determine a powerful abiotic stress, and consequently they are characterized by a particular climate with a certain degree of climatic resistance to the changes of the macroclimate [44]. This climatic resistance prevents the vegetation of the dominant climate from expansion, limits its competitive capacities, enabling the survival of the species tolerant to the local abiotic stress, characteristic to certain climatic periods long passed by [14,15,20,62].

An essential condition for the survival of the plant populations in these refugia is the persistence in time of the particular local climatic conditions, but this happens for a long time only in microclimatic – and more rarely in mesoclimatic – areas [44]. As for that, as early as 1929 Borza drew attention to these shelters of Tertiary flora ('sheltered valleys, gorges, rockslides') with particular microclimates so different from the general climate and of great importance in the ecological phytogeography [10]. An example of the importance of the microclimate is the vegetation of desertic character developing on the loess walls from the Carpathian Basin [49].

Such areas that satisfy the conditions above are the peatlands, the rockslides, the screes, where indeed we can find relict populations from different phytohistorical periods. Born at the base of rocky slopes, and subjected to a continuous process of crumbing that prevents the formation of deep zonal soils, the screes, for instance, are evidences of the cryogenic processes, which – although taking place even today – were more prominent in the periglacial climate of the Pleistocene. Consequently, they can be regarded as intrazonal fossil formations of a former morphoclimatic period [44]. This type of formations shelters species adapted to extreme ecological conditions and which – because of their diminished competitiveness – do not resist the processes of succession in other habitats. Thus, the screes are numbered among the ecotopes of conservative character, in most cases being mostly populated by plant communities of relict character [14]. The same holds true of the rupicolous communities, especially those developed on calcareous substrata (including dolomites and calcareous conglomerates), which are thus the richest in endemic, subendemic and relict species [2,3,14]. On the other hand, there is an obvious correlation between endemism and the age of the flora: the older the flora is, the more – geographically and systematically isolated –

endemic species it contains [3,47].

Due to the strict adaptation to the special ecological conditions of the habitat, many populations of these species remained isolated in these refugia, without migrating to the neighbouring areas. Thus, the refugial areas can be characterized by an increased floristic diversity [3].

Today it is widely accepted that the calcareous massifs accumulate and conserve the flora of the different phytohistorical periods, since on a limited area they offer a wide choice of ecotopes with particular microclimates [2,5,10,50], while the plain – with a diminished variety of habitats – always reflects the flora of the present-day climate [5,62].

The important role played by these massifs in the survival of the thermophilous flora of the cold climate is especially due to the thermal characteristics of the limestone. An indirect proof in this respect would also be the intensification of the limestone-dependence of a few species in the superior, colder zones of vegetation, while in the inferior ones this feature remains optional [18]. Under the influence of warmer conditions, the basiphilous character of certain calcareous species attenuates, colonizing also siliceous substrata.

A concrete example is that of the Alpine *Gentiana* species pertaining to the *Ciminalis* (Adans.) Dumort. section, which diversified during the Quaternary from a common calciphilous ancestor, while the calcifuge species *G. acaulis* and *G. alpina* are alleged to have originated in the interglacials, respectively in the postglacial period, when vast areas with siliceous substratum became free in the way of colonization [42].

Due to the large area (30%) occupied by limestone [22] and to the marked degree of fragmentation of the landscape, formed of massifs separated by the valleys and gorges of a rich hydrographical network, the Apuseni Mountains – with a more advanced fragmentation than that of the exterior arch of the Carpathians – consequently could constitute a vast refugia for the populations of the most different floristic elements [10,31,50].

In the light of these interpretations, Scărița-Belioara or Cheile Turzii, for instance, would represent famous collecting refugial areas, important from a phytohistorical and conservative point of view [10], where species of so different temporal and geographical origin often coexist in the same community. As for that, this latter fact has been emphasized in the case of many other localities by all the botanists who have studied the calcareous rockslides of the Apuseni and of other mountains [19].

Moreover, it is known that the calcareous massifs intermediated the expansion of the flora of the different climatic periods [5,62]. Thus, the Apuseni are alleged to have transferred the Pontic elements preserved in the refugia during the glacial periods towards the steppes within the Carpathian arch [9].

In addition, during the katathermal Würm climate, the vegetation of the Apuseni Mountains had been affected to a lesser extent by the direct action of the glaciers and more by the cold, arctic winds and the pronounced aridity caused by the vicinity of the continental ice-sheet, as well as by the southern limit of the permafrost, which – according to the geological evidences and the periglacial forms – reached the Northern Carpathians [10,43].

Thus, Berindei [4] concludes that in the case of the Apuseni we cannot speak of a Pleistocene glacial landscape, because the local geographical conditions did not allow the accumulation of so important quantities of snow that could have resulted in the formation of glaciers. In the Biharea Massif, the existing glacio-nival cirques are at most evidences of embryonary glaciers, like the one in Valea Cepelor on the northeastern slope of the Cucurbăta Mare Mountain, which is of a special floristic interest [16]. Likewise, the limit of the permanent snows in the Apuseni was at 1500 m.

Consequently, besides the less probable 'nunnataks' (which – as for them – are characteristic of high mountains), in the Apuseni the glacial refugia must be searched for in the 'microclimatic oases' mentioned above.

Of a special phytohistorical interest is the problem concerning the origin in these mountains of the populations of southern xerothermic elements. Many of these are connected to the rocky habitats of intrazonal character, which present the topo-climatic characteristics of certain refugial areas.

It is obvious that their migration routes from the Balcano-Illyrian regions crossed the Banat, and that this process was closely connected with the history of the Tethys Sea and the Alpine orogenic processes. The penetration of these elements into the Apuseni Mountains was possible only after the recession of the Sarmatic Sea from the Transylvanian Basin, because up to the Pannonian these formed a marine island still separated from the rest of the Carpathian ridgeline. South of the Apuseni, the waters of the Transylvanian Basin were communicating with the Pannonian basin in the Miocene through the corridor of the Mureş [48]. For the rest, the exchange of species between the Balkan mountains and the Carpathians took place without obstacles since this territory had been a contiguous dry land for a long time, and the isthmus formed in the Pontian period – and still marked today by the Danube corridor – was relatively narrow, so it could not represent a barrier in the way of the migration of plants [33].

Certain rupicolous calcareous communities of the Apuseni Mountains, such as *Seslerietum rigidae* or *Helictotrichetum decori* seem to originate in these preglacial times [14,31,37].

A 'problem' species from the composition of these communities is also the Submediterranean element *Saponaria bellidifolia*, considered by the specialized literature either a Tertiary relict [8,17] or a postglacial thermophilous relict [31]. The northernmost area of this species is the disjunct exclave from the Apuseni Mountains, more precisely Scărița-Belioara and the calcareous rocks of the adjacent valleys: Runc, Poşaga, Pociovaliştei, Craca (the Gilău-Muntele Mare Mountains), [7,8,30,41,52] as well as Piatra Urdaşului (the Trascău Mountains) [36]. Its presence on the Şuşcu Peak near Băile Herculane [21,53], respectively in other localities from the Cerna basin [55] is argued against [57].

If *S. bellidifolia* had reimmigrated into the Apuseni Mountains in the postglacial period, its appearance in certain stations from the south-west should be much more probable [17], the more so since the ecological conditions are highly offered by the calcareous rockslides of the Apuseni south of the Gilău - Muntele Mare and the Trascău Mountains. Thus, it seems easier to accept the hypothesis of the persistence of the species in its present habitat already since the Tertiary or the warm interglacials.

However, despite the age and the extremely specialized ecological character, the species does not present major differentiations regarding its taxonomical characteristics, compared to the populations of the Balkan Peninsula, even if the specialized literature described the infrataxon *Saponaria bellidifolia* Sm f. *borzae* Csűrös [28].

The partial studies at molecular level aimed at the population in Cheile Poşăgii [13] indicate an increased variability of the species in this locality, so it may be inferred that this species did not suffer genetic bottlenecks in the course of time. It is obvious that the population has not been formed recently starting from a low number of individuals and that it adopted efficient strategies which permitted to conserve an important part of the species' genofond [13].

The status of 'preglacial xerothermic relict' of certain species, such as *Centaurea atropurpurea*, *Allium flavum*, *Seseli gracile* [12], *Ferula sadleriana*, *Allium obliquum* [27,62] etc. is waiting to be reconfirmed also by studies in cytotaxonomy or molecular phylogeography, in order to complete the phytogeographic considerations.

Similar molecular studies have proved the preglacial age of the species *Gentiana clusii* in the mountains of Europe [42], unfortunately without also including material from the Romanian Carpathians.

Arctostaphylos uva-ursi is another 'problem' species that survives with certainty, in two localities on Romania's territory, namely in the Apuseni Mountains (Scărița-Belioara and Muntele Buscat, to be found at 15 km apart) [11,54], as well as in Bucovina [56].

It was often included in the same category of floristic elements that appeared in our flora during the glacial period, representing outposts of the Arctic-Alpine flora in its southward expansion.

However, the chemotaxonomic researches proved that the *Arctostaphylos uva-ursi* populations from the Apuseni are of Illyrian origin (pertaining to the southern 'chemical race'), contrary to those from Bucovina, which originate from the boreal populations [60,61]. Moreover, the Pliocene macrofossil remains of *Arctostaphylos uva-ursi* discovered on the territory of Bulgaria and Central Europe [11] should prove the preglacial origin of this species in the Apuseni.

Paradoxically, on the calcareous peaks of the massifs are to be found also glacial relict populations, apart from the peatbogs and the eutrophic marshes. For the first situation, highly controversial for that matter, we may find an ecological explanation in the fact that the calciphilous flora generally expanded in conditions of climatic aridity. Thus, the limestone-dependence of the oligothermal orophytes would mean at the same time also xerophytic adaptations, as a proof that many elements immigrated under the cold and dry climate of the Pleistocene glaciations [18].

It is not excluded – on the contrary, the floristic data prove – that the same calcareous peaks which during the glaciation served as glacial refugia for the xerothermal species, played the role of interglacial refugia for the Alpine species during the interglacials, a classic example being Scărița-Belioara, where the species *Saponaria bellidifolia* (Submediterranean element) and *Dryas octopetala* (Arctic-Alpine element) grow together only a few meters apart.

Similarly amazing is the case of the calcareous cliffs of Vidolm, which on the northern/northeastern slopes preserve the relict larch forest, and on the rockslides of southern exposure, a relatively large population of the Submediterranean element *Saponaria bellidifolia* [inedit., Csergő, A.-M.]. This is another concrete example cited in support of the hypothesis concerning the polygenetic origin of the calciphilous plants from the flora of the Romanian Carpathians, as it was highlighted by Boşcaiu [18].

Dryas octopetala was the representative species of the Tardiglacial, which in places with climate and soils characteristic of tundras constituted the so-called 'Dryas flora' together with a large suite of species. In the Apuseni its two relict populations are to be found at the lowest altitude in the Carpathians, where it survived the warm periods of the postglacial period: Scărița-Belioara [26,28,30,32] and the calcareous massif at Vidra, Alba county [24,29].

Many other species of the rockslides and meadows of the Apuseni have been included in the category of glacial relicts: *Arabis alpina*, *Pinguicula alpina*, *Poa alpina*, *Carex rupestris*, *Carex sempervirens* [31], *Pulsatilla alba*, *Saxifraga stellaris ssp. alpigena*, *Ligusticum mutellina*, *Lycopodium alpinum*, *Hieracium alpinum*, *Gnaphalium supinum*, *Thesium alpinum* [27], *Satureja alpina*, *Euphrasia salisburgensis*, *Kernera saxatilis*, *Carex brachystachys* [28], *Polystichum lonchitis*, *Cystopteris montana*, *Goodyera repens*, *Polygonum viviparum*, *Tozzia alpina* [17], without the possibility of proving with certainty this quality of theirs [51].

From among the woody species characteristic of the glacial maxima and the relict populations of which survive on the limestones of the Apuseni we mention *Pinus sylvestris* and *Larix decidua* var. *polonica*.

During the glacial maxima the dominant landscape was that of dry steppes with *Artemisia* and *Chenopodiaceae*, dispersed on account of the arid climate, which together with the rather frequent clumps of *Pinus* formed a periglacial forest steppe vegetation [1,43,46]. The pollen spectrum of the Pleistocene sediments from Sighiştel (the Beiuş basin) [34] offers a particularly relevant picture of the vegetation during the glacial maxima in the Apuseni. Especially shocking is the increased incidence of *Pinus sylvestris* (49-63,33%), besides which there were elms, oaks, hazels, willows and birches.

It is generally accepted that the *Pinus sylvestris* forest from Scărița-Belioara descends from the old clumps of forests of the glacial period [32]. This assertion can be explained by the fact that this species was the most frequent and the most widely expanded woody plant of the Pleistocene, and the characteristics of the present habitat from Scărița-Belioara allow the assumption that they favoured its survival. The ecology and the plasticity of the species are totally special [43].

It is from this period that the pine-forests with *Sesleria rigida* (*Seslerio rigidae-Pinetum sylvestris* (Csűrös et Spârchez 1963, Csűrös et all. 1988), to be found on the calcareous rockslides from Scărița-Belioara, must also originate.

Due to its increased resistance to frost, but also to the increased need for humidity, the larch also conquered space and mingled with the pine in the cold, but more humid stadial periods [43]. In the Apuseni Mountains, the *Larix decidua* var. *polonica* populations from Scărița-Belioara and Vidolm are considered glacial relicts [25,32,38].

It is worth mentioning the presence on the calcareous cliffs in the Apuseni of the steppe elements of both cryophile and xerophilous character, considered for a long time Arcto-Alpine elements, such as *Leontopodium alpinum* or *Aster alpinus*. Even if their origin in the Asian steppes is well known, the period in which they penetrated into our flora is still highly controversial. Thus, they are considered preglacial phytogeographical relicts [35,45], or, on the contrary, relicts of the Würm glaciation, originating from the periglacial steppes [1]. *Leontopodium alpinum* grows in the Apuseni at Întregalde [6], Râmeț [58], Vidra [24], at the lowest altitudes in the Carpathians.

With all the phytohistorical importance of these relict populations, the studies on the ecology and biology of populations are missing, while they could facilitate the understanding of their persistence, dynamic and temporal viability. The importance of these studies has been emphasized by Zólyomi [63].

Likewise, we shall have to reconsider the potential of certain – less known (and implicitly less affected by human activities) – calcareous massifs from the Apuseni to represent important refugial areas that preserve certain species of a special phytogeographical importance. As for that, this was the case with those from the proximity of Vidra village (Avram Iancu commune, Alba county), pertaining to the Poieni plateau, the region being considered 'a potential future national park' [24.]

Conclusions

Our current knowledge regarding the existence of the refugial areas in the Apuseni Mountains is based almost exclusively on the hypothesis of the traditional phytogeography.

However, due to the absence of the glaciers during the Ice Age, determined by the low altitudes, the fragmentation of the landscape, as well as the large calcareous surfaces, one can assume that the Apuseni Mountains offered a large number of habitats (screes, calcareous rockslides etc.), which could have facilitated the survival of some preglacial and glacial relict plant populations.

Cheile Turzii, Scărița-Belioara, Piatra Vidolmului, the calcareous rockslides from Vidra would represent, from this perspective, important refugial areas.

These are characterized by a certain climatic homeostasis and a high level of floristic and genetic diversity, which should draw the attention of the conservationists.

Their content in floristic elements is an evidence of the polygenetic origin of the calciphilous flora from the Carpathians.

The studies of the molecular phylogeography could confirm the current hypothesis related to the existence of the glacial and interglacial refugia, also on the territory of the Apuseni Mountains.

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PROBLEMA REFUGIILOR UNOR POPULAŢII RELICTARE PREGLACIARE ŞI GLACIARE DIN FLORA CALCIFILĂ A MUNŢILOR APUSENI (ROMANIA)

(Rezumat)

Cunoştinţele actuale privind existenţa şi localizarea ariilor refugiale din Munţii Apuseni se bazează aproape exclusiv pe ipotezele fitogeografiei tradiţionale.

Lucrarea de faţă se doreşte o sinteză a acestor ipoteze, precum şi a unor rezultate concrete ce pledează în favoarea existenţei refugiilor păstrătoare de populaţii relictare preglaciare şi glaciare din Munţii Apuseni, cu privire specială asupra masivelor calcaroase ca potenţiale zone refugiale.

O condiţie esenţială pentru supravieţuirea în refugii a populaţiilor de plante specifice unor perioade climatice anterioare este persistenţa în timp a condiţiilor climatice locale particulare, ceea ce se întâmplă îndeosebi în spaţiile microclimatice.

Asemenea spaţii, care îndeplinesc condiţiile amintite, sunt grohotişurile şi stâncăriile calcaroase, a căror floră are un profund caracter relictar.

Datorită lipsei gheţarilor în timpul glaciaţiunilor Pleistocene, a reliefului fragmentat, precum şi a suprafeţelor mari acoperite de calcare, se presupune că Munţii Apuseni au oferit o multitudine de asemenea habitate cu caracteristici microclimatice particulare, propice supravieţuirii populaţiilor relictare preglaciare şi glaciare.

Cheile Turzii, Scăriţa-Belioara, Piatra Vidolmului, calcarele de la Vidra ar reprezenta în această accepţiune câteva exemple de arii refugiale importante, a căror compoziţie în elemente fitogeografice este o dovadă a originii poligenetice a florei calcifile a Carpaţilor.

Studiile de filogeografie moleculară urmează să confirme ipotezele privind existenţa refugiilor glaciare şi interglaciare şi pe teritoriul Munţilor Apuseni.