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Frozen Chrysomelids from Alpine Glaciers – Witnesses of the Postglacial Resettlement[1]

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Abstract. In the last decades a significant retreat of alpine glaciers occurred. During these processes, some pieces of peat bogs melted out from below the glaciers. In this article, conclusions are discussed, which can be inferred from the Chrysomelidae fragments found in these pieces.

The first site is situated at Unteraar glacier in the Central Alps of Switzerland. The pieces of peat bogs are 3600 to 3800 years old and contained more than 5000 insect fragments. The Donaciinae remains showed a typical assemblage of a Cyperaceae fen peat. They contributed to a detailed assessment of the ecological conditions at this site 3600 years ago.

From below the Pasterze glacier, northeast of Grossglockner in Hohe Tauern, Austria, also pieces of peat bogs melted out. In the 8100 years old pieces, fragments of Chrysomelidae were found, which could be identified as *Oreina cacaliae* (Chrysomelinae). In the same pieces of peat bogs pollen of *Senecio* was found, too. With the *Oreina* fragments it was possible to narrow down the assignment to *Senecio fuchsii*, because *Oreina cacaliae* feeds only on this species of *Senecio*. But also interesting conclusions can be inferred concerning the postglacial resettlement. *Oreina cacaliae* has low dispersal ability. It persisted during maximum glacial extension in refugia far from its actual habitats, but managed to reach such a far site as the Pasterze 8100 years ago. This observation is contradictive to the theory of the "unfinished postglacial resettlement" due to lack of time. Other reasons for the restriction of the range of some species, which did not resettle obviously adequate habitats in the postglacial period, have to be discussed.

Key words. Holocene, beetle fragments, *Donacia, Oreina*, paleoecology, speed of dispersal, Pasterze, Unteraar glacier

1. INTRODUCTION

1.1. Retreat of glaciers and insect fragment analysis

In the last two decades a significant retreat of alpine glaciers could be observed. This retreat is not a new and singular event, it happened several times in the post-glacial period (HORMES et al. 2001). There were several intervals, lasting several hundred years each, with warmer climate compared to the average temperature of the 20th century (Fig. 1). During those intervals peat bogs established in the wetlands after the retreat of the glaciers. During the next period of lower temperature, these peat bogs were covered by the growing glaciers. Nowadays, in the relatively warm climatic period, pieces of peat bogs are melting out from below the glaciers.

In peat bogs insect fragments can be found, which are preserved for several thousand to more than hundred thousand years. The most abundant sclerites are remains of beetles. In the last 30 years, the method of insect fragment analysis was established, mainly by G. R. Coope and his team, who published a lot of very interesting results from sites in southern Great Britain, Scandinavia and Northern America (COOPE 1986). Almost all of these investigations were made from areas around the southern fringe of the northern ice shield. In Central Europe there was also a large ice shield during glaciation, which covered large parts of the alps and partly the areas of the surrounding lowlands (Fig. 2). After the retreat of the glaciers many lakes and peat bogs emerged. In some of these places insect fragments were found and investigated, but only selectively and not systematically.

There are two main causes for this situation: Firstly, the insect fragment analysis is more difficult here, because in Central Europe the number of beetle species is three times the number of species in Great Britain or in the Scandinavian sites. Secondly, in Central Europe we had not such an outstanding person like G. R. Coope, who performed these investigations systematically and continually for more than three decades, with a lot of experience and many co-workers. Therefore, in most cases, insect fragments were found only occasionally by macrophytic remains screening and identified only occasionally.

This article shows the results of two interesting sites in Central Europe, where Chrysomelid fragments were preserved in peat bogs and melted out from alpine glaciers. The first site is situated in the Central Alps of Switzerland and was studied by an interdisciplinary project at the Institute of Geology at the University of Bern. The other sample derived from the Pasterze glacier near Grossglockner, located in Hohe Tauern, Austria. From

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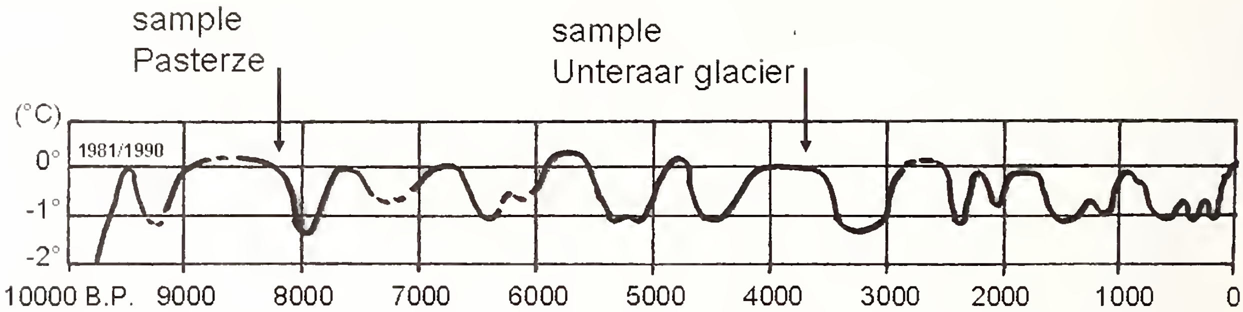

Fig. 1. Amplitude of the average summer temperature (May to September) in the Eastern Alps during the Holocene (graphics after SLUPETZKY et al. 1998).

Fig. 2. Maximum extension of the Würm glaciers in Central Europe, 22000 B.P. U: Unteraar glacier, P: Pasterze glacier.

both sites interesting conclusions can be inferred from the Chrysomelidae fragments.

1.2. Coleoptera fragment analysis provides additional results to the method of pollen analysis

The method of pollen analysis, palynology, is well established for more than 80 years und revealed many interesting results, especially on glacial, interglacial and postglacial ecology. Also almost all sediments with Coleoptera remains contain a variety of pollen. There are two aspects to why Coleoptera fragments provide additional knowledge.

Firstly, with Coleoptera fragments it is possible to narrow down the climatic conditions at a special site better than by palynology. The MCR (Mutual Climatic Range) method, developed by ATKINSON et al. (1986), demonstrated its usefulness in many cases. It was used also in the study of the fragments from Unteraar glacier (JOST-STAUFFER 2000). Secondly, Coleoptera fragments can provide also more precise information about the vegetation, in addition to the results of palynology. Whereas the tree pollen looks very characteristic and can be assigned to the tree species in most cases, the pollen of many herbs can be assigned only to genus level or even to genus group. Therefore, fragments of monophagous or oligophagous beetles, like Chrysomelids, support useful additional information and can narrow down the results of pollen analysis to species level.

2. DONACIINAE FROM THE WESTERN ALPS

2.1. Site, materials and methods

From the Vorfeld of the Unteraar glacier, at 1920 m a.s.l., located in the Central Alps of Switzerland (Fig. 2), 3600 to 3800 years old pieces of peat bogs melted out. They contained about 5000 insect remains; most of them were beetle fragments. The items were assigned to the beetle families by the co-workers of a research project from the Institute of Geology at the University of Bern and identified as exact as possible. Then specialists of the identified Coleoptera families were contacted and asked, to check the identification and to do it more precisely, if possible. I was asked to check the Chrysomelidae fragments, except the Alticinae (which were checked by Manfred Döberl, Abensberg, Germany), and then 150 well prepared items were sent to me.

2.2. Results and discussion

The Chrysomelidae (except Alticinae) species found at that site belonged to the subfamily Donaciinae. The following species were determined (Table 1).

Table 1. Donaciinae identified from the Vorfeld of the Unteraar glacier, Switzerland. Nomenclature according to KIPPENBERG (1994).

Donacia clavipes Fabricius, 1792
Donacia semicuprea Panzer, 1796
Donacia aquatica (Linnaeus, 1758)
Donacia impressa Paykull, 1790
Donacia brevitarsis Thomson, 1884
Donacia brevicornis Ahrens, 1810
Donacia marginata Hoppe, 1795
Donacia obscura Gyllenhal, 1813
Donacia thalassina Germar, 1811
Donacia vulgaris Zschach, 1788
Donacia simplex Fabricius, 1775
Plateumaris sericea (Linnaeus, 1758)

Only a few fragments (most of them are elytra or the distal fragment of one elytron) could be assigned exactly to one species, but often it was possible to narrow down the identification to two or three species. Sometimes it was possible to identify the genus only. Other fragments could be clearly assigned to the subfamily Donaciinae, but could not be identified more precisely.

The species mentioned in Table 1 are distributed in the whole of Europe, or, at least, in large areas of Europe. Their habitats are in such a wide temperature range that these Donaciinae were not used for the MCR, like some other Coleoptera species found at the Unteraar glacier. But these Donaciinae fragments contributed to more precise information about that habitat at this site 3800 years ago. In combination with the other identified beetle species it can be inferred that that habitat contained a marshy wetland with different sedges and reeds with *Phragmites communis, Glyceria maxima, Sparganium simplex, Sparganium ramosum, Scirpus lacustris, Scirpus palustris, Carex rostrata* and other *Carex* sp. (Botanical nomenclature according to FISCHER et al. (2005)).

3. *OREINA* FROM THE EASTERN ALPS

3.1. Site, materials and methods

The Pasterze glacier is the largest glacier in the Eastern Alps. It is situated northeast of Grossglockner in Carinthia, Austria (Fig. 2). In 1990 to 1996 pieces of peat bogs and stems of coniferous trees (*Pinus cembra*) melted out. They were collected by G. Lieb and H. Slupetzky during routine measurements of the glacier and then investigated thoroughly (SLUPETZKY et al. 1998; GEISER 1998).

Fig. 3. Sample of 8100 years old *Oreina cacaliae* fragments, found near Pasterze glacier (Photo: J. Burgstaller).

By the screening for macrophytic remains some beetle fragments were found (Fig. 3). These pieces of peat bog also yielded a rich pollen assemblage. It was 8180 ± 70 years old. The original site of the peat is still covered by the Pasterze glacier, about 0.5 to 4 km upwards of the actual glacier terminus at approximately 2100 to 2300 m a.s.l.

The pollen analysis and the macrophytic remains analysis revealed that during a period from 9000 to 8100 years B.P. a mountain forest was established at that site. The main tree species was *Pinus cembra*, and the typical assemblage of vascular plants was found there, especially the tall herbaceous vegetation with *Senecio* species. The forest also contained several peat bogs. This ecosystem is typical for the Hohe Tauern, but nowadays situated several hundred meters lower. This time period was the largest interval of relatively warm climate in postglacial times (Fig. 1).

The beetle fragments are stored in the collection of the author, which is designated to the Biologiezentrum in Linz, Austria.

3.2. Results and Discussion

3.2.1. Result of the identification of these beetle fragments: *Oreina cacaliae.* The fragments found at that site could be identified as *Oreina cacaliae* (Schrank, 1785). They belong to a minimum of three individuals.

Subfossil fragments of that genus are very rare. The evidence that this species was established at this site 8100 years ago is a very interesting fact.

3.2.2. Biology and actual distribution area of *Oreina cacaliae*. The habitat of the leaf beetle *O. cacaliae* is constituted by tall herbaceous vegetation in mountainous areas in Europe at 800 to 2500 m altitude. On some sites with adequate microclimatic conditions it can also be found down to 600 m a.s.l. This species is ovovivipar, like other Chrysomelids at the same altitude. For pupal development and hibernation *O. cacaliae* stays in the soil. Imagines up to three years old are known (ROWELL-RAHIER 1992).

Oreina cacaliae is oligophagous on Asteraceae, it feeds only on *Senecio ovatus* (syn. *Senecio fuchsii*) and *Adenostyles alliariae* (HÄGELE et al. 1996; there exists a remarkable variation in the nomenclature of that species, which was called *Senecio fuchsii* for decades. Mostly it is named now *Senecio nemorensis* or *Senecio ovatus* or *Senecio nemorensis* ssp. *fuchsii*. There exist further names and combinations of names. But the plant species is always the same.). The preference of the altitudes mentioned above, and the restriction to these two host plants are the reason for the fragmentation of their distribution area.

Oreina cacaliae shows an aposematic colour with high variation. They synthesise chemical defence secretions out of secondary plant compounds from their host plants (PASTEELS et al. 1994). Therefore, their restriction to their host plant species has evolved long ago. There is no indication to a host plant change in the last 10 000 years.

3.2.3. Supplementation of the pollen analysis. In the pieces of peat bogs, which contained the *O. cacaliae* fragments, pollen of *Senecio* could also be identified. No *Adenostyles* pollen was found. Therefore it can be inferred that the *Senecio* pollen identified at the Pasterze belong to *Senecio fuchsii*.

3.2.4. Glacial refugia of *Oreina*. The majority of today's distribution area of *O. cacaliae*, especially in the Alps, was covered with glaciers until 13 000 years ago. In many other locations of the actual range it was also impossible for the host plants to settle there, due to climatic reasons. Therefore, during the periods of large glacier extension, the majority of the populations of *O. cacaliae* had to persist in refugia far from their actual habitats. Figure 2 shows the maximum of the glacier extension in Central Europe at the period of Würm, 22 000 years ago.

3.2.5. Dispersal ability of *Oreina cacaliae* and its host plants. The host plants have very high dispersal ability, as usual in Asteraceae, which disperse easily with their pappi. Therefore they reached adequate habitats quickly during the periods of retreating glaciers and during their growing periods, also. On the other hand, *O. cacaliae* has relatively low dispersal ability. This is very difficult to observe directly, but there are some facts that support this assumption:

Field studies in the Swiss Alps showed that the adults moved only a few meters during summer, and a high percentage of individuals were recaptured in the next year, less than 5 m from the places where they were marked (ROWELL-RAHIER 1992).

Coloration of *O. cacaliae* is highly variable, even within one population. But the set of colour variations is very typical for different regions within the whole area of distribution. This indicates that the populations are isolated for a long time.

3.2.6. Dynamics of the postglacial resettlement. The majority of the animal and plant species of Central Europe have high dispersal ability. This is due to more than 50 periods of growing and retreating glaciers. The habitats shifted to the south and then to the north within a few thousand years. Therefore species with high dispersal ability had more chance to survive the Quaternary Ice Age. Species with high dispersal ability will spread to their habitats in Europe within a few 100 years (GEISER 1997). But also some species with relatively low dispersal ability managed to survive the climatic and therefore the habitat fluctuations. The species that didn't manage this became extinct in Central Europe.

The retreat of the glaciers after their maximum extension started about 20 000 B.P. This retreat was interrupted by some colder climate intervals. At 10 300 B.P. the glacier dimensions were similar to the dimensions in the 20th century. There were some small fluctuations in the Holocene (Fig. 1). The most recent retreat of the glaciers started in 1860, interrupted by a short growing period at 1920. Nowadays, a significant retreat can be observed since 1982.

The longest warm period lasted from 9000 to 8000 B.P. At a site that is still covered by the Pasterze glacier, a mountain forest with *Pinus cembra* could establish. The fragments of *Oreina cacaliae* show that even a species with such low dispersal ability could reach this remote site within a few thousand years.

3.2.7. Is "not yet finished postglacial resettlement" a relevant explanation for restricted distribution areas? There are several species known with a very patchy distribution area and adequate habitats in between. Some of these gaps in distribution are explained by "not yet finished resettlement" (since HOLDHAUS 1954) that implies that this is due to the lack of time in the postglacial period to reach that habitats. On the contrary, the example of *Oreina cacaliae* shows that a species with low dispersal ability could reach remote habitats within a few thousand years.

The extension of a definite distribution area of a definite species always changes dynamically, with lower or higher amplitude. Therefore, resettlement is never "finished". The restriction of distribution areas can be explained more probably as a result of the interaction of the following reasons:

- low dispersal ability
- low competitive ability
- highly specialised ecological demands
- geographical barriers (from the point of view of the species)
- and last, but not least, our lack of knowledge about the detailed biology and ecological demands of the definite species.

The dynamics of dispersal and the real process of the postglacial resettlement is inferred indirectly only, in most cases. Modern molecular methods, such as isoenzyme electrophorese (SCHMITT 2000) or DNA analysis, are very useful, but indirect, too. Real items on a real site with a definite age have to match the theory, if not the theory has to be revised.

Our knowledge about the causes of distribution, about postglacial resettlement and changes of climatic and other ecological conditions during the Quaternary, depends on pieces of a dazzling, but highly interesting puzzle, which is composed of many items and methods. The more such items we find and examine with different methods we have, the clearer our idea of the postglacial ecology will be.

Acknowledgements. All these interesting results derived from Chrysomelidae fragments, which were sampled and extracted by other scientists: the Doncaciinae fragments I received from Dr. Monika Jost-Stauffer were in excellent preparation and packing (that cannot be taken for granted!). Also, the cooperation with her and the Institute of Geology of the University of Bern was excellent.

The pieces of peat bogs, which contained the *Oreina* fragments, were sampled by Univ. Prof. Dr. Gerhard Lieb (Institute of Geology, University of Graz). The fragments were detected by Univ. Prof. Dr. Robert Krisai (Institute for Botany, University of Salzburg). Univ. Prof. Dr. Heinz Slupetzky (Department of Glaciology at the Institute of Geography, University of Salzburg) coordinated these investigations at the Pasterze glacier and supported me with useful information. He also initialized the cooperation with Mag. Johann Burgstaller (Salzburg), an experienced photographer of crystals, who managed to photograph that shiny surface of the *Oreina*-fragments.

My husband was, as always, a meticulous proof-reader and made a lot of critical comments. It is an inestimable advantage to be criticised by a real friend and expert Coleopterologist.

Cordial thanks to all these colleagues.

ZUSAMMENFASSUNG

Die Klimaerwärmung der letzten beiden Jahrzehnte hat zu einem Rückzug der Alpengletscher geführt. Bei diesen Schmelzprozessen wurden an mehreren Stellen der Alpen unter den Gletschern gelegene Torfstücke herausgeschwemmt. Die vorliegende Arbeit berichtet über die Ergebnisse von zwei Fundstellen, an denen subfossile Chrysomelidenreste gefunden wurden.

Die erste Fundstelle befindet sich am Unteraargletscher in den Schweizer Zentralalpen. Die ausgeschwemmten Torfstücke waren 3600 bis 3800 Jahre alt und enthielten über 5000 Insektenreste, die im Rahmen eines Projektes des Geologischen Institutes der Universität Bern untersucht wurden. Die Autorin überprüfte und bestimmte die Reste der Unterfamilie Donaciinae. Die Artzusammensetzung entsprach der typischen Donacien-Fauna eines Cyperaceen – Flachmoores. Diese Befunde trugen zusammen mit den anderen Käferresten zu einer sehr genauen Einschätzung der ökologischen Verhältnisse an dieser Stelle der Alpen im genannten Zeitraum bei.

Die zweite Fundstelle befindet sich unter der Pasterze nordöstlich des Grossglockners (Hohe Tauern, Österreich). Die herausgeschwemmten Torfstücke enthielten Reste eines 8100 Jahre alten Bergblattkäfers: *Oreina cacaliae*. Dieser Fund einer oligophagen Chrysomelidenart trägt zu einer Präzisierung der botanischen Befunde durch Pollen- und Großrestanalyse bei. Dadurch ist die Aussage möglich, dass es sich bei den ebenfalls in dieser Probe nachgewiesenen *Senecio*-Pollen um die Art *Senecio fuchsii* handelt. Weiters liefert dieser Fund einer wenig ausbreitungsfreudigen Art an einer Stelle, die von den Glazialrefugien dieser Käferart weit entfernt ist, einen interessanten Hinweis über den Verlauf bzw. die Geschwindigkeit der postglazialen Wiederbesiedlung.

Die eingeschränkte Verbreitung mancher Arten, trotz Vorhandenseins zahlreicher (anscheinend!) geeigneter Habitate wird immer wieder mit einer „nicht abgeschlossenen nacheiszeitlichen Wiederbesieldung" erklärt, mit dem Argument, dass seit dem Ende der letzten maximalen Gletscherausdehnung im Hochwürm vor 20 000 Jahren die Zeit noch nicht ausreichte für die Arealausweitung auch von wenig ausbreitungsfreudigen Arten. Wenn aber Arten wie *Oreina cacaliae* bereits vor über 8000 Jahren die entlegensten Habitate in den Alpen besiedelt haben, dann erscheint diese Theorie wenig

stichhaltig und die Ursache der eingeschränkten Verbreitungsgebiete muss neu diskutiert werden.

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