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Lepidoptera associated with peatlands in central and northern Europe : a synthesis

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Abstract

A comparison of the peatland faunas of Central Europe, southern Fennoscandia and Lapland is made by choosing 50 Lepidoptera species obligatorily associated with peatlands (so-called tyrphobionts) at least in one area. Characteristic for the tyrphobionts is that they occur as isolated, island-like communities which are often endangered by the human activities. The strength of association of the species with the habitat increases southwards and towards lower elevations. An exception is formed by 12 purely Palaearctic species which mostly live in Central Europe in xerotherm, sandy biotopes but are obligatorily associated with the peatlands in southern Fennoscandia. The typical meso- and microclimate is concluded to be the most important ecological factor affecting the composition of the fauna. The ordinary tyrphobionts are historically cold-adapted species which have had their origin in other biotopes than peatlands. Presumably the 22 (58 %) Holarctic species out of 38 had their origin in the Subartic and the remaining 16 (42 %) in the Subarctic or in the southern mountainous areas.

Introduction

The peatland Lepidoptera obligatorily associated with oligotrophic bogs (= tyrphobionts) have been investigated separately in several parts of Central and Northern Europe, but only few comparative studies have been published (e.g. Petersen, 1954). The tyrphobionts occur in Central Europe and southern Fennoscandia as relict populations, mostly of boreo-montane distribution. The peatlands are island-like, isolated edaphic climax communities which have a characteristic micro- and meso-climate, vegetation and insect fauna (see Peus, 1928, 1932 ; Rabeler, 1931 ; Krogerus, 1960 ; Dohnal, 1965 ; Povolný *et al.*, 1965 ; Novák & Spitzer, 1972 ; Mikkola, 1976 ; Meineke, 1982a and b ; Roháček, 1982 ; Roháček & Mára, 1982).

The peatlands of Central Europa and southern Fennoscandia conform with the category of "Reisermoore" ("Hochmoore"), raised bogs, bogs with ericaceous shrubs and with the central parts higher than the marginal areas (Peus, 1932 ; Krogerus, 1960 ; Ruuhijärvi, 1960, 1970). For survival of tyrphobiont populations in these isolated refugia the following conditions are essential : 1) an area large enough, 2) stable hydrological conditions and 3) distribution of refugia as described by the theory of island biogeography (Diamond & May, 1976 ; Spitzer, 1981).

The peatlands of central and northern Fennoscandia form a more dense network : the aapa mires of central and northern Finland and the palsa mires of northernmost Lapland (cf. also Sjörs, 1965 ; Sonesson, 1980 ; Goodwillie, 1980). The plant communities and the general ecology of the Finnish oligotrophic peatlands have been described by Ruuhijärvi (1960, 1970) and Eurola (1962), and reviewed by Schenk (1970).

For our study in Central Europe, the oligotrophic raised bogs with the autochtonous plant community Pino rotundatae – Sphagnetum (Kästner & Flössner, 1933 sec. Neuhäusl, 1972) are taken into consideration, with a special emphasis on wide areas in southern Bohemia, Czechoslovakia (cf. Spitzer, 1975, 1981). But published data on peatland Lepidoptera from some other areas were used as well, e.g. Orava in the Carpathians (Králiček, 1981), northern Austria (Foltin, 1954, Klimesch, 1971), Switzerland (Geiger, 1980, Rezbanyai, 1980) and Germany (Wagener, 1980 ; Meineke, 1981, 1982a and b).

From Finland, there is a number of local faunistic records of Lepidoptera from different types of peatlands available, but the only comprehensive review was published by Krogerus (1960). The subarctic or arctic palsa mires of fjeld Lapland represent an extreme and unique habitat which is still little known from entomological point of view (cf. Krogerus, 1960, Mikkola, 1976, Koponen *et al.*, 1982). The review on the conservation biology of European peatlands, published by Goodwillie (1980), contains but few entomological data.

The classification and definition of the insect fauna of peatlands was originally proposed by Peus (1932), and subsequently elaborated and summarized for temperate Europe by Roubal (1934 ; Coleoptera), Povolný, Spitzer & Marek (1965 ; Lepidoptera), Spitzer (1975, 1981 ; Lepidoptera), Meineke (1982a ; Lepidoptera) and Roháček & Máca (1982 ; Diptera). This classification of ecological groups of peatland fauna seems to be useful for our comparative study of the temperate and boreal regions.

Fig. 1. Montainous raised peat bog near Kvilda, Šumava mountains, Czechoslovakia. Growths of *Pinus mugo* and *Betula nana* visible.

Fig. 2. Raised peat bog near Tvärminne, Hanko Peninsula, southern Finland, recently ditched (visible in the background).

Fig. 3. An aapa peat bog near Muonio, central Lapland. Growths of *Betula nana* visible.

Fig. 4. A palsa peat bog near Kevo, northern Finnish Lapland. The height of the palsa formation in the figure is roughly 3 metres. – All photos : K. Spitzer.

Our aim is 1) to list the Lepidoptera species most strictly associated with the peatlands of Central Europe as well as of southern and northern Fennoscandia, 2) to find out the common features and differences of the faunas and 3) to discuss which ecological and zoogeographical factors are essential for the faunas. We hope that the study will encourage further investigation of these endangered communities and that it will prove useful for conservation purposes.

Ecological classification of the lepidopterous fauna

The tyrphobionts are stenotopic psychrophilous species entirely confined in their life history to peatlands (bogs, mires), i.e. they depend on the characteristic micro- and mesoclimate, trophic relations and/or vegetation of their habitat. As the strength of the association to the mires varies geographically, it was decided that "a tyrphobiont" must show strict association to the peat bogs at least in one region studied. The tyrphophilous species show weaker association to the peatlands and, thus, a wider ecological amplitude in a given geographical region; They regularly occur also on some other biotopes, usually on other types of wetlands, on heathlands or in conifer forests.

If the whole geographical range of a species is taken into account, it is easily seen that the border between tyrphobiont and tyrphophilous species is far from abrupt: many species which are highly stenotopic tyrphobionts in more southern latitudes fly on the tundra and in the alpine region of the fjelds in many biotopes, i.e. are eurytopic. On the other hand, several species which are associated with sandy biotopes in the south behave themselves as tyrphobionts in southern Fennoscandia (cf. Povolný *et al.*, 1965, Mikkola, 1976).

The tyrphophilous species include some Lepidoptera which formerly used to be more eurytopic but now prefer peatland environments ("Kulturflüchter" sensu Peus, 1932, see Spitzer, 1981, Roháček & Máca, 1982), e.g. *Phyllodesma ilicifolium* (L.), *Eriogaster lanestris* (L.) or even *Endromis versicolora* (L.) used to be more widely distributed in Central Europe 20-30 years ago.

In Fennoscandia, a classification of peatland arthropods was originally proposed and published by Krogerus (1960). The category tyrphobionts corresponds to the definition of Krogerus "euzön a" and in a few cases of Lepidoptera to his "euzön b". The tyrphophilous species are chiefly included in the category "tychozön" of Krogerus (for a comparative review of Diptera, see Roháček & Máca, 1982).

1. Tyrphobionts

We included in the Table 1 species of Lepidoptera which show at least in one of the zones obligatory association with the peatlands, i.e. are tyrphobionts. By "obligatory" we indicate that the species is only seldomly and in low numbers found outside peatlands. E.g. the foraging flights of *Colias palaeno* (see Meineke, 1982a) or erratic flights to foreign biotopes of *Acronicta menyanthidis* and *Eugraphe subrosea* do not mean that these species are not tyrphobionts. On the other hand, if a species seems to have, by side of peatlands, another biotope where it occurs regularly and independently of peatlands, it is not included: e.g. *Lacanobia w-latinum* (Hfn.) which in Finland has mostly been found on peatlands but also on dry esker biotopes.

Table 1. – Association of different tyrphobiont species of Lepidoptera with peatlands

Species	Central Europe	Southern & Central Finland	Lapland	General distribution
A. Strong association both in Central Europe and in southern Fennoscandia (not necessarily in Lapland)				
Glyphipteryx haworthana (Steph.)	xxx	xxx	xx	H/bm
Coleophora ledi Stt.	xxx	xxx	xx	H/ ?
Athrips pruinosella (Lien. & Zell.)	xxx	xxx	x	H/bm
Chionodes viduella (Fabr.)	xxx	xxx	xx	H/bm
Olethreutes ledianus (L.)	xxx	xxx	xx	P/bm
Olethreutes turfosanus (H. S.)	xxx	xxx	xx	H/bm
Crambus alienellus (Germ. & Kaulf.)	xxx	xxx	xxx	H/bm
Pediasia truncatella (Zett.)	xxx	xxx	xx	H/bm
Colias palaeno (L.)	xxx	xxx	xx	H/bm
Proclossiana eunomia (Esp.)	xxx	xxx	xxx	H/bm
Carsia sororiata (Hb.)	xxx	xxx	xxx	H/bm
Eugraphe subrosea (Steph.)	xxx	xxx	O	H/bm
Anarta cordigera (Thnbg.)	xxx	xxx	x (F)	H/bm
Apatele menyanthidis (Esp.)	xxx	xxx	xx ?	P/bm
Syngrapha microgamma (Hb.)	xxx	xxx	xxx	H/bm
B. Strong association only in Central Europe				
Epinotia gimmerthaliana (Lien. & Zell.)	xxx	xx ?	xx ?	P/ ?
Vacciniina optilete (Knoch)	xxx	x (H)	x (F, H)	H/bm
Boloria aquilonaris (Stich.)	xxx	xx (W)	x (F, W)	P/bm
Eupithecia gelidata Möschl.)	xxx	xx (C)	x (C, B)	H
Arichanna melanaria (L.)	xxx	xx (P)	O	P/bm
Lithophane lamda (Fabr.)	xxx	x (C)	O	P/bm
Amphipoea lucens (Frr.)	xxx	xx (W)	O	P/bm
Celaena haworthi (Curt.)	xxx	x (W)	x (W)	P/bm

Species	Central Europe	Southern & Central Finland	Lapland	General distribution
C. Strong association only in Fennoscandia				
Tischeria heinemanni Wocke	– (S ?)	xxx	O	P
Rhagades pruni (D. & S.)	x (S)	xxx	O	P
Pachytelia villosella (Ochs.)	– (S)	xxx	xx (H)	P
Phalacropterix graslinella (Boisd.)	xx (S)	xxx	xxx	P/bm
Clepsis pallidana (Fabr.)	– (S)	xxx	O	P
Philedone gerningana (D. & S.)	x ?	xxx	O	P
Coenonympha tullia (Müll.)	xx	xxx	xx	P/bm
Thalera fimbrialis (Scop.)	– (S)	xxx	O	P
Scopula virgulata (D. & S.)	x (S)	xxx	O	P
Idaea muricata (Hfn.)	x (S)	xxx	O	P
Hypoxystis pluviaria (Fabr.)	– (S)	xxx	O	P
Aspitates gilvaria (D. & S.)	– (S)	xxx	O	P
D. Does not occur in Central Europe (some in the Alps but not in peatlands)				
Coleophora obscuripalpella Kan.	O	xxx	xxx ?	P
Agriphila biarmica (Tgstr.)	O	xxx	xxx	H/sa
Pyrgus centaureae (Rbr.)	O	xxx	xx (F)	H/sa
Clossiana freija (Thnbg.)	O	xxx	xx (F)	H/sa
Clossiana frigga (Thnbg.)	O	xxx	xxx	H/sa
Erebia embla (Thnbg.)	O	xxx	xx (H)	P/sa
Chloroclysta infuscata (Tgstr.)	O	xxx	xx (C)	P/sa
Semiothisa carbonaria (Cl.)	O (alp.)	xxx	x (F)	P/aa
Lycia lapponaria (Boisd.)	O	xxx	xx (F, B)	P/sa
Orgyia ericae (Germ.)	O	xxx	xxx	P/sa
Eilema cereolum (Hb.)	O (alp.)	xxx	O	P/bm
Nola karelica (Tgstr.)	O	xxx	xxx	P/sa
Sympistis funebris (Hb.)	O (alp.)	xxx	xx (F)	H/aa
E. Occurrence only in Lapland				
Erebia disa (Thnbg.)	O	O	xxx	H/sa
Lasionycta skraelingia (H. S.)	O	O	xxx	H/sa
Total 46 species				

xxx = strong, xx = moderate and x = weak association, – = no association, O = does not occur in the area. Alternative biotopes are given in the brackets : F = fjeld (tundra), B = subarctic *Betula* forest, P = *Pinus* and *Betula* forest, C = coniferous forest, H = heath with shrubs (*Calluna*, *Empetrum*, etc.), W = wet meadows, S = sandy or other xerotherm biotopes, alp. = occurs in the alpine region. General distribution : P = Palaearctic, H = Holarctic (sec. Hodges *et al.*, 1983), bm = boreo-montane, aa = arcto-alpine, sa = subarctic.

Very few species are strongly associated with the peatlands in all of the zones. There is a general trend of weakening of the association towards the northern and/or alpine timber line. Species which in the southern areas are obligatorily associated with the peatlands may be only weakly

tyrphophilous in the north. In fact, this change happens often on a narrow belt around the timber line : quite in the same geographical area the species behaves as a tyrphobiont in the conifer forest zone but is eurytopic up in the alpine region.

The most well-known tyrphobiontic association is represented by the ecological group which is in southern Fennoscandia and Central Europe exclusively confined to the peatlands (subcontinental raised bogs, cf. Eurola, 1962 ; Ruuhijärvi, 1960, 1970 ; Dohnal, 1965 ; Neuhäusl, 1972), e.g. *Olethreutes lediana* (L.), *Colias palaeno* (L.), *Carsia sororiata* (Hb.), *Eugraphe subrosea* (Steph.) and *Anarta cordigera* (Thnbg.). Many of such species are not obligatorily associated with the peatlands above the timber line.

Several species are tyrphobionts in Central Europe but less so in Fennoscandia : e.g. *Vacciniina optilete* (Knoch.), *Arichanna melanaria* (L.), *Lithophane lamda* (Fabr.) and *Celaena haworthi* (Curt.). Perhaps some peatland species of alpine endemitic origin should be considered as tyrphobionts, e.g. *Blastethia mughiana* (Z.) (not included in the Table 1), cf. Elsner *et al.* (1981).

The group of tyrphobionts of southern and central Fennoscandia which do not occur in Central Europe contains several subarctic species like *Pyrgus centaureae* (Rbr.), *Clossiana freija* (Thnbg.), *C. frigga* (Thnbg.), *Erebia embla* (Thnbg.) and *Chloroclysta infuscata* (Tgstr.). Two species have a arcto-alpine distribution, *Isturgia carbonaria* (Cl.) and *Sympistis funebris* (Hb.), but they do not occur on peatlands in southern high alpine parts of their distribution, e.g. in the Alps and on some Siberian mountains.

Only a few tyrphobionts occur exclusively in the subarctic zone : *Erebia disa* (Thnbg.) and *Lasionycta skraelingia* (H. S.). The following species are found also in the central parts of Fennoscandia and are closely associated with the peatlands of the aapa type, though occur also on raised bogs : *Lycia lapponaria* (B.), *Orgyia ericae* (Germ.) and *Nola karelica* Tgstr. *Oeneis jutta* (Hb.) is a widely distributed subarctic species, now extinct in most southern localities near the Baltic Sea.

A remarkable shift of biotopes from dry, often sandy environments in Central Europe to peatlands in southern Fennoscandia is observed in several species : *Rhagades pruni* (D. & S.), *Thalera fimbrialis* (Scop.), *Scopula virgulata* (D. & S.), *Idaea muricata* (Hfn.), *Hypoxystis pluviaria* (Fabr.), *Aspitates gilvaria* (D. & S.) and *Lacanobia w-latinum* (Hfn.). In Central Europe these species mostly occur only in low numbers or not at all on peatlands (see Meineke, 1982a), but in the south of Fennoscandia most of them behave as tyrphobionts.

As far as the Microlepidoptera are concerned, the Table 1 is still incomplete. It is to be hoped that this article has such a positive effect that in the near future a more comprehensive list can be published. Among the Macrolepidoptera, the apparent deficiencies probably are caused by subjective judgements : the border between the classes of tyrphobionts and tyrphophilous species is subject to consideration, and for accurate solutions of problems very exact information about the frequencies of species in different biotopes is needed.

2. Tyrphophilous species

The tyrphophilous association to peatlands is weaker than in the preceding group and the species in question have alternative habitats. The group of tyrphophilous species is not included in the Table 1, but often species which are tyrphobionts in one or two zones (marked with xxx) show tyrphophilous association elsewhere (marked with x and xx). Tyrphophilous species live usually, by side of peatlands, on various types of wetlands or heathlands.

From the big group of tyrphophilous species some examples are listed below : *Sterrhopteryx standfussi* (Wck.), *Pleurota bicostella* (Cl.), *Acleris lipsiana* (D. & S.), *Metriostola vacciniella* (Lien. & Zell.), *Udea inquinatalis* (Lien. & Zell.), *Callophrys rubi* (L.), *Plebejus argus* (L.), *Brenthis ino* (Rott.), *Clossiana euphrosyne* (L.), *Chlorissa viridata* (L.), *Scopula immutata* (L.), *Eulithis testata* (L.), *Itame brunnearia* (Thnbg.), *Ematurga atomaria* (L.), *Lasiocampa quercus* (L.), *Comacla senex* (Hb.), *Eilema lutarellum* (L.), *Diacrisia sannio* (L.), *Nola aerugula* (Hb.), *Lycophotia porphyrea* (D. & S.), *Anarta myrtilli* (L.), *Orthosia opima* (Hb.), *Photedes pygmina* (Haw.), *Syngrapha interrogationis* (L.), *Callistege mi* (Cl.) and *Hypenodes turfosalis* (Wck.) (see Krogerus, 1960 ; Povolný *et al.*, 1965 ; Mikkola, 1976 ; Geiger, 1980 ; Meineke, 1981, 1982a ; Spitzer, 1981). Some tyrphophilous species occur exclusively in the subarctic area, e.g. *Euphydryas iduna* (Dalm.), *Oeneis bore* (Schn.) and *Pararctia lapponica* (Thnbg.). As a whole, the category of tyrphophilous species is diverse and heterogeneous with regard to the faunistic components and elements.

Discussion

The peatland fauna might not be especially ancient, since probably no or few peatlands existed in Europe before the Pleistocene (see Petersen, 1954). Most species might have their origin in other biotopes, alternatively in the subarctic area or in the more southern mountainous areas.

Therefore, it is not unexpected that many peatland species occur in some other biotopes, too. If they do not, it may be that the original population has become extinct. One of the few species which is not known to occur outside boreal peatlands is *Erebia disa* (Thnbg.) (Petersen, 1954). Basically, the peatland species are cold-adapted ones which found adequate conditions near the glaciated areas. Some of them may have invaded Fennoscandia already during the interstadials, but since most part of Finland was covered by water still some 9000 years ago, the dispersal of the Finnish peatland fauna is a relatively recent one.

Great proportion of the ordinary tyrphobionts have a circumpolar distribution in the Holarctic zone : 87% of the 15 species with a strong association with peatlands both in Central and in Northern Europe and 58% of all the 38 species. The Holarctic species probably have had their origin in other biotopes of the Subarctic than peatlands, and the rest (42%) might have originates in the Subarctic or in the southern mountainous areas. The remaining 12 species form a distinct group : they are purely Palaearctic, and most of them live in Central Europe in xerotherm habitats and behave as tyrphobionts only in Fennoscandia. They are essentially southern lowland species (cf. Table 1).

Unfortunately, only few and mostly preliminary ecofaunistic studies are known from Siberia and North America (cf. Kurentzov, 1948, 1967 ; Munroe, 1968 ; Spitzer, 1968 ; Danks, 1978). Our Table 1 is based on our field studies and on all published records available (cf. the list of references), but is relatively uncomplete as regards Microlepidoptera. The list presents an outline for the corpus of European Lepidoptera obligatorily associated with oligotrophic peatlands at least in some part of their distribution.

Few peatland species are stenotopic over the whole area of distribution, but for most of them the timber line forms an ecological frontier between the stenotopic, more isolated occurrences and the eurytopic, more continuous distribution. Generally the strength of the association to peatlands increases southwards and towards lower elevations.

Most species live as larvae on plants which would be available on other biotopes, too. Thus, their strict occurrence on peatlands must be dependent on the bog physiognomy, most probably on the characteristic meso- and microclimate of the bogs. It is well-known that the weak conductivity of the peat layer leads to conditions with extreme temperature amplitudes : the days are hot and the nights cold. This feature probably also explains the change of biotopes of many species from sand to peatland. The sandy biotopes also show very wide temperature amplitudes.

Many tyrphobionts live in temperate Europe as relict populations of a boreo-alpine distribution. *Eugraphe subrosea* (Steph.), *Anarta cordigera* (Thnbg.), *Carsia sororiata* (Thnbg.) and *Colias palaeno* L. are separated in such a way and have formed many subspecies during the holocene postglacial period.

We would like to emphasize the fragility of the unique isolated communities of tyrphobionts. For these sensitive species already minor changes of environment may be fatal. Bog drainage has in great extent restricted possibilities of survival of these species. In southern and central Finland, for instance, over half of the peatlands have been ditched. Krogerus (1960) notes a case when *Clossiana freija* (Thnbg.) and *C. frigga* (Thnbg.) disappeared from a bog soon after it was ditched.

For evaluation of the vulnerability of individual species both the strength of association to the biotope and the power of dispersal should be taken into account. In the tyrphobionts these are generally high and low, respectively. Thus, in SW Germany, all tyrphobionts are classified as endangered (Meineke, 1982b). The communities of tyrphobionts provide excellent subjects for further ecological and evolutionary investigations. They urgently need projects of conservation (cf. Petersen, 1954 ; Mikkola, 1976 ; Spitzer, 1981 ; Meineke, 1982 a and b).

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