Pirineos, 156: 69 a 85, JACA; 2001

VERTICAL DISTRIBUTION OF THE ALPINE LEPIDOPTERA IN THE CARPATHIANS AND IN THE BALKAN PENINSULA IN RELATION TO THE ZONATION OF THE VEGETATION

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ABSTRACT.– The vertical distribution of arctic-alpine, alpine and Balkanic oreal species is discussed in connection with the vertical zonation of the vegetation, climatic conditions, substrate, type of alpine vegetation and co-occurrences of related species. Arctic-alpine species have mostly a Eurasian distribution and occur in the Arctic and in the alpine and subnival zones of the Central and Southern European high mountains with expressed glacial morphology and alpine vegetation. Alpine species are mostly European species and they are connected to the alpine and subnival zones of Central and South European high mountains. Balkanic oreal species are mostly southeast European species which in some cases occur locally in the southern parts of the Alps and Carpathians. Balkanic oreal species are most numerous at the timberline, preferred habitats being grasslands in the upper subalpine belts. The more diverse habitats of limestone mountains are usually home to a higher number of alpine (s. l.) species than that of the mountains consisting of acidic rocks. The apparent petrophily of several alpine and tundro-alpine species correlates with their sheltering behaviour. The vertical distribution of butterflies is probably influenced also by the competition of closely related species. Closely related species often show some types of habitat partitioning. Data on species numbers and vertical distribution of species are presented in the tables 1-4.

ZUSAMMENFASSUNG.– Die vertikale Verbreitung der arktisch-alpinen, alpinen und balkanischen Orealarten wird hier im Zusammenhang mit den vertikalen Stufenfolgen der Vegetation, den klimatischen Verhältnissen, den geologischen und geomorphologischen Bedingungen, den Vegetationstypen und dem Vorkommen der verwandten Arten behandelt. Die arktisch-alpinen Arten haben meist eine eurasiatische Verbreitung, und sie kommen sowohl in der Arktis und in den alpinen-subnivalen Stufen der mittel- und südeuropäischen Hochgebirge vor. Die alpinen Arten sind meistens auf Europa beschränkt, und sie sind ebenfalls zu den alpinen-subnivalen

Stufen der mittel- und südeuropäischen Hochgebirge gebunden. Die balkanischen Orealarten haben einen südosteuropäschen Arealschwerpunkt. sie kommen jedoch lokal auch in den Südalpen und Süd-bzw. Ostkarpaten vor. Die balkanischen Orealarten kommen am zahlreichsten in der Nähe der Waldgrenze vor, und die Wiesen der oberen subalpinen Stufe gelten als ihre am meisten besiedelte Lebensräume. Die mehr mannigfaltigen Habitate der Kalksteingebirge beherbergen meistens eine höhere Anzahl der alpinen (s. l.) *Arten, als die azidischen Urgesteinsstöcke. Die scheinbare Petrophilie zahlreicher alpinen und tundro-alpinen Arten ist durch ihre spezifische Verhaltensweise bedingt. Die vertikale Verbreitung der Arten ist wohl auch durch die Kompetition der verwandten Arten bedingt. Die nahe verwandten Arten weisen oft eine charakteristische Habitat-Aufteilung auf. Artenzahle und Angaben über die vertikale Verbreitung werden dargestellt (Tabellen 1-4).*

RESUMEN.– *Los autores estudian la distribución de las especies de montaña árticoalpinas, alpinas o balcánicas y su relación con la zonación altitudinal de la vegetación, las condiciones climáticas, el sustrato, el tipo de vegetación alpina y la presencia de especies relacionadas. Las especies árticoalpinas tienen sobre todo un área de distribución euroasiática y se dan tanto en las regiones árticas como en los niveles alpino y subnival de las cordilleras de Europa central y meridional, las cuales presentan morfología glaciar y vegetación alpina. Las especies alpinas son principalmente europeas y están relacionadas con los pisos alpino y subnival de las altas montañas del centro y sur de Europa. Las especies orófitas de los Balcanes son principalmente de Europa sudoriental, si bien algunas de ellas alcanzan puntos meridionales de los Alpes y de los Cárpatos. Dichas especies orófitas de los Balcanes se muestran numerosas en el límite superior del bosque e incluso prefieren los hábitats de pasto en el piso subalpino alto. Los hábitats más diversos de las montañas calizas albergan mayor número de especies alpinas* (s. l.) *que sus homólogos de montañas silíceas. La aparente petrofilia de algunas especies alpinas o de la tundra alpina se correlaciona con el hecho de que allí acuden buscando protección. Seguramente la distribución vertical de las mariposas está influida también por la competencia entre especies estrechamente relacionadas. Estas últimas muestran con frecuencia ciertos tipos de hábitats fragmentados. Finalmente se presetan datos sobre el número de especies y su distribución vertical en las tablas 1 a 4.*

Keywords: Faunal types, alpine, arctic-alpine and Balkanic oreal species, vertical zonation, petrophily, sheltering behaviour, food-plant and habitat preferences, habitat partitioning.

1. Introduction

The paper covers the traditional "macro-Lepidoptera", mostly butterflies (*Papilionoidea* and *Hesperoidea*), as a consequence of the relative abundance of the data. Several important families of "micro-Lepidoptera" are not considered, because we do not have comparable data sets on their vertical distribution in most of the South European high mountains. We follow the conse-

quent distinction in the vertical belts of the biota (see: "*Stufenfolgen*" in WALTER & STRAKA, 1970: 340-341) from the general horizontal zonation. Thus, we have considered here only the *oreal fauna*, i. e. the set of species, which are attached to *orobiomes* (sensu WALTER, 1968; WALTER & BRECKLE, 1991: 15-27). Consequently, the oreal fauna is considered here as a major biogeographical unit in its own right, which is correlated with orographically determined non-arboreal ecosystems (VARGA, 1996).

Alpine vs. xeromontane (eremoreal) faunal types can be distinguished in the European orobiomes (VARGA, 1996). The alpine type, which is characteristic of humid high-mountains, is closely connected with the Quaternary glaciations, resulting in some long-distance area translocations and disjunctions, and, as a consequence, a great number of arctic-alpine disjunct species. Widespread European alpine and European/Eurasiatic arctic-alpine species predominate in the heavily glaciated European high mountains, e. g. in the Northern and Central Alps, Carpathians, etc. On the other hand, there are also numerous stenotopic alpine species which survived the last glaciations in the partially glaciated or unglaciated South European high mountains (e. g. Pyrenees, SW and SE Alps, Balkans).

The xeromontane faunal type prevails in the summer-arid Mediterranean high mountains and the arid high mountains of Western and Central Asia. Its members have a more continuous evolutionary history, less influenced by the Quaternary glaciations. They often have a high potential for speciation in taxonomic groups which are adapted to cold and arid conditions (e. g. many Orthoptera, '*cutworm*' Noctuidae, rodents), and have close connections with the eremic zonobiome. The distribution of the two faunal types overlap in for example the Central (Wallis, Upper Engadin, Upper Inn valley) and SW Alps. There are also areas of overlap in the Balkan high mountains (e. g. Dinarids, Pindos, Pirin, Ali-Botus and Rhodope Mts.), while the xeromontane faunal type predominates in the southern Balkanic mountains, e. g. Parnassos, Tymphrystos, Taigetos, and also in the high mountains of Creta.

Here we discuss the vertical distribution of arctic-alpine, alpine and Balkanic oreal species. The definition of faunal types follows VARGA (1975; 1977, 1996); and the nomenclature of Lepidoptera is after HUEMER & TARMANN (1993) and TOLMAN & LEWONTIN (1997)[1]. The general rules of their distribution can be summarized as follows:

1. Arctic-alpine species have mostly a Eurasian distribution and occur in the Arctic and in the alpine and subnival zones of the Central and Southern European high mountains with expressed glacial morphology and alpine vegetation.

1 The full names of species with Authors and years of original description are presented in the annexed list.

2. Alpine species are mostly European species and similarly to arctic-alpine species are connected to the alpine and subnival zones of Central and South European high mountains. However, they are absent from the arctic tundra and from most Asian high mountains.
3. Balkanic oreal species are mostly southeast European species which also occur in some cases locally in the less glaciated southern parts of the Alps and Carpathians. Their main area of distribution is in the high mountains of the Balkan Peninsula. In Asia Minor, they occur only in the north-west, in the more humid part of the Pontic Mts.

2. Species diversity, substrate, climate and vegetation

Species Numbers

Generally known that the highest number of alpine and arctic-alpine species occur in the mountains which have the most extended alpine and subnival belts, e. g. Central and Eastern Pyrenées, Central Alps, highest massifs of the Southwestern and Southern Alps, Southern Carpathians, highest mountains of the Balkan peninsula (Sar-planina, Korab, Rila, Pirin). Numerous data of vertical distribution of Lepidoptera in the Carpathians and in the Balkanic high mountains have been already published e. g. by ABADJIEV (1992-95), ALEXINSCHI (1960), ALEXINSCHI & KÖNIG (1963), BESHKOV (1995, 2001), COUTSIS & GHAVALAS (2001), DRENOWSKY (1910, 1925), KÖNIG (1959, 1982), KOUTSAFTIKIS (1974), KRZYWICKI (1963), MICHIELI (1963), PAMPERIS (1997), POPESCU-GORJ (1963, 1971), RÁKOSY (1992a, 1992b), SIJARIC (1971, 1980), THURNER (1964), VARGA (1975, 1995), VARGA & SLIVOV (1976) & ZÜLLICH (1936). The species numbers and the extent of glaciations in SE Europe are presented and figured in HOLDHAUS (1954) and VARGA (1995), respectively (Table 1). From these data we can conclude, that the total number of species and the number of endemic species are only partly correlated (see also HUEMER, 1997; WILLIAMS *et al.*, 1999).

Table 1. The numbers of Artic-alpine, Alpine and Balkanic oreal species.

Species	*North Carpathians*	*East Carpathians*	*South Carpathians*	*Crna Gora-N Albania*	*Sar-planina & Korab*	*Rila*	*Pirin*
Arctic-alpine	5	10	9	12	11	8	8
Alpine	19	18	17	19	20	18	16
Balkanic oreal	0	1	2	8	9	9	9
Total	**24**	**29**	**28**	**39**	**40**	**35**	**33**

The connection of the vertical distribution of Lepidoptera with the climatic conditions and vertical zonation of the vegetation

The distribution of oreal species mostly depends on the elevation of the timberline, however, it is often influenced by meso- and micro-climatic conditions. Arctic-alpine and alpine species occur e. g. on the northern slopes of the Carpathians at relatively low altitudes because of a suppression of the timberline due to the unfavourable climatic conditions (e. g. Tatra Mts., Rodna and Retezat Mts.). The overall number of oreal species in the Carpathians (especially in the High Tatra Mts.) is lower than that in the highest mountains of the Balkan peninsula where the extent of the subalpine and alpine zones is much larger (Table 2). In the karstic high mountains the zone-inversion is often observed in the cool, deep valleys or in karstic depressions (called *dolina* or locally called *ponjikve* in the Kroatian mountains).

The vertical belts or «*Stufenfolgen*» (ADAMOVIC, 1909; HORVAT, 1962; WALTER & STRAKA, 1970; GRABHERR *et al.*, 1994) of the vegetation show at least four different major types in the European high mountains. In the Nordic and Central European high mountains the timberline is formed by Coniferous forests. In the Northern and Central Alps the Helvetic type of zonation predominates with a timberline formed by the Spruce (*Picea abies*), often with groups of *Pinus cembra*. In the continental Inner Alpine areas (e. g. parts of Wallis, Upper Engadin, parts of Ötztaler Alps) the Penninian type of zonation is widespread with three different Coniferous belts: a Scotch Pine belt (often with birch), a zone of Spruce and the highest level is predominated by the Larch (*Larix decidua*). In the Submediterranean zone either some variations of the Helvetic type can be observed, e. g. in the Balkans at the uppermost forested belts often with endemic coniferous species: *Pinus heldreichii, P. peuce*, or the Insubric type of zonation occurs with sub-alpine beech forests at the uppermost forested belt, often with inserted tall-grass or scrubby mountain steppe-like formations (Insubric Alps, Dinaric Mts.). Finally, the Mediterranean zone is characterised by some special types of high mountain Coniferous forests (e. g. Balkanic *Abies* species), scrubs, cusheon plant formations and dry grasslands of Oro-Mediterranean type. In the humid high mountains with the Helvetic and Penninian type of vertical zonation the high-lying open biomes are bordered, as a rule, by a nearly continuous timberline. In addition, the zonation of dense alpine scrub- and tall-forb communities («*Krummholz*», scrub-like *Pinus, Juniperus, Betula, Rhododendron* and different *Ericaceae*) typifies the «*Kampfzone*» of arboreal and non-arboreal biomes.

The occurrence of the tundro-alpine and alpine species is usually connected with the Helvetic and Pennini type of vertical zonation. They need the presence of a "true" alpine elevation with adequate types of vegetation (alpine turfs: "*Matten*", cusheon plants, dwarf scrubs of lattice - "*Spalier*" - vegetation, etc.

They reach a southern boundary of occurrence in the Balkan peninsula at the "*Adamovic-line*" due to the basic change of vertical zonation (VARGA, 1975, 1995).

Table 2. List of high mountain Macrolepidoptera occurring in the Rila and Pirin Mts.

Pirin	Rila
Arctic-alpine species	
Pyrgus andromedae	
	Erebia pandrose ambicolorata
Entephria nobiliaria	
Entephria flavicinctata	Entephria flavicinctata
Eupithecia cretaceata fenestrata	Eupithecia cretaceata fenestrata
Glacies coracina bureschi	
	Syngrapha devergens rilaecacuminum
Apamea zeta cyanochlora	Apamea zeta cyanochlora Varga
Apamea maillardi oxygrapha.	Apamea maillardi oxygrapha
Anarta melanopa rupestralis	Melanarta melanopa rupestralis (Hübner, 1799)
	Agrotis fatidica Hübner
Alpine species	
	Pyrgus cacaliae
Boloria pales rilaensis	Boloria pales rilaensis
Euphydryas cynthia drenowskyi	Euphydryas cynthia leonhardi
Erebia oeme vetulonia	Erebia oeme vetulonia
Erebia gorge pirinica	Erebia gorge pirinica
Erebia cassioides macedonica	Erebia cassioides macedonica[2]
Erebia pronoe fruhstorferi	Erebia pronoe fruhstorferi
Entephria cyanata	Entephria cyanata
Nebula tophacearia	Nebula tophaceata
Nebula nebulata	Nebula nebulata
Nebula achromaria	Nebula achromaria
Colostygia aptata	Colostygia aptata
Colostygia aquaeata	Colostygia aquaeata
	Perizoma obsoletarium
Aplocera simpliciata	Aplocera simpliciata
Charissa glaucinaria peruni	Elophos glaucinaria peruni
Mythimna andereggii pseudocomma	Mythimna andereggii pseudocomma
Xestia ochreago	Xestia ochreago
Balkanic-oreal species	
Colias caveasica balcanica	Colias balcanica
Lycaena candens leonhardi	Lycaena candens leonhardi
Boloria graeca balcanica	Boloria graeca balcanica
Erebia orientalis infernalis	Erebia orientalis orientalis
Erebia rhodopensis rhodopensis	Erebia rhodopensis rhodopensis
Erebia ottomana balcanica	Erebia ottomana balcanica
Erebia melas leonhardi	Erebia melas leonhardi
Coenonympha rhodopensis rhodopensis	Coenonympha rhodopensis rhodopensis
Charissa certhiata	Charissa certhiata

2 Erebia cassioides centrorilica Abadjiev, 2001 is considered here as junior synonym of E. cassioides macedonica Buresch, 1918.

The vertical distribution of Balkanic oreal species shows several characteristic differences. Balkanic oreal species are most numerous at the timberline, preferred habitats being grasslands in the upper subalpine belts. Only some few species are connected to the (mostly lower!) alpine elevations (2000-2400 m), and they exceptionally also occur at lower altitudes near to the timberline (*Erebia orientalis, E. rhodopensis, Aplocera simpliciata*). Some other species display a transitional character: They occur predominantly in lower-alpine and sub-alpine elevations with a mosaic-like scrub and grassland vegetation (e. g. in the Pirin Mts: *Pinus mugo* and *Juniperus sibirica* scrubs, *Bruckenthalia spiculifolia* and *Daphne oleoides* dwarf scrubs amd grassy vegetation predominated by *Festuca paniculata* and *Stipa* spp., see: Figure 2), or in steppe-like grasslands with abundant tall-forbs. As species with this character can be mentioned: *Polyommatus eroides, Boloria graeca, Coenonympha rhodopensis, Erebia ottomana, Anaitis lithoxylata, Xestia ochreago*, while other species occur mostly in humid sub-alpine meadows and tall-forb habitats, e. g. *Lycaena candens*. Some Balkanic oreal species and also the xeromontane species (x) are confined to rocky habitats with scarce vegetation, e. g. *Agriades pyrenaicus rebeli* (x), *Erebia melas, Pseudochazara graeca* (x), *P. sintenisi* (x), *P. geyeri occidentalis* (x), *P. graeca* (x), *Elophos certhiatus, Hadena clara macedonica* (x), *H. vulcania urumovi* (x), *Hadena drenovskyi* (x), *Rhyacia nyctimerides stavroitiacus* (x), *Rhyacia* (*Epipsilia*) *cervantes* (x), *Chersotis laeta leonhardti* (x), *Dichagyris* (*Yigoga*) *gracilis etoliae* (x), *Euxoa decora macedonica* (x), etc.

The influence of the substrate and food plants on the vertical distribution

The vertical distribution of butterflies is generally influenced by substrate type and by the vertical belts of vegetation. The occurrence of some arctic-alpine species, e. g. *Melanarta melanopa rupestralis, Pyrgus andromedae* seem to be connected with tundra-like geomorphological formations, as the polygonic soils. Many species prefer the slopes covered by erratic blocks or gravel. The apparent petrophily of several alpine and tundro-alpine species correlates with their sheltering behaviour under unfavourable weather conditions, e. g. in daily active geometrid species, as *Pygmaena fusca, Sciadia tenebraria* and several species of the genus *Glacies* or in some *Titanio* species (*Pyralidae*).

The food plants of arctic-alpine butterflies and moths are often cushion plants and low herbaceous plants such as species of *Androsace* (e. g. *Elophos* and *Glacies* spp.), *Dianthus, Gentiana, Plantago* (e. g. *Euphydryas cynthia*), *Silene* and *Viola* (e. g. *Boloria pales*), or grasses (e. g. *Erebia* spp. and *Apamea* spp.). Vegetation and surface type can also provide shelter from cold and rain; e. g. in high altitudes of Pirin Mts. (Bulgaria) *Pyrgus andromedae* was observed

under cushions of *Dryas octopetala*. We have observed that *Boloria pales*, *Euphydryas cynthia*, *Erebia orientalis* and *E. rhodopensis* regularly overnight under dwarf scrubs of *Juniperus nana*. Other species, e. g. *Erebia gorge*, *E. melas*, *Entephria nobiliaria*, *Glacies coracina*, etc. shelter under stones.

Habitat preferences

The habitat preferences of alpine species are rather diverse. The more diverse vegetation of limestone mountains is usually home to a higher number of alpine species of Lepidoptera than that of the mountains consisting of acidic rocks. Examples include the calcareous Belanské Tatry vs. the granite-gneiss High Tatra of the western Carpathians: *Erebia pharte*, *Calostygia austriacaria* and *Glacies noricana* occur only in the calcareous Belanské Tatry. The calcareous conglomerate summits of the Bucegi Mts. are inhabited by much more alpine species than the granite-gneiss Fagaras Mts. in the Southern Carpathians. *Zygaena exulans*, *Erebia pronoe*[3], *Glacies coracina*, *G. noricana* and *Grammia quenselii* e.g. occur only in the Bucegi massif. Similarly, *Boloria pales*, *Entephria nobiliaria*, *E. cyanata* Hübner and *Glacies coracina* Esper occur only in the calcareous Vichren-Kutela group and are lacking in the granitic parts of the Pirin Mts. Some species with typical alpine distribution occur mostly in the humid sub-alpine or lower alpine grasslands near to the timberline, e.g.: *Erebia epiphron*, *E. manto*, *E. pharte*, *E. eriphyle*, *E. melampus*, *E. sudetica*, *E. albergana*, *Psodos quadrifarius*, etc. Outside the Alps, some of these species (*Erebia epiphron*, *E. manto*, *E. pharte*, *E. sudetica*, *Psodos quadrifarius*) occur also in similar habitats of the Carpathians.

However, they are absent or rather sporadically occur in the Balkan high mountains, because of the lack of suitable habitats, with the exception of *E. epiphron* which seems to be fairly widespread in the W Balkans, and also has a sister species, *E. orientalis* (subdivided into three subspecies: *E. o. orientalis* in Rila, *E. orientalis infernalis* in the Pirin Mts. and *E. orientalis macrophthalma* in the central Stara Planina) in the eastern Balkan high mountains. *E. manto* (as *E. manto osmanica*) occurs exclusively in the Dinarids of Bosnia, *E. albergana* (as *E. albergana phorcys*) only at moderate altitudes (1200-1600 m) near to the beech-forest timberline, on the southern slopes of the central Stara Planina.

Many other alpine species are connected to the rocky and gravelly habitats with scarce vegetation, e. g. *E. gorge* (widespread in European high mountains), *Erebia pluto* De Prunner (Alps, Central Appenines), *E. lefebvrei*

3 Erebia pronoe (as *E. p. regalis* Hormuzachi) occurs also in the calcareus Piatra Craiului.

Boisduval (Pyrenées, Cantabrian Mts.), *E. melas* Herbst (Balkans, Slovenian Karst, Southern and Eastern Carpathians, Mti Apuseni); most species of the genera *Glacies*, *Elophos* and *Charissa* (Geometridae).

Habitat partitioning in closely related species

The vertical distribution of butterflies is probably influenced also by the competition of closely related species. We have only very scattered data on the butterfly assemblages (e. g. the detailed publications of BALLETTO *et al.* 1982a, 1982b) and on the horizontal vs. vertical movements of butterflies in the European mountains. The interpretation of vertical creeps and shifts is based mostly on anecdotic informations and only rarely on the analysis of abiotic vs. biotic factors. It would be necessary to form a data-basis from literary and museal data, and to compare it with the results of recent surveys, carried out in high mountains of different geographical latitudes.

Closely related species often show different types of habitat partitioning. A humid vs. dry partitioning, combined with some vertical shifts, characterises the sibling species of the *Boloria pales*-species group (Figure 1). A typical sward vs. gravel partitioning has been observed for example in *Erebia mnestra* (grasslands) and *E. gorge* (gravel) in the western Central Alps, in *E. rhodopensis* (grasslands) and *E. gorge* (gravel) in the Balkans.

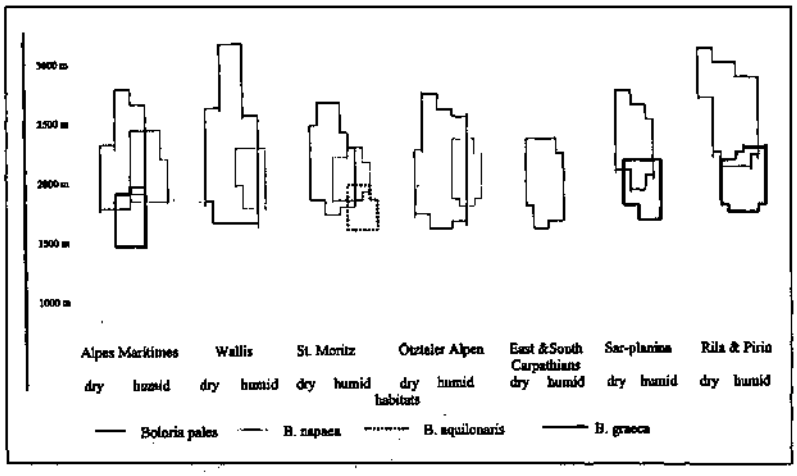

Figure 1. Vertical distribution of the sibling species of the Boloria pales species-group in different European high mountains.

Table 3. Vertical distribution (in 1000 m´s) of some butterfly and day-flying moth species in the Carpathians and in some high mountains of the Balkan Peninsula.

Species	*Tatra*[4] *Mts.*	*Bucegi Mts.*	*Retezat Mts.*	*Durmitor Mts.*	*Sar-planina*	*Rila Mts.*	*Pirin Mts.*
Zygaena exulans		2.0-2.3		2.1-2.45	2.1-2.6		
Pyrgus cacaliae		1.9-2.3				2.2-2.7	
Pyrgus andromedae				2.2-2.5	2.3-2.7		2.5-2.7
Boloria pales	1.6-2.3	1.8-2.4		1.95-2.3	2.2-2.65	2.2-2.7	2.4-2.8
Boloria graeca				1.7-2.1	1.8-2.25	1.6-2.3	1.7-2.3
Euphydryas cynthia						2.2-2.7	2.4-2.8
Erebia epiphron	1.3-1.9	1.5-2.2	1.35-2.3	1.7-2.2	2.1-2.6		
Erebia orientalis						2.1-2.7	2.3-2.7
Erebia sudetica		1.5-1.7	1.6-1.95				
Erebia pharte	1.6-2.1		1.5-2.1				
Erebia manto	1.1-1.7	1.25-2.1	1.3-2.1				
Erebia gorge	1.7-2.3	1.8-2.45	1.8-2.35	1.9-2.35	2.1-2.7	2.2-2.75	2.4-2.9
Erebia rhodopensis					2.1-2.5	2.2-2.7	2.1-2.6
Erebia melas			1.8-2.1	1.6-2.1	1.7-2.35	1.7-2.2	1.55-2.55
Erebia cassioides			1.55-2.1	1.9-2.3	1.95-2.5	2.2-2.6	2.3-2.6
Erebia ottomana				1.55-2.1	1.7-2.1	1.65-2.25	1.7-2.35
Erebia pronoe		1.5-2.1		?	?	1.85-2.3	2.1-2.3
Erebia pandrose	1.75-2.3	2.1-2.4	1.8-2.4	2.1-2.4	2.1-2.6	2.3-2.75	
Anaitis simpliciata			1.8-2.2	1.6-2.3	1.7-2.3	1.9-2.5	1.95-2.55
Psodos coracinus	1.9-2.1	2.1-2.3	1.9-2.5		2.5-2.7		2.5-2.9
Psodos canaliculatus		1.9-2.3	1.85-2.3	2.1-2.5			
Psodos bentelii		2.1-2.3	2.15-2.4				
Grammia quenselii		2.3-2.4					
Syngrapha devergens						2.3-2.7	

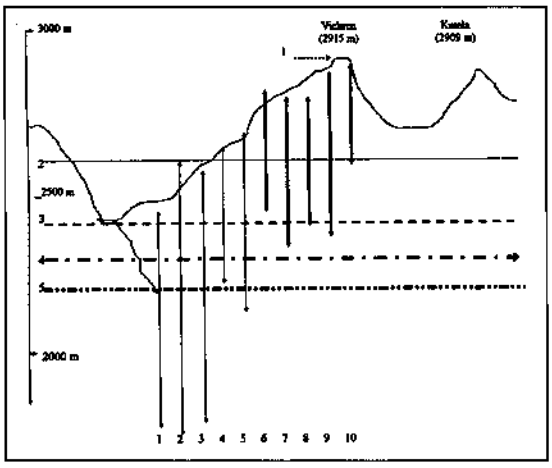

Figure 2. Important limits of vegetation and vertical distribution of Lepidoptera in the Pirin Mts. (Bulgaria).

4 Incl. Belanské Tatry.

Table 4. Vertical distribution of alpine - balkanic-oreal species pairs.

Mountains	Alpine	Balkanic I	Balkanic II
	Boloria pales	*Boloria graeca*	
Tatra Mts.	1600-2300 m		
Piatra Craiului	1700-2100 m		
Bucegi	1800-2400 m		
Durmitor	1950-2300 m	1700-2100 m	
Sar-planina	2200-2650 m	1800-2250 m	
Rila	2200-2700 m	1600-2300 m	
Pirin	2400-2800 m	1700-2300 m	
N Pindos		1700-2100 m	
	Erebia cassioides	*Erebia ottomana*	
Retezat Mts.	1550-2100 m		
Durmitor	1900-2300 m	1550-2100 m	
Sar-planina	1950-2500 m	1700-2100 m	
Rila	2200-2600 m	1650-2250 m	
Pirin	2300-2600 m	1700-2350 m	
Rodopi Mts.		1600-2100 m	
N Pindos		1700-? m	
	Erebia gorge	*Erebia melas*	*Erebia rhodopensis*
Tatra Mts.	1700-2300 m		
Bucegi	1800-2450 m		
Piatra Craiului	1850-2200 m		
Retezat	1800-2350 m	1800-2100 m	
Durmitor	1900-2350 m	1600-2100 m	
Sar-planina	2100-2700 m	1700-2350 m	2100-2500 m
Rila	2200-2750 m	1700-2200 m	2200-2700 m
Pirin	2400-2900 m	1550-2550 m	2100-2600 m
N Pindos		1700-2300 m	1900-2300 m

The vertical distribution of the alpine species displays a characteristic trend. While they often occur in the Alps and Carpathians near (and not exclusively above) the timberline, their distribution is essentially higher in the Balkan mountains (DRENOVSKY, 1925; RÁKOSY, 1992a, b; VARGA, 1975; Table 3, Figure 2). They do not occur at the sub-alpine meadows, at the clearings of the uppermost coniferous zone or of the *'krummholz'* belt. These habitats are populated by the Balkanic oreal group of species (Figure 2). The Balkanic oreal butterfly species populate mostly the tall-grass dry grasslands near the timberline (e. g. *Festucetum paniculatae, Stipa* grasslands), e. g. *Boloria graeca, Erebia orientalis, E. rhodopensis, E. ottomana* as do numerous typical Balkanic Orthoptera species such as *Psorodonotus* spp. and *Anterastes serbicus*. The Balkanic endemic *Pinus* species, *P. heldreichii* and *P. peuce* form open stands

and Balkanic oreal butterfly and grasshopper species regularly occur in the natural clearings of these forests near the timberline. At these elevations normally no arctic-alpine and alpine species occur. It is not clear, that this is the consequence of the differences of the habitats or the effect of some kind of competitive exclusion (Table 4, Figures 2, 3).

Some other Balkan oreal species are connected to rocky habitats. The species of the genus *Erebia* display many interesting combinations of vertical and habitat type (swards vs. rocky habitats) partitioning. Species of the *Erebia pluto* group and the ecologically similar *E. melas* are shown in five mountains. In many areas of the Alps, Carpathians, Balkan high mountains more species occur sympatrically, but with restricted habitat overlaps. *E. cassioides neleus*, for example, has a relatively wide sub-alpine to alpine range (1550 m - 2100 m) in the Retezat Mts., where the Balkanic *E. ottomana* does not occur, while the Balkanic subspecies *E. neleus macedonica* seems to be restricted to the alpine zone (2200 m - 2600 m) in the Rila and Pirin Mts., where the sub-alpine zone is occupied by large populations of *E. ottomana*. The only ecologically closely related Balkanic *E. melas* shows a nearly complete vertical exclusion with the taxonomically not very closely related alpine *E. gorge* in many Balkanic high mountains. *E. gorge* is

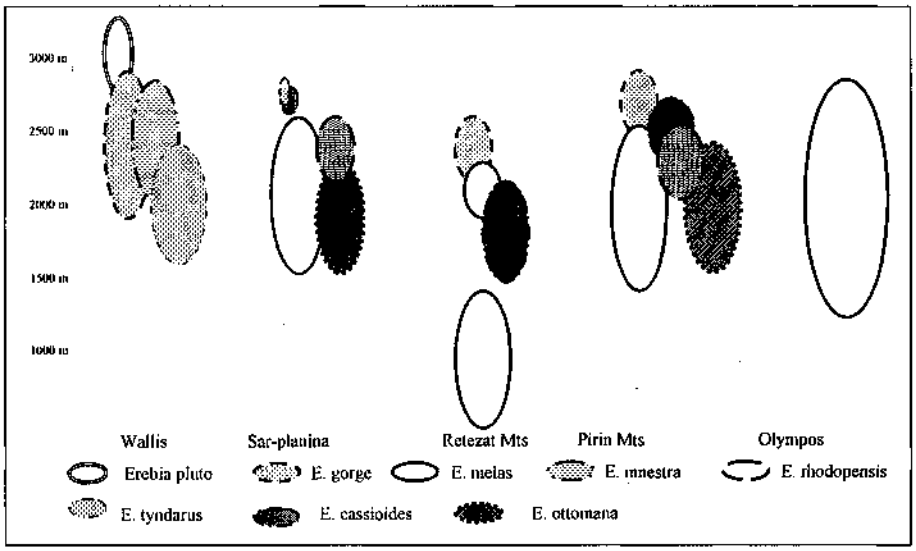

Figure 3. Vertical distribution of the species of the *Erebia pluto* and *E. tyndarus* species-groups in different European high mountains.

restricted to the alpine zone, where the montane/sub-alpine *E. melas* does not occur. On the contrary, in the Olympus Mts., where no other *Erebia* spp. occur, *E. melas* occupies a wide range of rocky habitats, to the highest alpine levels.

We cannot claim, on the basis of these rather anecdotal data, to demonstrate the existence of competitive exclusion, however, there is a clear indication of some geographical trends.

Acknowledgements. The paper is dedicated to the memory of the late professors Z. LORKOVIC (Zagreb) and S. MICHIELI (Ljubljana), who introduced me into the study of the Balkan high mountain Lepidoptera. Authors are highly indebted to Dr. A.V. SLIVOV for his kind helpfulness during our study trips in the high mountains of Bulgaria, to Dr. L. VILLAR for the translation of the *Resumen* and helpful suggestions, to Mr. L. NAGY for linguistic corrections and to Mr. P. KOZMA for technical assistance.

List of arctic-alpine, alpine, Balkanic oreal and xeromontane species, mentioned in the text

Zygaenidae: *Zygaena exulans* (HOHENWARTH, 1792)

Hesperiidae: *Pyrgus andromedae* (WALLENGREN, 1853), *Pyrgus cacaliae* (RAMBUR, 1840)

Pieridae: *Colias caucasica balcanica* REBEL, 1903

Nymphalidae: *Boloria pales pales* (DENIS *et* SCHIFFERMÜLLER, 1775), *B. pales contempta* (REBEL *et* ZERNY, 1931), *B. pales rilaensis* VARGA, 1972, *Boloria graeca balcanica* (REBEL, 1903), *Euphydryas cynthia cynthia* (DENIS *et* SCHIFFERMÜLLER, 1775), *E. cynthia drenowskyi* (RÖBER, 1926), *Euphydryas cynthia leonhardi* (FRUHSTORFER, 1917), *Erebia manto manto* (DENIS *et* SCHIFFERMÜLLER, 1775), *E. manto osmanica* SCHAWERDA, 1909, *E. manto trajanus* HORMUZACHI, 1895, *Erebia epiphron* (KNOCH, 1783), *Erebia orientalis orientalis* ELWES, 1900, *Erebia orientalis infernalis* VARGA, 1972, *E. orientalis macrophthalma* VARGA, 1999, *E. melampus* FUESSLY, 1775, *Erebia sudetica sudetica* STAUDINGER, 1861, *Erebia pharte pharte* (HÜBNER, 1804), *E. pharte eupompa* FRUHSTORFER, 1918, *E. pharte belaensis* GOLTZ, 1937, *E. eriphyle* (FREYER, 1839) *Erebia albergana phorcys* (FREYER, 1836), *Erebia oeme spodia* STAUDINGER, 1871, *Erebia pluto* DE PRUNNER, 1798, *Erebia gorge gorge* (HÜBNER, 1804), *E. gorge hercegovinensis* REBEL, 1903, *E. gorge pirinica* BURESCH, 1919, *E. gorge fridericikoenigi* VARGA, 1999, *Erebia*

mnestra (HÜBNER, 1804), *Erebia rhodopensis rhodopensis* NICHOLL, 1900, *Erebia ottomana balcanica* REBEL, 1903, *E. ottomana drenovskyi* VARGA, 1976, *Erebia cassioides cassioides* (HOCHENWARTH, 1792), *E. cassioides illyrica* LORKOVIC, 1933, *E. cassioides illyromacedonica* LORKOVIC, 1933, *E. cassioides macedonica* BURESCH, 1919 (= *E. cassioides centrorilica* BESHKOV, 2001), *E. cassioides kinoshitai* BESHKOV, 1996, *Erebia melas melas* (HERBST, 1796), *E. melas leonhardi* FRUHSTORFER, 1918, *E. lefebvrei* (BOISDUVAL, 1828), *Erebia pronoe pronoe* (ESPER, 1780), *E. pronoe fruhstorferi* WARREN, 1936, *Erebia pandrose* (BORKHAUSEN, 1788), *E. pandrose ambicolorata* VARGA, 1972, *Coenonympha rhodopensis rhodopensis* ELWES, 1900, *Pseudochazara graeca* (STAUDINGER, 1870), *P. geyeri occidentalis* (REBEL *and* ZERNY, 1931)

Lycaenidae: *Lycaena candens leonhardi* (FRUHSTORFER, 1917), *Agriades glandon* (DE PRUNNER, 1798), *A. pyrenaicus* (BOISDUVAL, 1840); *A pyrenaicus rebeli* (TULESCHKOW, 1932)*Polyommatus eroides* (FRIVALDSZKY, 1835)

Geometridae: *Entephria nobiliaria* (HERRICH-SCHÄFFER, 1852), *Entephria cyanata* (HÜBNER, 1809), *Entephria flavicinctata* (HÜBNER, 1813), *Nebula tophaceata* (DENIS *et* SCHIFFERMÜLLER, 1775), *Nebula nebulata* (TREITSCHKE, 1828), *Nebula achromaria* (DE LA HARPE, 1853), *Perizoma obsoletarium* (HERRICH-SCHÄFFER, 1838), *Colostygia aptata* (HÜBNER, 1813), *Colostygia aquaeata* (HÜBNER, 1813), *Eupithecia cretaceata fenestrata* MILLIERE, 1874, *Aplocera simpliciata* (TREITSCHKE, 1835), *Aplocera lithoxylata* (HÜBNER, 1813), *Pygmaena fusca* (THUNBERG, 1792), *Charissa glaucinaria peruni* (VARGA, 1975), *Charissa certhiata* (REBEL *et* ZERNY, 1931), *Sciadia tenebraria* (ESPER, 1806), *Glacies coracina bureschi* VARGA, 1975, *Glacies noricana* (WAGNER, 1898), *Psodos quadrifarius* (SULZER, 1776)

Arctiidae: *Grammia quenselii* (PAYKULL, 1791)

Noctuidae: *Syngrapha devergens rilaecacuminum* VARGA *et* RONKAY, 1982, *Apamea zeta cyanochlora* VARGA, 1977, *Apamea maillardi oxygrapha* VARGA, 1977, *Apamea michielii* VARGA, 1977, *Mythimna andereggii pseudocomma* (REBEL *et* ZERNY, 1931), *Hadena clara macedonica* BOURSIN, 1959 *(x)*, *H. vulcania urumovi* (DRENOVSKY, 1931) *(x)*, *Hadena drenovskyi* (REBEL, 1930) *(x)*, *Melanarta melanopa rupestralis* (HÜBNER, 1799), *Mythimna andereggi pseudocomma* (REBEL *et* ZERNY, 1931), *Xestia ochreago* (HÜBNER, 1909), *Rhyacia nyctimerides stavroitiacus* (Tuleschkow, 1950) *(x)*, *Dichagyris (Yigoga) gracilis etoliae* DUFAY, 1971, *Rhyacia (Epipsilia) cervantes* REISSER, 1935 *(x)*, *Chersotis laeta leonhardti* (REBEL,1904) *(x)*, *Euxoa decora macedonica* THURNER, 1936 *(x)*,

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