

## BIOGEOGRAPHY AND EVOLUTION OF OREAL LEPIDOPTERA IN THE PALAEARCTIC

Z. VARGA

Department of Zoology and Evolution, Kossuth L. University  
H-4010 Debrecen, Hungary

The concept of the orear fauna can be defined as that typifying orographically caused non-arboreal biomes. It is considered here as a major biogeographical unit in its own right, not only as a component of the oreotundral fauna. The orear fauna is correlated with orographically determined non-arboreal ecosystems and its members have, as a rule, insular, often strictly endemic or disjunct areas of distribution. Its chorological centres can be regarded mostly as only potential centres of dispersal. They can be recognised by accumulated occurrence of stenochorous species and by the high species-diversity of some typical genera. The orear fauna can be subdivided into an *alpine* type, as the faunal type of humid high mountains with prevailing glacial morphology and with strong connections to the tundra zonobiome, and *xeromontane* type, as the faunal type of arid high mountains with prevailing physical weathering and with manifold connections to the *eremic* zonobiome. The formation of the *alpine* faunal type is closely connected to the Quaternary glaciations. Its history can be characterised by long-distance translocations and disjunctions, resulting in a great number of arctic-alpine species. On the contrary, the *xeromontane* faunal type displays a more continuous evolutionary history extending far back into preglacial times and also demonstrates a high potential for speciation in such groups which are adapted to the cold-arid conditions. A major part of the *xeromontane* fauna appears to have been stationary with a great number of relict-like species, especially in some core areas of Central and Inner Asia. *Xeromontane* species could only populate Central and Northern Europe during the extreme continental late-glacial and early post-glacial phases. In Europe and adjacent areas, most *xeromontane* species occur in the summer-dry Mediterranean high mountains from the Atlas to Asia Minor. The *xeromontane* fauna can be subdivided into a W Palaearctic (Mediterranean-*xeromontane*) and a Central- and Inner-Asiatic (Continental) subtype. This bifurcation arose through the influence of a "xeromontane filter" on a set of ancestral species coming mostly from seasonally humid, southeastern Asiatic mountains. Thus, the fauna of subtropical, monsoonic orobiomes (e.g. in southern China and the Himalaya region) displays a somewhat intermediate, less differentiated (ancestral) character. The core areas of allopatric speciation, dispersal and evolutionary history of Palaearctic *xeromontane* Noctuidae are considered.

Key words: biogeography, orear fauna, core areas, alpine type, *xeromontane* type, Palaearctic *xeromontane* Noctuidae

### OREAR FAUNA: CONCEPTS, PRINCIPLES AND DEFINITIONS

#### *Zonobiomes and orobiomes*

The fauna of high mountains deserves special attention as a kind of continental-insular fauna. It presents us with an important source for the study of the spatio-temporal aspects of evolution.



In lowlands the biotic composition of the most recent faunal range extensions predominate interacting with the prevailing zonobiomes. Even minor differences in the relief, e.g. canyon-like, deep, rocky valleys in table-lands, gorges or step-like escarpments of plateaux can result in a heterogeneity of the general faunal picture. The compositional homogeneity of the prevailing zonobiome breaks down in response to narrow-scale environmental factors which promote the survival of relict-like populations. We observe essentially the same phenomena in mountainous regions, where the macroclimatically influenced zonal arrangement of major biomes is disturbed by orographic factors. These conditions are expressed in the high biotic diversity within a limited area and in the coexistence of different faunal types. Some of them are relicts of more ancient faunal invasions, which have survived in restricted refuges. They are, as a rule, often members of relict-like communities or community fragments, that were more widely distributed in some former phases of the Quaternary climatic fluctuations. During climatic oscillations the more successful fraction of such previously restricted populations can irradiate, hence mountains also often serve as centres of dispersal. Thus, several components of orobiomes could be transformed during their evolutionary history into components of zonobiomes. These facts provide the basis for several ideas concerning the origin and history of tundra, taiga and steppe zonobiomes (e.g. ANDER 1949, BORBÁS 1908, HEPTNER 1959, PETERSEN 1954, SOÓ 1929, 1940, 1959, STEGMANN 1932, 1938 1958, VARGA 1975a, b, 1989a, c, 1995b, ZÓLYOMI 1949, 1953, 1964).

#### *The concept of the oreal fauna*

The fauna specific to high mountains is often referred to as the "*oreal fauna*" in the zoogeographical literature, although mostly without a satisfactory definition of this notion. I will try to place this concept within the context of the basic of the biomes division.

Biomes not only represent types of ecosystems, but also types of primary production. Perhaps the most striking feature of the biosphere, shown on the map of RODIN & BAZYLEVICH (1965), is the relatively sharp delimitation of the regions with a rather low (i.e. less than  $25 \text{ g ha}^{-1}$  per year) level of primary production, caused by the restriction of the water circulation to less than 3 months per year (BUDYKO 1977). Essentially the same picture is presented on the map based on the life-zone concept of HOLDRIDGE (1962, see GROOMBRIDGE 1992). If we define all these regions of low bioproduction as "*non-arboreal*", as opposed to the *arboreal* ones (where primary production is more than  $25 \text{ g ha}^{-1}$  per year), we can define the oreal fauna as "*the faunal types of orographically caused non-arboreal biomes*" (VARGA 1975a, 1995b: Table 1).

This paper discusses the general features of distribution and faunal history of Palaearctic oreale Lepidoptera. A detailed analysis of the patterns of speciation



in xeromontane Noctuidae with a survey of their biogeographical types will be presented in a subsequent paper.

#### *Oreal and tundra fauna*

Here I recognise the oréal fauna as a main zoogeographical unit, not only as a component of the "*oreotundra*" one (cf. DE LATTIN 1967), although a very intimate geographical and historical connection between the tundra and oréal biomes is evident. Their interaction can be seen during the entire Quaternary period as a vast faunal mixing in the periglacial belts still continuing at present along the mountain ranges of Eastern Siberia and Pacific North America (Fig. 1).

On the other hand, one also has to consider the main differences between tundra and oréal faunas. The tundra fauna belongs to one of the major zono-biomes, and most of its members have a circumpolar or amphi-Beringian distribution (the possibility of an amphi-Atlantic connection is rejected, see KONONENKO *et al.* 1989, LAFONTAINE & WOOD 1988, MIKKOLA 1987, MIKKOLA *et al.* 1991). The oréal fauna, in contrast, is essentially not of a zonal nature. Its members are connected to numerous orographically determined ecosystems and they occur, as a rule, in spot-like, "insular", often highly endemic or widely separated areas, with an essentially higher diversity of areal types (i.e. "faunal elements" in the German tradition), than the members of the generally more uniform tundra fauna (the exceptional position of Beringia is discussed in several recent papers of KONONENKO *et al.* 1989, LAFONTAINE & WOOD 1988 and MIKKOLA *et al.* 1991, see above). The frequently discussed arctic-alpine (or tundra-alpine) distribution is only a specific case of formerly expansive, but recently restricted and disrupted distribution ranges, occurring equally well as convergent area regressions in species of oréal and tundra origin, or sometimes having closely related sibling species in such areas (EHRlich 1958, PETERSEN 1954, VARGA 1989c, 1995a, b, c).

There are, however, extended oréal biomes without any connection or any compositional or physiognomical similarity to the tundra ones, e.g. the *puna* vegetation, the tall Compositae-Euphorbiaceae formation in East African high mountains, the xerophytic "polster"-scrub vegetation in the mountains of the Middle East and Central Asia etc. (AGACHANJANTS 1981, BRECKLE 1974, MÜLLER 1977, VUILLEUMIER 1970, VUILLEUMIER & SIMBERLOFF 1980, WALTER & BRECKLE 1986). The oréal biomes which have no or rather poor connections with tundra ones (i.e. most of the arid or at least seasonally arid oréal biomes), are usually not delimited by a timberline, or (depending on the exposition) only by a rather scattered one (AGACHANJANTS 1981, WALTER & BRECKLE 1986). At the same time they usually have manifold contacts with deserts and semi-deserts (i.e. eremial biomes) and/or with the seasonally dry, unforested or only sparsely forested arboreal biomes (e.g. tall-grass steppe, savanna, some Mediterranean



xerophytic formations). Thus, the widely accepted definition of the orear biomes: "biomes above the timberline" is unsatisfactory for similar reasons (VARGA 1975a, b, 1977).

#### *Survival and evolution of the orear fauna*

In the zoogeographical literature – influenced by the polemic sentences of some classic works (DANSEREAU 1957, DARLINGTON 1959, UDVARDY 1981 vs. CROIZAT 1978, CROIZAT *et al.* 1974, PLATNICK & NELSON 1978, ROSEN 1978) – a rather fruitless conflict of the categorical migrationist vs. the conservationist-vicarist views has taken place (see also: IABLOKOFF-KHNZORIAN 1968 vs. KRYZHANOVSKY 1969 on the origin and evolution of alpine Coleoptera). This debate is essentially similar to that over the faunal history of islands. It means that the faunal history of high mountains can also be described and discussed in terms of colonisation and survival vs. extinction and evolution (see also MACARTHUR & WILSON 1963, 1967, VUILLEUMIER 1970, 1973).

Careful analyses of the European arctic-alpine insects (ANDER 1949, AS-PÖCK 1963, BURESCH & ARNDT 1926, HOLDHAUS & LINDROTH 1939, HOLDHAUS 1954, WARNECKE 1959, VARGA 1989c, 1995a) have shown that the faunal diversity of an isolated mountain range depends in some cases on the distance from the "source" of the colonisation (see also: interaction between distance, survival and diversity, MACARTHUR & WILSON 1963, 1967). The comparatively low NW Dinarids, which also have a relatively small extension but lie near to the SE Alps, have e.g. a rich fauna of terricolous (often petrophilous) insects with low mobility (e.g. small, flightless Carabidae, see HOLDHAUS 1954, HOLDHAUS & LINDROTH 1939, MARAN 1946 etc.).

In other cases, conditions favourable for survival seem to be more significant, e.g. the more remote, but extensive and high massifs of the Balkan peninsula (Rila, Pirin, Šar-planina etc.) are much richer in alpine and tundra-alpine butterflies and "macro"-moths than the Dinarids or the Carpathians (VARGA 1975b, 1995a). The concept of "better survival" often implies the possibility of further evolutionary differentiation, leading either to more or less differentiated allopatric subspecies or to "autochthonous" neo-endemic species, often vicariants to related ones isolated in some other remote massifs (MARAN 1946, VARGA 1975a, 1989c).

Whether only a geographical subspeciation within the range of a widely distributed polytypic species, or a "punctuational" emergence of rapidly evolved species-flocks takes place, depends mainly on the tempo of the evolutionary changes in the group studied. The examples of the classical ("dumbbell model") geographical subspeciation are present in numerous families of "Macrolepidoptera", Orthoptera, passerine birds etc., while the latter are represented by numerous torrenticolous insects (e.g. the trichopteran genera *Drusus*, *Plectrocnemia*,



*Rhyacophila*), by the petrophilous Carabidae and land snails, e.g. the limestone-rock inhabiting *Alopi*a species in the East Carpathians (BOTOSANEANU 1962, HOLDHAUS 1954, MARAN 1946, SOÓS 1943, VARGA 1995a, b).

In summary, one may believe that mountain faunas provide several possibilities for both phenomena: survival of relict species belonging to ancient biota and – according to the *founder principle* – for rapidly evolving, “*peripatric*” neo-endemics. Both main types of “*allopatric*” (I prefer the term “*area-dynamic*”, as opposed to the stasipatric model of speciation) evolution can be regularly observed:

- *refugial isolation* connected with evolving vicariant taxa by area regression and disjunction;
- *isolation by dispersal* (“post-dispersal”, more exactly “propter”-dispersal) connected with the peripheric fluctuation of the range (VARGA 1971).

#### *Faunistical and biogeographical survey of Palaearctic Noctuidae*

The facts on which the following discussions and conclusions are based, come from two main sources.

The taxonomy and distribution of the European Noctuidae is relatively well-known. We have numerous check-lists from different parts of Europe (BOURSIN 1964, LERAUT 1980, HACKER 1990, TARMANN & HUEMER 1993 etc.), as well as some check-lists of all European species (HARTIG & HEINICKE 1973, FIBIGER & HACKER 1990). In recent years a monographic book series and an atlas of distribution maps have been started as well (FIBIGER 1990, 1994, RONKAY & RONKAY, 1994, 1995, SVENDSEN & FIBIGER 1993). There is much information on the Noctuidae of the Palaearctic (Mediterranean) Northern Africa and Asia Minor, too (e.g. HACKER 1986, 1987, 1990, HACKER *et al.* 1986, 1988, HACKER & WEIGERT 1986, RUNGS 1945, 1972, 1981, WILTSHIRE 1948, 1957). Data from huge areas of Asia are much more incomplete and scattered. Many species are known only from a few type specimens collected during the last decades of the 19th century and preserved in some “classic” collections (e.g. STAUDINGER, PÜNGELER and BANG-HAAS collections in the Zoological Museum of the Humboldt University in Berlin, many famous collections in The Natural History Museum, London, the collection of the Grand Duke NIKOLAI MICHAJLOVICH ROMANOFF in St. Petersburg, the CORTI collection in the Natural History Museum of Basel etc.).

After a long period of very scattered collecting in the first half of this century, the surveys of Palaearctic Noctuidae were intensified during the 1960s and the 1970s by systematic collecting trips with more modern tools (portable generators, mercury vapour lamps, fluorescent tubes) by several highly qualified entomologists in different parts of Western and Central Asia (Turkey, Armenia, Iran, Afghanistan, Pakistan, Mongolia e.g. by G. EBERT, G. FRIEDEL, F. KASY, Z.



KASZAB, C. M. NAUMANN, R. PINKER, J. PLANTE, E. VARTIAN) and by the immense taxonomical achievements of CH. BOURSIN. However, the majority of this material could only be evaluated during the last two decades, after the death of BOURSIN. Because the collection and taxonomic notes of this author unfortunately have become practically inaccessible in the meanwhile, the specialists who tried to continue his work were forced to re-study all the type materials originally examined and photographically documented by him.

These difficulties became, however, the starting block for new revisions with a more up-to-date attitude and with more sophisticated methods (e.g. the new information coming from the "lock-and-key" structures of the everted inner genitalia of both sexes: LAFONTAINE & MIKKOLA 1987, MIKKOLA 1992). The geopolitical changes of the last twenty years had two outcomes. Large areas became inaccessible to entomologists due to political unrest (e.g. SE Turkey, Afghanistan, Tibet), but very important new material could be collected by several expeditions and also by indigenous collectors in many parts of the former Soviet Union (e.g. Turkmenistan, Kazakhstan, Kyrgyzstan, Uzbekistan, Tadjikistan, Siberian parts of Russia), in Pakistan, Northern India, Nepal, Mongolia, Korea, Taiwan etc.

Due to these recent faunistic investigations carried out in many, hitherto very poorly studied parts of Eurasia, a vast amount of new information on the taxonomic composition and geographical distribution of the Palaearctic noctuid fauna was obtained. The survey of these several tens of thousands of noctuid specimens resulted in the description of several hundred new species and thousands of data on the distribution of hitherto incompletely known species. This descriptive and data collecting work occurred during a very intensive phase (see: References). Due to the description of a very large number of new species and by the study of many taxonomically incompletely known or misinterpreted species, some monographic studies have been started on taxonomically complicated and highly diverse genera of Noctuidae. Thanks to these monographs, we can now understand better the evolutionary processes and phylogeographic relations in many groups of Noctuidae. A new, "post-BOURSIN" generation of noctuid specialists has emerged, for whom team-work and close cooperation is natural. This is the reason why a large part of the distributional data of Noctuidae materials preserved in different museums and private collections could be taken into consideration for the purposes of the present paper.

#### *Taxonomic revisions of Palaearctic Noctuidae*

The extraordinary richness of the new noctuid material, and the favourable conditions for a close cooperation in taxonomical surveys, made possible the publication, during the last ten to fifteen years, of a large number of longer revisional papers on many complicated and taxonomically-phylogenetically import-



ant genera (*Trichosilia*, *Eugnorisma*, *Xestia* [subg. *Anomogyna*, *Pachnobia*, *Schoyenina*,] *Xenophysa*, *Lasionycta*, *Hadena*, *Bryopolia*, *Bryoxena*, *Cucullia*, *Polymixis*, *Auchmis*, *Pseudohadena*, *Victrix* etc.) of Palaearctic/Holarctic Noctuidae (BEHOUNEK 1992, HACKER 1992a, 1995, HACKER & RONKAY 1991, 1992, HARDWICK 1970, HREBLAY 1992, 1994a, b, 1995, HREBLAY & RONKAY 1994, HREBLAY *et al.* 1994, LAFONTAINE 1981, 1987, LAFONTAINE & KONONENKO 1986, LAFONTAINE *et al.* 1983, 1986, MIKKOLA *et al.* 1987, RONKAY 1986, 1989, RONKAY & RONKAY 1994, 1995, RONKAY & VARGA 1989, 1990a, b, 1993a, b, RONKAY *et al.* 1995, VARGA 1983, 1989b, VARGA & RONKAY 1987, 1989, 1991a, b, c, 1996, VARGA *et al.* 1990, WILTSHIRE 1979).

Some of these papers contain maps of distribution, biogeographical and phylogenetic considerations which could be used for the areographic and faunal historic surveys of this paper. Further monographic works are imminent or are in a very intensive phase of preparation (*Euxoa*, *Dichagyris*, *Chersotis*, *Rhyacia*, *Diarsia*, *Cardiastrea*, *Cardepija*, *Discestra*, *Hadula*, *Thargelia*, *Odontelia*, *Haderonia*, *Ctenoceratoda*, *Tricheurois*, *Polia*, *Saragossa*, *Sideridis*, *Conisania*, *Perigrapha*, *Harutaeaographa*, *Orthosia*, *Mythimna*, *Xylomoia* etc.) and will be published during the next few years. Because of these monographic works many hitherto unsolved phylogenetic problems and biogeographical questions can be answered (e.g. the major phylogenetic division of Noctuinae, Cuculliinae and Hadeninae s. str.).

The detailed results of the phylogenetic and biogeographical analyses of several xeromontane noctuid genera and species groups, based on these revisional works, will be discussed in a subsequent paper. Here, I can only present some general ideas about the taxonomic and biogeographic diversity of xeromontane Noctuidae, which is obviously one of the most ancient and important sources of the Palaearctic fauna.

#### *Chorological principles: "core areas" in oreol biomes*

In the zoogeographical literature the term "core areas" (in German: *Arealkerne*, *chorologische Zentren* etc: DE LATTIN 1957, 1967, MÜLLER 1973, 1974, REINIG 1950, SCHINTLMEISTER 1989, VARGA 1967, 1975a, b, 1977) is used for restricted areas of high species-diversity with a great number of *stenochorous* ("endemic") species. They are often interpreted as areas of survival (refuges) and, consequently, as "centres of dispersal" ("*Ausbreitungszentren*" in the German tradition) of a given faunal type. They are identified by an areographic analysis, consisting of some consecutive steps. The term "areas of endemism", widely employed in biogeographical literature, seems to me to be less clear-cut, because the notion of "endemism" can be referred to biogeographical regional units of very different size (realms, regions, provinces etc.). In addition, species of restricted range ("endemic" ones) and more or less expansive species can equally



belong to the set of species with the same "core area" (cf. the principle of "*equiformal progressive areas*" of HULTÉN 1937). Repetitive geographical patterns of these "core areas" and their significance in survival, speciation and dispersal of biota can also be confirmed by a phylogenetic (cladistic) analysis (CRACRAFT 1982, 1983, CRACRAFT & PRUM 1988, ENGHOFF 1995, OOSTERBROEK & ARNTZEN 1992, ROSEN 1978 etc.). New possibilities of the combined areographical and phylogenetic analyses are supplied by the modern molecular "tool-box" of "phylogeography" (reviewed by RODERICK 1996).

The somewhat complex meaning of "core areas" contains the following main components:

1. Core areas are regions of *accumulated occurrence* of *stenochorous* ("endemic") species, which can equally be older *relict endemics* and "in situ" differentiated *neo-endemic* ones, respectively. A differentiation between these main types can usually be achieved by a phylogenetic analysis.

2. Core areas are regions of *accumulated occurrence* of isolated *subspecies* (or simply populations) of widely dispersed *polytypic species* with *disjunct* range and/or of *allopatric* members (i.e. *semispecies* or *sibling species*) of *superspecies* or *closely related species groups*.

3. Core areas are often *centres of high species-diversity* of characteristic *genera* of a given faunal type, e.g. in the oreol biomes: *Erebia*, *Parnassius*, *Pseudos* and numerous noctuid genera, discussed below (cf. VARGA 1975b, 1977, 1989b, VARGA & RONKAY 1987, 1991a, c, VARGA *et al.* 1989 etc.). Such core areas can be regarded as especially valuable from a historical point of view due to the possibility of a phylogenetic analysis (see also: HENGVELD 1990, "geographical nesting of species").

Core areas are usually *centres of survival of species and communities during regressive phases of the given biome and faunal type*, respectively, but in some cases they do not simultaneously represent centres of speciation and supra-specific differentiation (cf. cases 1 and 3, *partim*).

Because in hilly or mountainous regions a short-distance shift ("creep") is often enough for survival, centres of survival and dispersal of the Palaearctic arboreal fauna often lie in hilly or mountainous regions (cf. DE LATTIN 1949, 1952, 1957, 1967, REINIG 1937, 1938, 1950). Faunal richness and high level of endemism of European butterflies in mountainous regions of Southern Europe has also been clearly demonstrated by DENNIS *et al.* (1991) and DENNIS (1993). It is widely accepted that during the last glaciations the main survival centres of the Western Palaearctic arboreal fauna were restricted to e.g. some parts of the Mediterranean peninsulas. In this phase of the genesis of the fauna, the arboreal biomes were disconnected into several larger or smaller "islands". Due to the post-glacial re-afforestation, however, the *zonal character* of these biomes could be restituted, combined with the reorganisation of forested biocenoses.

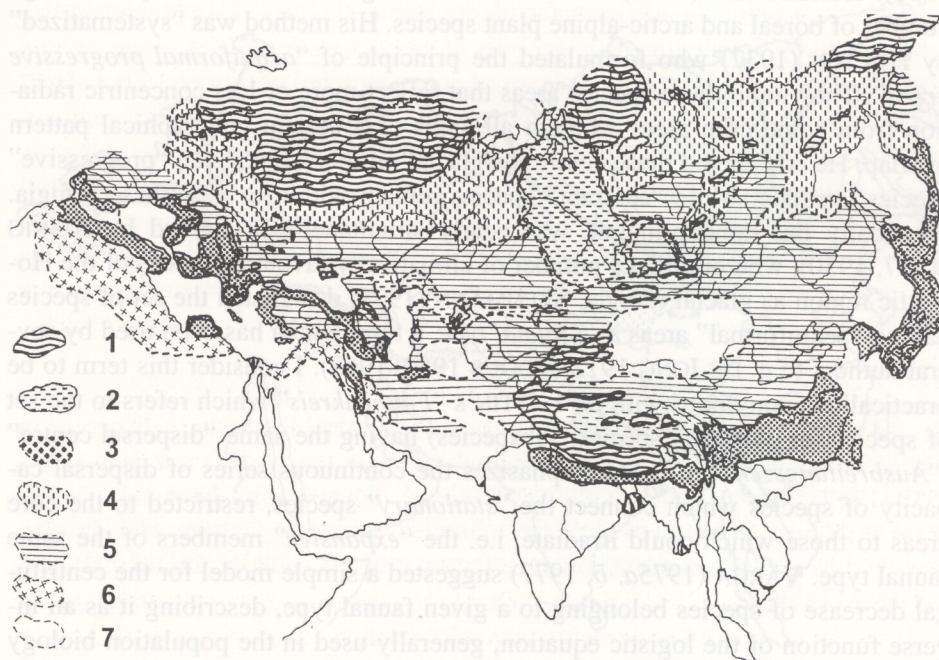


On the other hand, the core areas of the oréal fauna at present hardly (or do not) represent centres of dispersal, as opposed to the arboreal and eremial ones, because the postglacial expansion of the arboreal biomes has fragmented these habitats into patches which could remain suitable for the biota of the orobiomes. Nevertheless, they may become expansive, e.g. in the case of a future glaciation or also by aridisation, which would lead to a retreat of the arboreal biomes.

From these general principles it can be concluded that the core areas of the oréal fauna in this phase of our work can be defined mainly as

- i. centres of occurrence of a large number of stenochorous ("endemic") species,
- ii. centres with an accumulated occurrence of disjunct subspecies of widely dispersed species with scattered distribution.
- iii. centres with higher than average representation of genera, which are typical for orobiomes.

It seems quite evident that the same basic patterns are repeated in the distribution of the monophyletic, very closely related allopatric species groups and



**Fig. 1.** Paleogeographical conditions during the last maxima of Würm glaciations in Eurasia. Legend: 1 = main ice shields, 2 = inland brackish water, 3 = major forest refugia, 4 = periglacial tundra belts, 5 = pseudoperiglacial cold steppe and forest-steppe belts, 6 = Mediterranean (western part), 7 = continental desert and semi-desert areas



also in the subspecific divisions of many widely distributed polytypic species with disjunct areas. A detailed chorological survey and the phylogeographical analysis of some monophyletic species groups, and polytypic species of the Palearctic Noctuidae (mostly Noctuinae and Hadeninae) will be published in a subsequent paper.

*The problem of the unit of the biogeographical analysis:  
the species, the genus or both?*

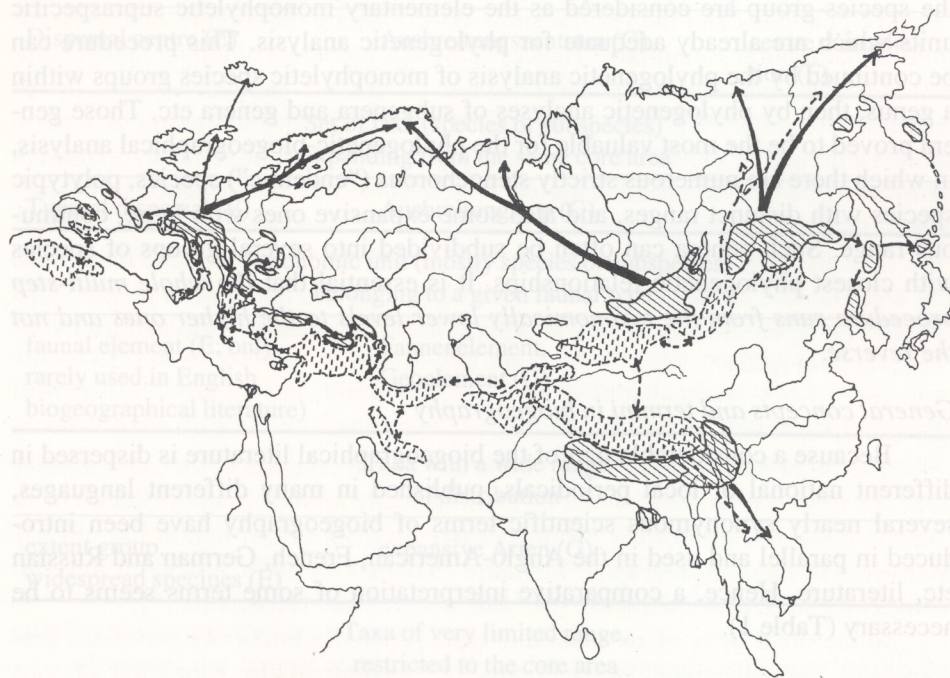
Most biogeographical and taxonomic publications deal with the description, mapping and analysis of ranges of species. As "*faunal elements*", species (or subspecies of polytypic species, see DE LATTIN 1967) are usually considered as the units of biogeographical typisation. It appears to be evident that the ranges of species with some geographical congruences can be accepted as "imperfect repetitions", considered as basic objects of "Geographical Ecology" (MACARTHUR 1973: 77). There are numerous closely related concepts in the biogeographical literature which reflect essentially the same regularity: the partial overlap of a large number of ranges in well-defined regions (see the review of UDVARDY 1981). KULCZYNSKI (1923) demonstrated the regularities of overlap in a large number of boreal and arctic-alpine plant species. His method was "systematized" by HULTÉN (1937) who formulated the principle of "*aequiformal progressive areas*". They unite those species areas that reflect more or less concentric radiation from some core areas wherein all areas of a certain geographical pattern overlap. He considered these centres as glacial refugia from which "progressive" species irradiate, while "centrant" species remain within or near these refugia. Practically the same principle was nearly simultaneously applied by REINIG (1937, 1950), who outlined a number of climatically favourable areas of the Holarctic region as glacial refugia. STEGMANN (1938) designated the set of species having "aequiformal" areas as a *faunal type*, a term which has been used by several authors (e.g. DE JONG 1972, VOOUS 1960, 1963). I consider this term to be practically synonymous with DE LATTIN's "*Faunenkreis*" which refers to the set of species (in polytypic species: subspecies) having the same "dispersal centre" ("*Ausbreitungszentrum*"). He emphasizes the continuous series of dispersal capacity of species which connect the "*stationary*" species, restricted to the core areas to those which could irradiate, i.e. the "*expansive*" members of the same faunal type. VARGA (1975a, b, 1977) suggested a simple model for the centrifugal decrease of species belonging to a given faunal type, describing it as an inverse function of the logistic equation, generally used in the population biology (Fig. 2).

Based on this model, the vicarious stationary species and the disjunct subspecies of polytypic species were characterised by a "*refugial*" type of speciation. On the other hand, the "*post-dispersal*" marginal isolates of the expansive species



were contrasted with the former ones as cases of peripheric speciation and subspeciation, respectively. In addition, the necessity of the analysis of the core areas of species-rich genera was pointed out, especially in those ones which consist of a large number of "stationary" species (e.g. in the case of Lepidoptera species connected to orobiomes). The same conclusion can be drawn by the analysis of stenochorous high mountain species of Orthoptera (LA GRECA 1977, LA GRECA & MESSINA 1977, 1979, PRAVDIN & MISTSCHENKO 1980, WILLEMSE 1971, 1972, 1973, 1977, 1984).

The idea that supraspecific taxa can be considered as units of biogeographical analysis, is also possible. KOSTROWICKI (1969) considered genera as useful tools for statistical comparisons to outline faunal types and faunal regions as well. Other authors emphasized the phylogenetic significance of supraspecific taxa. KRYZHANOVSKY (1965) argued that genera are units of zoogeographical analysis by "common origin", by essentially the same morphology and ecology of species belonging to the same genus. PRAVDIN & MISHTSHENKO (1980) ex-



**Fig. 2.** Main areas of distribution and area connections of alpine and xeromontane biota. Legend: 1 = major areas of alpine biota (horizontally hatched with full lines), alpine and tundra-alpine area connections: black arrows; 2 = major areas of xeromontane biota (vertically striped), xeromontane areal connections: broken arrows



tend this view with the idea that the centres of species diversity of genera give information on their origins and history, which is essentially not a new idea. Many new approaches deal with the area cladograms of species groups, genera or suprageneric groups in order to "translate" a phylogenetic hypothesis about organisms with a given geographical distribution into a hypothesis about distributional history of these taxa (ENGHOFF 1993, 1995, DE JONG 1974, 1978, OOSTERBROEK & ARNTZEN 1992 etc.). Noctuid moths, providing the bulk of the factual data of this paper, are also considered to be very suitable for a phylogenetic-biogeographical analysis LAFONTAINE 1981, LAFONTAINE & KONONENKO 1986, LAFONTAINE *et al.* 1983, VARGA 1989b, VARGA *et al.* 1989, 1990).

Thus, it appears to be evident that the integral biogeographical analysis consists of several subsequent steps (VARGA 1977). Working hypotheses outlined by comparative areographic methods can be tested by phylogenetic biogeographical methods. Units of the areographical analysis are the ranges of species. Core areas drawn by the distribution of stenochorous ("endemic") species can be affirmed by the allopatric subspecies of polytypic species, and by allopatric semi-species or sibling species of superspecies. Superspecies consisting of allopatric taxa of the species-group are considered as the elementary monophyletic supraspecific units which are already adequate for phylogenetic analysis. This procedure can be continued by the phylogenetic analysis of monophyletic species groups within a genus, then by phylogenetic analyses of subgenera and genera etc. Those genera proved to be the most valuable for the phylogenetic-biogeographical analysis, in which there are numerous strictly stenochorous ("endemic") species, polytypic species with disjunct ranges, and also some expansive ones with large, continuous range. Such genera can often be subdivided into several groups of species with closest phylogenetic relationships. It is essential that *the whole multi-step procedure runs from the taxonomically lower levels to the higher ones and not the reverse.*

#### *General concepts and termini in biogeography*

Because a considerable part of the biogeographical literature is dispersed in different national or local periodicals, published in many different languages, several nearly synonymous scientific terms of biogeography have been introduced in parallel and used in the Anglo-American, French, German and Russian etc. literature. Hence, a comparative interpretation of some terms seems to be necessary (Table 1).



**Table 1.** Comparative interpretation of some biogeographical terms

Biogeographical entity consisting of taxa (species or subspecies) sharing the same core area		
Faunal type (E)	Faunenkreis (G)	Tip fauny (R)
Faunal unit (only nearly synonymous, see DENNIS <i>et al.</i> 1991) equiformal progressive areas (only nearly synonymous, see HULTÉN 1937, 1963)		
Area of congruence in ranges of species		
Area nuclei, nuclear areas, core areas (E)	Arealkerne (G)	
Area of survival of a set of taxa (species or subspecies) or assemblies of species under unfavourable ecological conditions (e.g. glaciations)		
Refuge (E)	Refugium (G)	réfuge (F)
Core area of dispersal of a set of taxa (species or subspecies)		
Dispersal centre (E)	Ausbreitungszentrum (G)	centre d'irradiation (F)
Set of taxa (species or subspecies) expanding from the same core area		
Type of dispersal (E)	Ausbreitungstyp (G)	
Taxonomic unit (mostly species or subspecies) belonging to a given faunal type:		
faunal element (E; only rarely used in English biogeographical literature)	Faunenelement, Goelement (G)	
Taxa with a wide range of distribution		
extent group, widespread species (E)	expansive Arten (G)	
Taxa of very limited range, restricted to the core area		
endemic, stenochorous (rarely used), stationary, "centrant" species (E)	stenochore Arten, stationäre Arten (G)	



## DIVISION AND BIOGEOGRAPHICAL CONNECTIONS OF THE OREAL FAUNA

The most plausible division of oréal biomes and faunal types is possible by reviewing the factors which determine the "non-arboreal" conditions.

### *The fauna of the humid high mountains (of alpine s. l. type)*

Many high mountains extend to humid regions where fluvial erosion predominates in lower and moderate altitudes, and the snow-line is relatively low. The alpine and higher belts are characterized by the well-known alpine geomorphological features, e.g. sharp ridges, glacial cirques and long glacier tongues reaching into the deep valleys (usually with a zone-inversion), sometimes down to the forested belts, especially in the regions of expressed oceanic climate. These high-lying open biomes are bordered, as a rule, by a timberline, and in the "Kampfzone" of arboreal and non-arboreal biomes, the zonation of a scrub-community ("Krummholz" scrub-like *Pinus*, *Juniperus*, *Betula*, *Rhododendron* and different *Ericaceae*) is characteristic. Seasonal humidity, solifluction, the occurrence of peat-bogs and the regular snow-cover of long duration resemble conditions in the tundra zonobiome. Hence, numerous members of alpine faunal complexes became pre-adapted for dispersal into tundra (i.e. periglacial) belts by the retreat of forests during glacial phases. Of course, upward migration of tundra species into alpine elevations was equally possible, brought about by extensive inter- and post-glacial re-afforestation, which has led to the formation of characteristic oreo-tundra disjunctions.

The alpine (s. l.) faunal type was subjected to the most extensive migrations and area translocations during the oscillating glacial and interglacial phases. This faunal type is, on the other hand, at present most restricted in its dynamics by arboreal belts (Fig. 2).

### *The oréal fauna of arid high mountains*

The other basic type of oréal biome and faunal complex is the *xeromontane* one. The term "*eremoreal*" would be grammatically more correct (a Greek-Greek combination), but the former "chimaera-like" (Greek-Latin) notion has already been used in the zoogeographic literature (STEGMANN 1938, VOOUS 1963), although in a more restricted sense (as "*paleomediterran-xeromontane*").

In the oréal belts of *xeromontane* type, *physical weathering* processes predominate: thermal- (incl. frost) fluctuation, leading to the formation of vast masses of clastic rocks and gravels subjected to gravitational movements and to the establishment of gravel pediments, ravine pyramids etc. It is also important to note that *xeromontane biomes* often do not cover *whole* mountains, but form mosaic-like patterns of habitats, often surrounded by alpine belts, e.g. in several Eu-



ropean or Southern Siberian high mountains. On mountains (or parts of mountains) of xeromontane character the snow-line lies essentially higher than in comparable mountains of the alpine type (cf. MANI 1968: 28), and the snow-cover is often irregular and sparse. Primary production is inhibited not only by the often extremely cold winter season, but also by the seasonal aridity. Hence, the level of bioproductivity is often lower here than in the mountains of the alpine type, and their vegetation is semidesert- or desert-like (e.g. Pamir plateau, Gobi Altaj Mts, parts of the Tibetan plateau etc., WALTER & BOX 1983, WALTER & BRECKLE 1986).

Because the xeromontane belts are now surrounded mostly by eremial zoniobiomes, their ecosystems are not, or only insignificantly, delimited by the timberline. Hence their elements are not inhibited from dispersal into the zonal steppes and deserts. This situation was essentially similar during the whole Quaternary, less influenced by the alternation of the cold and temperate phases. Thus, the xeromontane fauna could serve as an important source for the genesis of the eremic one. We can observe a nearly continuous transition of xeromontane and eremic patterns of distributions in numerous genera of Noctuidae, being typical for arid belts in Central and Inner Asia.

#### *Quaternary dynamics in the xeromontane fauna*

Therefore, in the xeromontane fauna the range fluctuations and translocations have been, as a rule, not as extreme as in the alpine one. Only during the extremely continental late glacial and earliest postglacial ("kryoxerotic") phases (before the major postglacial re-afforestation) a major fraction of continental elements, connected to open habitats, could spread into Europe, and the most Mediterranean-xeromontane species could populate only the typical summer-dry Mediterranean mountainous regions (Atlas, arid parts of the Iberian peninsula, southern Balkan peninsula, Asia minor etc.). During the postglacial vegetation history of Central Europe, there was not a single climatic phase which could have promoted the dispersion of xeromontane species. Hence, no extra-Mediterranean zoniobiome, as opposed to e.g. the southern Balkanic – W Asiatic *Astragalo-Acantholimetalia* orobiome, consists of a number of xeromontane species. Their scarce representatives in Central and Northern Europe are mostly "pre-Litorina" relicts, occurring either above the tree-line in xeric habitats (e.g. Central Alps) or in the unforested habitats of moderate and low altitudes, determined by extreme edaphic and/or microclimatic conditions.

However the largest and obviously richest xeromontane biomes of the Palearctic occur, mostly in the mountainous massifs of Central and Inner Asia. The highlands of Inner Anatolia and Armenia already represent a fraction of this fascinating world, but the greatest part of the Tien-Shan mountain system, the Pamir-highland, the magnificent chains of Hindukush, Karakoram and Trans-Hi-

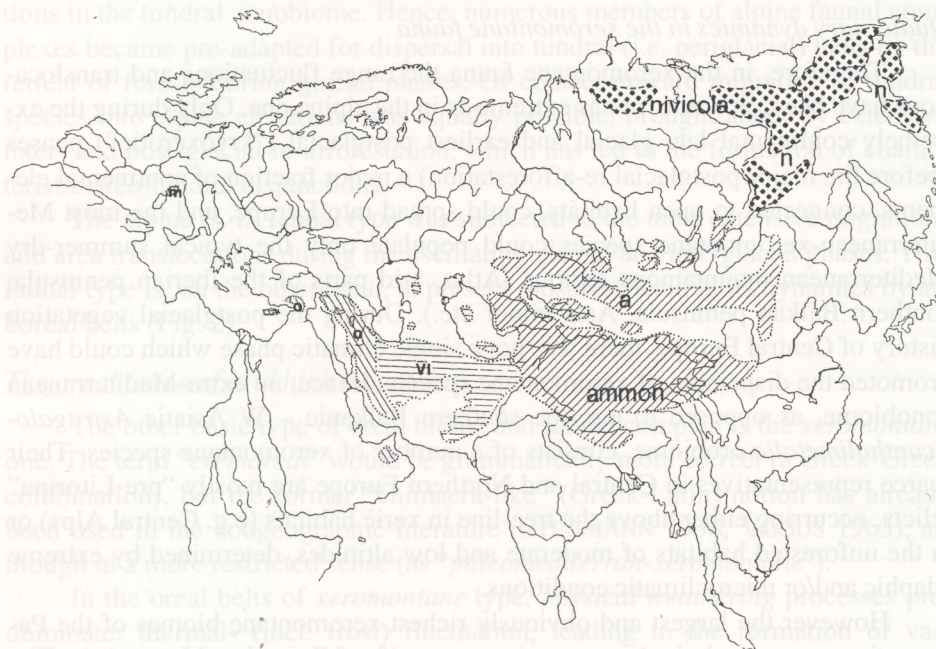


malaya, the high massifs of Mongolia, Tibet and Ladakh are the true "home-lands" of this faunal type: the faunal type of Marco Polo's Argali (Fig. 3), Altai Ibex, Snow leopard, Bearded and Griffon Vultures, Chukar Partridge, Snowcocks (*Tetraogallus*), Redstarts (*Phoenicurus*), many endemic flightless grasshoppers (e.g. *Conophyma*, *Paraconophyma*, *Bienkoia*, *Saxetania* etc., see: PRAVDIN & MISHTSHENKO 1980) and last but not least, grass-root feeding cutworms (Noctuidae, mostly Noctuidae).

We conclude that both the alpine and xeromontane faunal types are of general importance for the composition and genesis of the Palaearctic fauna, and despite the existing differences mentioned above, they also have some parallel features in their regional division (Fig. 2).

#### *Disjunctions in the arboreal vs. orear fauna*

The macrogeographic division of the orear biomes is obviously the consequence of their *antagonistic dynamics* in relation to the arboreal zonobiomes. The expansion of the arboreal ecosystems in temperate belts, iterating in interglacial



**Fig. 3.** Distribution of the major taxa of mountain sheep: *Ovis ammon* species-group. Legend: m = *O. musimon*, o = *O. orientalis* (probably conspecific with the former one) vi = *O. vignei*, ammon: *O. ammon ammon*, a = *O. ammon altaicus*, nivicola + n: *O. nivicola*



cial/interstadial periods and also in the Holocene, resulted, in these latitudes, in a general regression and disjunction of the oréal biomes and also of the distribution areas of their inhabitants. The expansion of the arboreal biomes caused a wide diversification of sizes and shapes in the ranges of their faunal elements with a nearly continuous variance. Hence, it is often not simple to recognize the stationary and expansive extremes of the same faunal type (cf. DE LATTIN 1975, 1964, 1967), e.g. stationary Mandzhurian species vs. trans-Palaeartic Eurosiberian ones, or stenochorous Mediterranean elements vs. widely distributed Mediterranean-Central European ones.

On the other hand, the regressive disjunctions caused superficially similar shapes of geographical ranges in oréal and oreo-tundral species of different origin. Thus, the revision of the stenochorous species, or of the genera rich in such species, may be highly significant for the analysis of the oréal fauna. The phylogenetic-biogeographical analysis of several such cases will be attempted in a subsequent paper.

#### *Chorological review of the alpine fauna*

Because the alpine fauna is generally better known and carefully analysed in its details, I will present only a short, thesis-like review of statements on its main features and tendencies here.

1. The tundra-alpine disjunction, analysed in numerous publications (e.g. ANT 1965, ANDER 1949, ASPÖCK 1963, EHRLICH 1958, HOLDHAUS 1954, HOLDHAUS & LINDROTH 1939, IVERSEN 1958, KULCZINSKY 1923, DE LATTIN 1957, 1967, VARGA 1975a, b, 1989c, 1995b, WALTER & STRAKA 1970, WARNECKE 1959), is a general phenomenon in vascular plants and also in most major groups of animals.

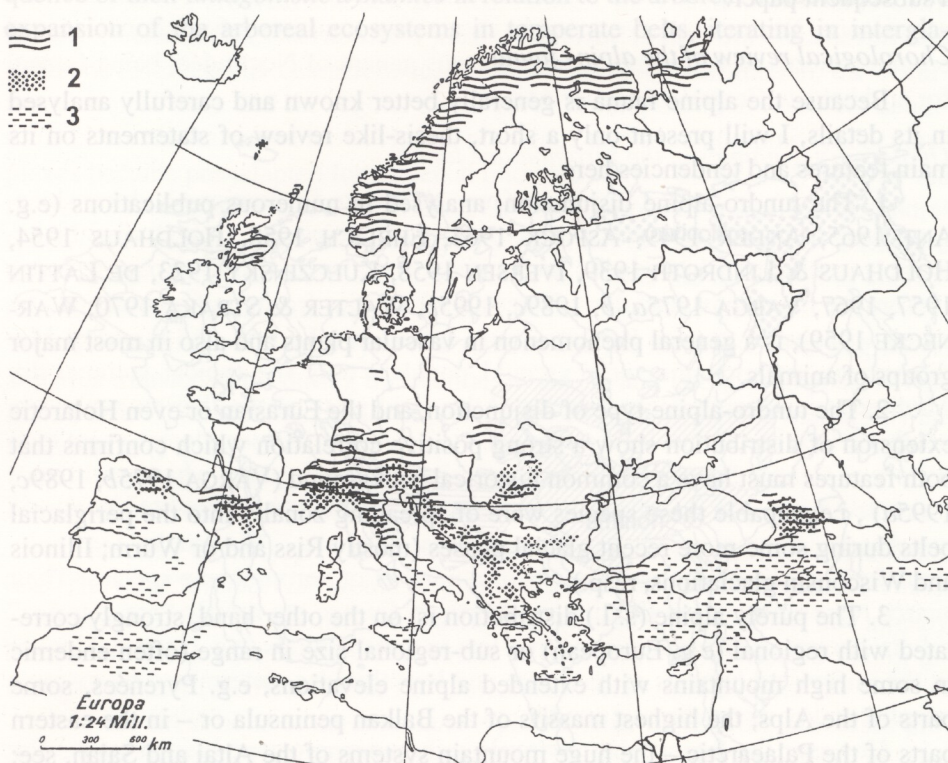
2. The tundra-alpine type of disjunction, and the Eurasian or even Holarctic extension of distribution show a strong positive correlation which confirms that both features must have a common historical background (VARGA 1975b, 1989c, 1995a), i.e. capable these species were of spreading zonally into the periglacial belts during some more recent glacial phases (mostly Riss and/or Würm; Illinoian and Wisconsin glaciations, resp.).

3. The purely alpine (s. l.) distribution is, on the other hand, strongly correlated with regional (e.g. European) or sub-regional size in range (often endemic in some high mountains with extended alpine elevations, e.g. Pyrenées, some parts of the Alps, the highest massifs of the Balkan peninsula or – in the eastern parts of the Palaeartic – the huge mountain systems of the Altai and Sajan, see: VARGA 1989c). These species could survive the glacial periods in mountainous refugia at the margin of the mountain glaciations (e.g. "massifs de refuge", in the less glaciated alpine belts (e.g. in the high mountains of the Mediterranean penin-



sula) or – in special cases – in refugial patches within the major glaciations (i.e.: “nunatak” refuges, JANETSCHEK 1956).

4. Numerous widely distributed alpine species do not occur in the Northern Calcareous Alps or in the Northern Carpathians. These mountains also seem to be poor in endemic high mountain species. The relatively small and scattered extension of the alpine belts, combined with unfavourable climatic conditions (“Nordstaulage”) in these mountains can explain this fact. Numerous species groups which are mostly distributed in southern European high mountains of alpine type, are often represented by vicariant species pairs in southwestern and southeastern Europe, respectively, separated by this “gap”. The presence of this N Alpine – N Carpathian “gap” gives us the possibility for basic regionalisation of the European orcal fauna of the alpine type (Fig. 4).



**Fig. 4.** Glacial events as factors of regional division in the Western Palearctic orcal fauna. 1 = Territories directly influenced by glaciations: only alpine and arctic-alpine species; 2 = Areas of survival of relict-like alpine species displaying a western-eastern European subdivision, often with vicariant sister species/subspecies; 3 = Main areas of distribution of xeromontane species



5. The alpine type of fauna has a typical insular character. A high level of similarity was found among certain parts of the Alps, and also among some more remote mountain massifs (Pyrenées, Sar-planina, Rila and Pirin) which have extended "islands" of alpine belts, and thus permit the survival of numerous alpine species (VARGA 1975b, 1995a).

6. Preliminary considerations on phylogenetic patterns of some alpine Lepidoptera suggest the possibility of very large heterogeneity in their origins. Only some typical cases can be mentioned here:

- Long-distance isolates, with vicariant species (or only subspecies!) in Southern or Eastern Siberia and/or Northern America (*Erebia christyi* RÄTZIUS, *E. flavofasciata* HEYNE, *E. tyndarus* ESPER -group, *Euphydryas ichnaea wolffensbergeri* FREY, *Euxoa culminicola* STAUDINGER, *Agrotis fatidica* HÜBNER etc.).
- Alpine endemisms probably evolved from their arboreal relatives, distributed at medium altitudes in close proximity, e.g. *Mellicta varia* MEYER-DÜR (*M. parthenoides* KEFERSTEIN), *M. asteria* FREYER (*M. aurelia* NICKERL -group), *Euphydryas debilis* OBERTHÜR (*E. aurinia* ROTTEMBURG, in which the speciation process is seemingly not yet complete!), etc.
- Alpine endemisms with more widely dispersed oreol and/or oreotundral relatives which indicate their probably autochthonous evolution as neo-endemisms, e.g. numerous species of *Setina*, *Psodos*, *Gnophos*.

An analogous heterogeneity is also evident among SE European ("ponto-mediterranean oreol") species. Ponto-atlantomediterranean or ponto-mediterranean-W-alpine disjunctions are often to be observed (*Boloria graeca* STAUDINGER, *Erebia ottomana* HERRICH-SCHAEFFER, *E. rhodopensis* NICHOLL / *aethiopella* HOFMANNSEGG, *Anaitis simplicata* TREITSCHKE etc.), but some of the ponto-mediterranean oreol species have their closest relatives among the members of the Siberian faunal type (such species-pairs are e.g. *Lycaena candens* HERRICH-SCHAEFFER / *hippotoe* LINNAEUS, *Aricia montensis* VERITY / *artaxerxes* FABRICIUS, *Coenonympha rhodopensis* ELWES / *tullia* MÜLLER etc., see also VARGA 1989c).

#### *Chorological review of the xeromontane fauna*

*Taxonomic and evolutionary aspects of biodiversity in the xeromontane fauna.* Like its alpine counterpart, the xeromontane faunal type also has a general trans-Palaeartic (or trans-Holarctic) range of distribution, sometimes with marginally fragmented exclaves in tropical latitudes of Asia, Africa and South America. Its importance becomes evident from its richness of entirely xeromontane genera, e.g. Satyridae: *Karanasa* (AVINOFF & SWEADNER 1951), *Paralasa*, *Boeberia*, *Pseudochazara*; Noctuidae: *Pachyagrotis*, *Hemiexarnis*, *Ledereragrotis*, *Xenophysa*, *Bryopolia*, *Bryoxena*, *Margelana*, *Victrix*, etc.; (a large num-



ber of coleopteran groups of this nature is mentioned by KRYZHANOVSKY 1965), or by a large number of widely distributed, highly diverse genera, which have the highest number of species in the xeromontane belts, e.g. Papilionoidea: *Parnassius*, *Colias*, *Oeneis*, *Agrodiaetus* (examples: Fig. 5), *Polyommatus*; Noctuidae: *Euxoa*, *Dichagyris*, *Yigoga*, *Parexarnis*, *Protexarnis*, *Rhyacia*, *Chersotis*, *Eugnorisma*, *Discestra*, *Ctenoceratoda*, *Sideridis*, *Conisania*, *Polymixis*, *Dasypolia*, *Cucullia*, *Oncocnemis* etc. (HACKER 1993a, b, RONKAY 1988, RONKAY & VARGA 1986, 1989, 1990a, b, VARGA 1975, 1989a, 1990a, b, 1992a, b, VARGA & RONKAY 1987, 1989, 1991, VARGA *et al.* 1989, 1990 etc.).

It is quite typical that the noctuid fauna of Turkey, with its large xeromontainous areas, consists of about 1300 species (1032 spp. are enumerated by HACKER 1990), as opposed to the whole European fauna which can equally be estimated at about 1300 species (1104 spp. are mentioned by HARTIG & HEINICKE 1973, 1291 spp. are listed by FIBIGER & HACKER 1991). Good evidence for the high species-diversity of the xeromontane Noctuidae is shown by HACKER (1990).

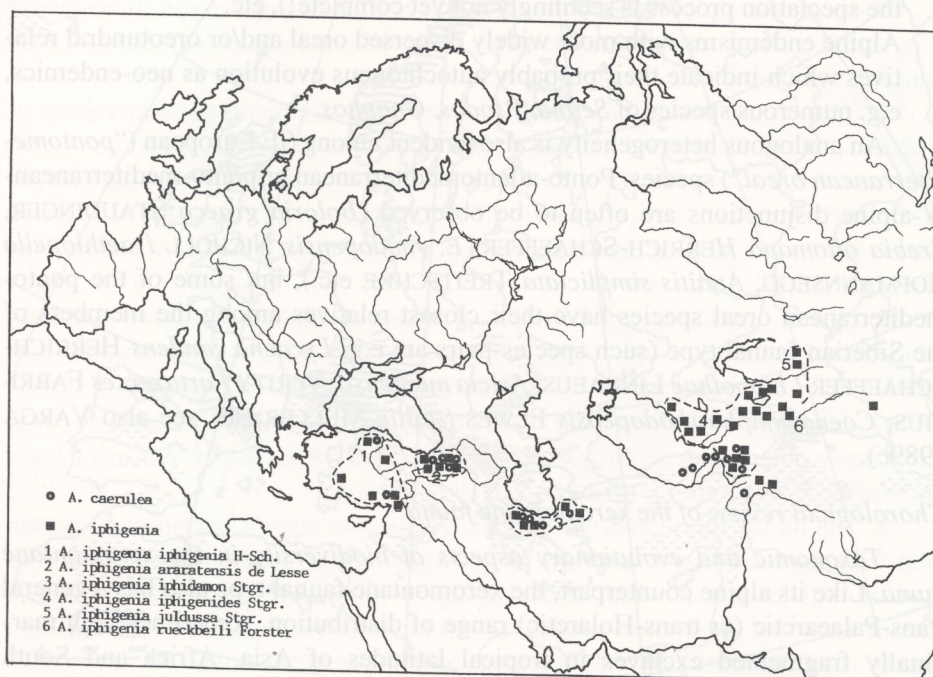


Fig. 5. Distribution of two polytypic-polycentric xeromontane species of the Lycaenidae genus *Agrodiaetus*: *A. caerulea* STAUDINGER and *A. iphigenia* HERRICH-SCHAEFFER displaying an evident division according to the core areas of the xeromontane fauna. The boundaries of the eastern subspecies of *A. iphigenia* are not completely clarified



Numerous, obviously monophyletic groups of closely related species (i.e. groups of sibling species, pairs of sister-species, or simply subspecies of widely dispersed polytypic species) of these genera are exclusively xeromontane and are highly characteristic for some regional units of Palaearctic mountain systems, e.g. *Eugnorisma* subg. *Metagnorisma* (VARGA & RONKAY 1987), *Euxoa* subg. *Pleonectopoda hilaris* FREYER-group, *Dichagyris psammochroa* BOURSIN-group (VARGA 1993, Fig. 6), *Xenophysa junctimacula* CHRISTOPH -group (VARGA 1989), *Chersotis capnistis* LEDERER-group (VARGA & RONKAY 1996), *Rhyacia subdecora* STAUDINGER-group, *Dichagyris clara* STAUDINGER-group, the whole genus *Ostheldera* (RONKAY & VARGA 1991 several species-groups of the genera *Bryopolia* and *Bryoxena* for details and maps of distribution, see VARGA *et al.* (1990).

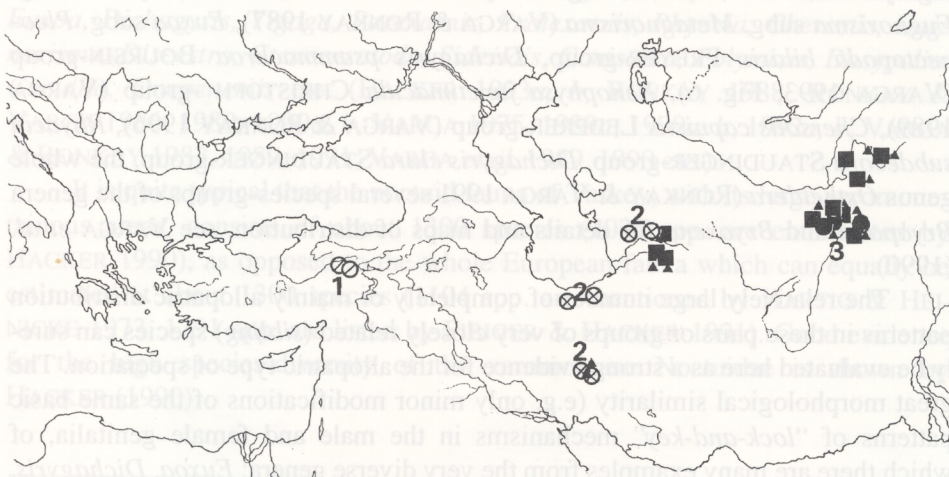
The relatively large number of completely or mainly allopatric distribution patterns in these pairs or groups of very closely related (*sibling*) species can surely be evaluated here as a strong evidence for the allopatric type of speciation. The great morphological similarity (e.g. only minor modifications of the same basic patterns of "lock-and-key" mechanisms in the male and female genitalia, of which there are many examples from the very diverse genera: *Euxoa*, *Dichagyris*, *Eugnorisma*, *Xestia*, *Apamea*, *Conisania*, *Sideridis* etc., see LAFONTAINE 1981, 1987, LAFONTAINE *et al.* 1983, LAFONTAINE & MIKKOLA 1987, VARGA & RONKAY 1987, 1991, VARGA 1991) and close taxonomic relations of members in these species groups suggest a relatively rapid speciation.

In some species groups the restricted occurrence of some closely related species is combined with a much wider distribution of a "successful" sister species which could transgress some ecological barriers. This fact becomes evident e.g. from the taxonomical-chorological analysis of the *Chersotis elegans* EVERSMAAN – species-group in which the expansive, partially already overlapping, secondarily "Mediterranean-xeromontane" areas of two, "successful" species (*Ch. anatolica* DRAUDT, *Ch. elegans* EVERSMAAN), which were obviously separated earlier, is combined with the marginally isolated areas of two stenochorous species (*Ch. kacem* LE CERF, *Ch. eberti* DUFAY & VARGA), which are more closely related to *Ch. elegans* EVERSMAAN (DUFAY & VARGA 1995, Fig. 7). This step in evolution is often combined with a change of life-strategy (aestivation of imagines, connected with a strong development of fat bodies: *Chersotis capnistis*-group, VARGA & RONKAY 1995, see also Fig. 10) or of the habitat (*Euxoa cursoria* HUFNAGEL-group, *Agrotis ripae* HÜBNER – group: a rapid, Quaternary adaptation and dispersal in riparian and halophytic habitats).

Here is the place to mention that not only are there numerous important cultivated plants of xeromontane origin (e.g. cereal crops, maize, alfalfa etc.) but so are some widely dispersed insect pests (e.g. from genera: *Euxoa*, *Agrotis*, *Discestra* etc.).



**Fig. 6.** Distribution of the *Dichagyris psammochroa* species-group (white circles with markings & black circles): 1 = *D. cataleipa*, 2 = *D. psammochroa*, 3 = *D. afghana*. Distribution of *Euxoa sigmata* (black squares) and *E. aneucta* (black triangles)



#### *The xeromontane-eremic and xeromontane-tundral faunal connections*

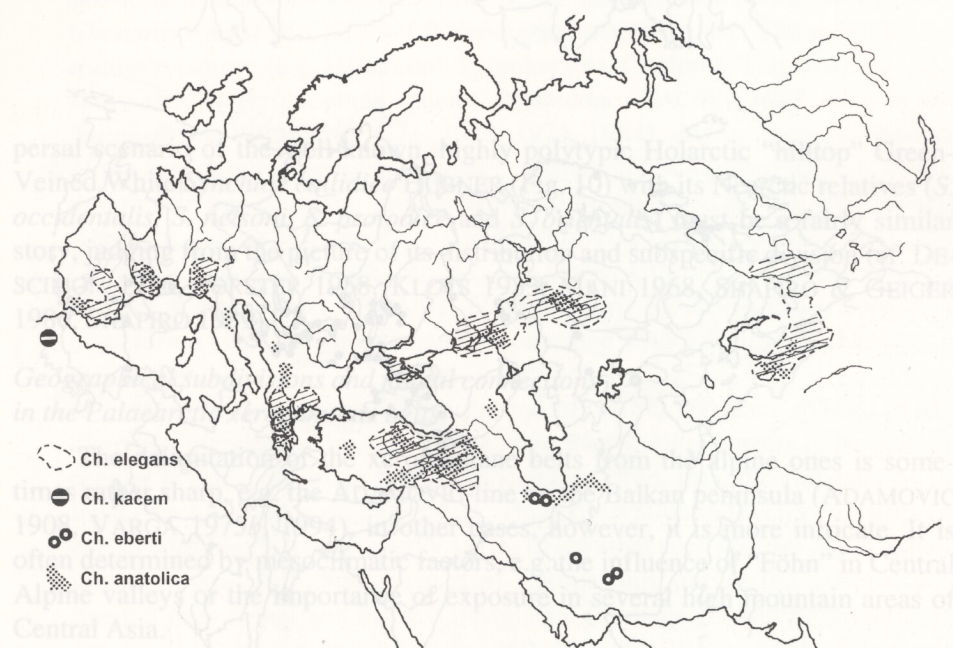
The xeromontane biomes and fauna have manifold contacts and connections with other open, non-arboreal belts. Most obvious is their contact with the eremic zonobiomes. A major fraction of prevailing xeromontaneous genera has widely dispersed representatives in the eremic regions, e.g. *Dichagyris imperator* BANG-HAAS, distributed from southern Spain and N Africa to the deserts of Arabia, closely related to the xeromontane *D. melanura* KOLLAR – *D. grisescens* STAUDINGER-complex; *Euxoa fallax* EVERSMAAN, a desert species which occur from Transcaspia and Kazakhstan to the Dzhungarian and Transaltai Gobi in Mongolia, and is closely related to *E. praestigiosa* BRANDT (Iran) and *E. cespitis* SWINHOE (Afghanistan and W Pakistan). *Euxoa c. cursoria* HUFNAGEL and *Agrotis r. ripae* HÜBNER, generally occurring in littoral sand-dune or semidesert-like halophytic ecosystems, have closely related stenochorous vicariants (often only infraspecific taxa!) in Western and Central Asia. The taxonomic relations within the *Agrotis ripae*-group need further revision. Similar cases can also be mentioned in the eremic genera *Cardepija*, *Cardiestra*, *Hadula*, *Saragossa*.

It should be mentioned here that the species of xeromontane origin made an important contribution to the genesis of the steppe fauna. There are numerous species which have a wide range of distribution in the Palearctic steppe belts as well, e.g. several species of the *Lycaenid* genus *Agrodiaetus* (Fig. 5), a great number of Noctuidae, Noctuinae: numerous *Euxoa*, *Dichagyris* (Fig. 6), *Eugnor-*



*isma* etc. species. The total number of such species in the Palaearctic certainly exceeds one hundred. The terricolous "cutworm" life-form of their larvae, probably evolved in xeric mountainous regions, surely has an outstanding (but incompletely studied) importance in the trophic organisation of the temperate grassland ecosystems.

The tundra connections of some, originally xeromontane genera display a complicated picture. In the genera *Colias* and *Oeneis*, those species that have a southern-eastern Siberian and Mongolian high mountain distribution, are also dispersed through the tundra areas. The mountain tundras ("goltsy") of the eastern Siberian Pacific mountains could serve as "stepping-stones" for their dispersal to the north. Numerous species of *Colias* and *Oeneis* (e.g. *Colias tyche* BOEBER, *C. melinos* EVERSMAAN, *C. mongola* ALPHERAKY, *C. hecla sulitelma* AURIVILLIUS, *Oeneis norna* THUNBERG, *Oe. jutta* HÜBNER, *Oe. tarpeia* PALLAS, *Oe. mongolica* OBERTHÜR, *Oe. sculda* EVERSMAAN, *Oe. melissa* SAYER, *Oe. bore* SCHNEIDER) are inhabitants of southern Siberian – northern Mongolian high mountains. Some of the subspecies of *C. hecla*, *Oe. norna*, *Oe. jutta*, *Oe. melissa*,



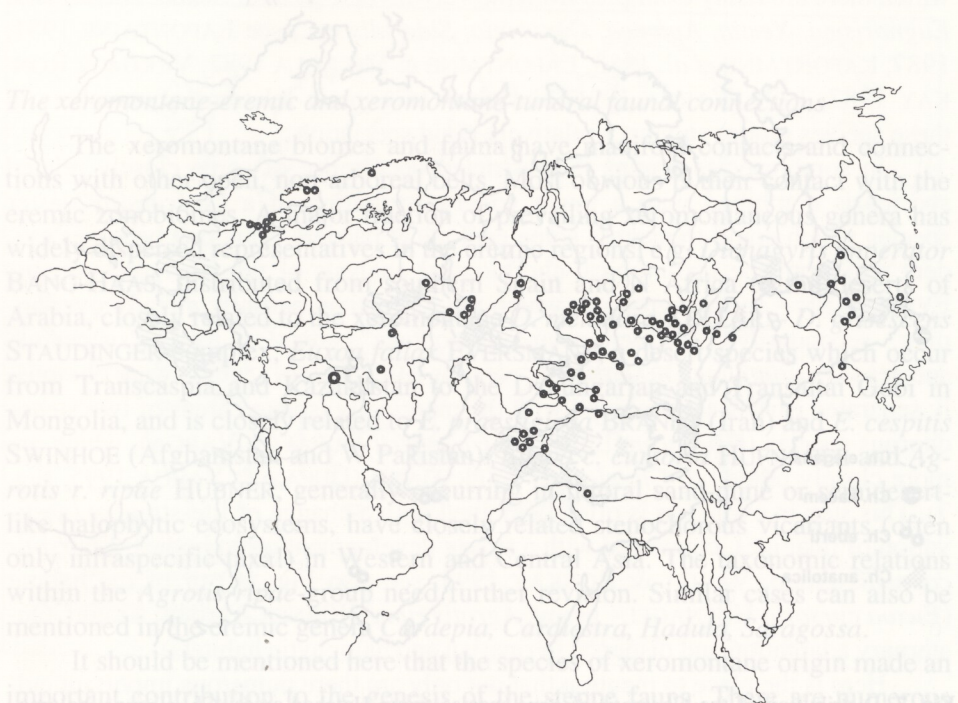
**Fig. 7.** Distribution of the *Chersotis elegans* species-group. Hatched areas: *Ch. elegans*, holomediterranean-xeromontane species with wide area in the steppe zonobiome; black circles with white bar: *Ch. kacem*, Mauretanian-xeromontane species; black circles with white dot: *Ch. eberti*, Iranian-xeromontane species; dotted areas: *Ch. anatolica*, Holomediterranean-xeromontane species with local exclaves in the steppe zonobiome



*Oe. bore* were also able to populate vast areas of the Eurasian and North American tundra belts. On the other hand, they do not occur in the European high mountains. They were obviously inhibited by some barriers (probably by the western Siberian – Caspian glacial sea, see Fig. 1, so they were unable to populate the Western Palearctic periglacial belts. As a contrasting example we can mention the European alpine species *Colias phicomone* ESPER and *Oeneis glacialis* MOLL which – although closely related to the xeromontane and tundra species of their genera – do not occur in northern territories.

In Holarctic Noctuidae, the xeromontaneous origin of the *Anarta* (s. l.) generic complex (closely related to *Discestra*) and of the typical arctic-alpine *Sympistis* (almost impossible to separate from *Oncocnemis*) can be accepted as strong evidence supporting the importance of the continental xeromontane fauna in the formation of the Holarctic tundra faunal complex.

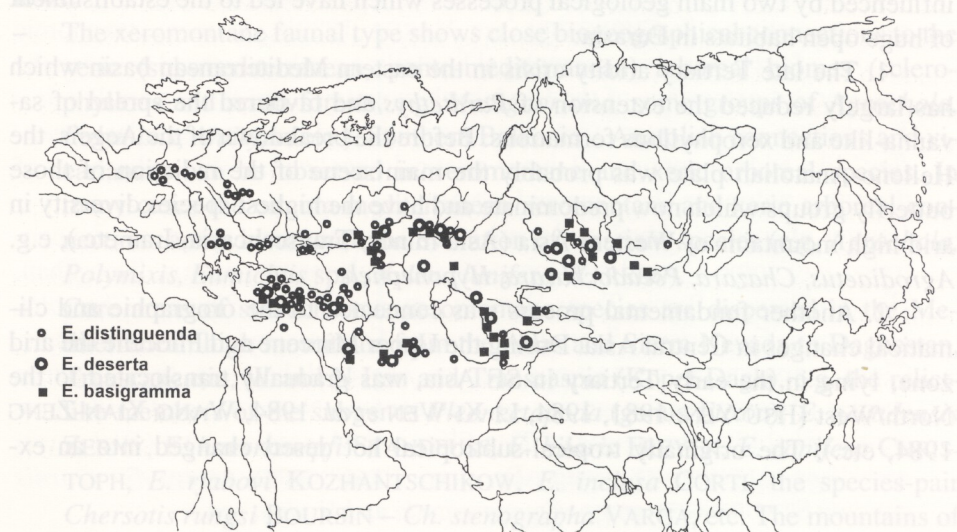
As a model example, the evolutionary history of the mountain sheep: *Ovis ammon-nivalis* species group can be mentioned here (HEPTNER 1966, NADLER *et al.* 1973, Fig. 3). They form a Holarctic superspecies of xeromontane origin with an eastern Siberian – North American irradiation into the tundra biome. The dis-



**Fig. 8.** Distribution of *Euxoa* (*Chorizagrotis*) *lidia* (incl. *E. [Ch.] inexpectata*, *arenacea*, *flavogrisea*, *expugnata* etc.). A polymorphic xeromontane species with littoral and montane exclaves in NW Europe



Fig. 9. Distribution of three *Euxoa* species: xeromontane species with irradiation into the zonal steppe areas (*E. distinguenda*, *E. basigramma*, *E. deserta*) and edaphic grasslands of S European mountains (*E. distinguenda*)



persal scenario of the well-known, highly polytypic Holarctic "hilltop" Green-Veined White *Synchlœ callidice* HÜBNER (Fig. 10) with its Nearctic relatives (*S. occidentalis*, *S. nelsoni*, *S. protodice* and *S. orientalis*) must be a fairly similar story, judging from the picture of its distribution and subspecific division (cf. DESCIMON 1986, FORSTER 1958, KLOTS 1933, MANI 1968, SHAPIRO & GEIGER 1986, SHAPIRO 1989).

#### *Geographical subdivisions and faunal connections in the Palearctic xeromontane belts*

The delimitation of the xeromontane belts from the alpine ones is sometimes rather sharp, e.g. the ADAMOVIC-line on the Balkan peninsula (ADAMOVIC 1908, VARGA 1975b, 1994), in other cases, however, it is more intricate. It is often determined by mesoclimatic factors, e.g. the influence of "Föhn" in Central Alpine valleys or the importance of exposure in several high mountain areas of Central Asia.

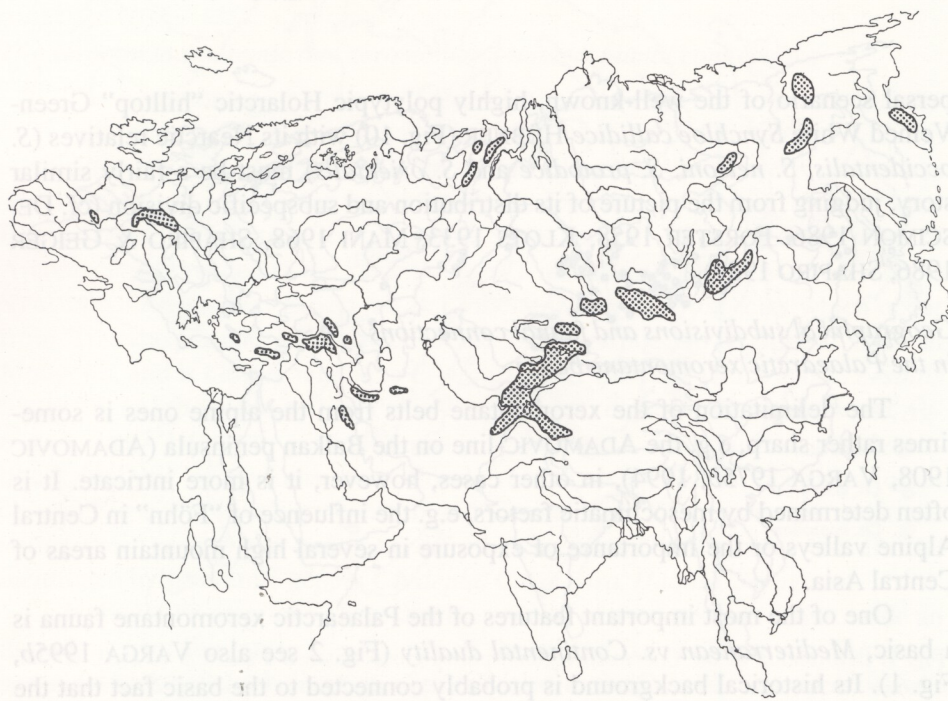
One of the most important features of the Palearctic xeromontane fauna is a basic, *Mediterranean vs. Continental duality* (Fig. 2 see also VARGA 1995b, Fig. 1). Its historical background is probably connected to the basic fact that the Balkans and the western part of Asia Minor (the Hellenic – Anatolian plate) were, since 17 MYBP, newly separated by the *Paratethys* from East Asia Minor and



from the other eastern parts of the Eurasian continent (OOSTERBROEK & ARNTZEN 1992, RÖGL & STEININGER 1983, 1984, STEININGER *et al.* 1985). Further evolution (since approximately the latest Miocene) of this faunal type has been influenced by two main geological processes which have led to the establishment of huge open habitats in Eurasia:

1. The late Tertiary aridity crisis in the eastern Mediterranean basin which has largely reduced the extension of *Paratethys* and favoured the spread of savanna-like and xerophyllous formations. Before the breakdown of the Aegeis, the Helleno-Anatolian plate was probably the main scene of the radiation of those butterfly groups which now predominate and have the highest species diversity in arid high mountains of Western Asia (Asia minor, Transcaucasia, Iran etc.), e.g. *Agrodiaetus*, *Chazara*, *Pseudochazara*, *Hyponephele*.

2. Another fundamental process was connected to the orographic and climatical changes in Central Asia. During the Upper Miocene and Pliocene the arid zone, lying in the early Tertiary in SE Asia, was gradually translocated to the North/West (HSÜ YEN, 1981, 1984, LI XI-WEN *et al.* 1984, WANG XIAN-ZENG 1984, etc.). The originally tropical-subtropical hot desert changed into an ex-



**Fig. 10.** Eurasiatic distribution of the Holarctic Green-Veined "hilltop" White: *Synchloe callidice*



tremely continental, cool temperate one, surrounded by older (Tien Shan, Altai) and newly emerged mountain systems (Himalaya, Karakoram, Pamir).

The main consequences of these palaeogeographical processes are as follows.

- The xeromontane faunal type shows close biogeographical connections to the xeric (sub-mediterranean, ponto-mediterranean) arboreal biomes (sclerophyllous and scrub-forests, e.g. *Metagnorisma*, some groups of *Agrochola*, *Polymixis*, *Antitype*, etc.). Southern Balkanic – Anatolian connections and vicariations can be observed in xeromontane and xeric arboreal species. In many cases the circum-mediterranean xeromontane and xeric arboreal connections are evident, with the evolution of vicariant species (e.g. *Agrochola*, *Polymixis*, *Eumichtis* spp., *Xylena lunifera* WARREN).
- Core areas of stenochorous xeromontane species are dispersed in the Mediterranean high mountains from the Atlas and Sierra Nevada to Daghestan, Transcaucasia, W and N Iran and Transcaspia (Kopet-Dagh), e.g. the relict-like members of the subgenus *Pleonectopoda* (genus *Euxoa*): *E. nevadensis* ZERNY, *E. haverkampfi* STANDFUSS, *E. hilaris* FREYER, *E. conifera* CHRISTOPH, *E. rjabovi* KOZHANTSCHIKOW, *E. inclusa* CORTI, the species-pair *Chersotis rungsi* BOURSIN – *Ch. stenographa* VARGA, etc. The mountains of southern Greece (e.g. Parnassos, Tymphrystos, Chelmos, Taigetos) are especially rich in xeromontane species (Noctuidae: HACKER 1989; also in *Orthoptera*, see WILLEMSE 1971, 1972, 1973, 1984), due to the predominance of the xerophytic “*oromediterranean*” formations. A smaller “island” of mediterranean-xeromontane species can also be observed in the southwestern Alps (e.g. *Euxoa hastifera* DONZEL, *Dichagyris* [*Yigoga*] *celsicola* BELLIER, *Chersotis fimbriola* ESPER, Fig. 11, *Ch. larixia* GUENÉE, *Ch. elegans* EVERSMANN, *Ch. anatolica* DRAUDT, *Hadena clara* STAUDINGER, *Heterophysa dumetorum* GEYER) which is surely connected with the refugial character of this region.
- In contrast to the patterns of distribution of the xeromontane species in Mediterranean areas and in Asia Minor, their distribution appears to be quite irregular in European extra-Mediterranean territories, influenced mostly by the local edaphic conditions of the sites. This observation indirectly confirms our earlier formulated hypothesis (VARGA 1975b) that such species could expand into the extra-Mediterranean part of Europe only during the extreme continental late-glacial and earliest postglacial (kryoxerotic and protocratic, respectively GRICHUK & GRICHUK 1960, IVERSEN 1958) phases. Their relatively regular occurrence at rocky littoral habitats of Fennoscandinavia and the British Isles, as “*Pre-Litorina relicts*”, also seems to support this explanation.



- Eastern borders of range in expansive, polycentric West-Palaeartic species or superspecies frequently occur in the western Tien Shan, eastern Hindu-kush, Nuristan or NW Pakistan (*Euxoa homicida* STAUDINGER, *Dichagyris leucomelas* BRANDT, *D. afghana* BOURSIN, *D. chrysopyga* BOURSIN, *Xenophysa junctimacula* CHRISTOPH, see VARGA 1989b). In many taxonomic groups a fairly sharp biogeographical borderline can be observed between the easternmost extensions of the Hindukush mountains and the eastern Pamir – Karakorum ranges, resp. (see: the distribution of western, smaller, “moufflon”-like and the continental, inner-asiatic, larger “argali”-like subspecies of the rather polytypic *Ovis ammon* LINNAEUS).
- Centres of species diversity of many typical xeromontane genera are concentrated into some Central and Inner Asiatic high mountains, e.g. Tien Shan, Hissaro-Darwaz, Pamir, Trans-Himalaya ranges (*Euxoa*, *Rhyacia*, *Chersotis*, *Dichagyris*, *Eugnorisma*, *Spaelotis*, *Discestra*, *Ctenoceratoda*, *Dasypolia* etc.).
- Close taxonomical connections can be observed between the allopatric species of some species groups of xeromontane Noctuidae and Hadeninae genera inhabiting the ranges of Tien Shan and Mongolian Altai (*Dichagyris umbrifera* ALPHERAKY-group, *D. clara* STAUDINGER-group, *Parexarnis candida* STAUDINGER-group, *Ctenoceratoda* and *Hadula* spp.).



Fig. 11. A holomediterranean–pontomediterranean xeromontane sibling species pair: *Chersotis fimbriola* (black circles with white dots) and *Ch. laeta* (black squares)



- Numerous faunal connections are present among the mountain systems of Zerawshan, Hissaro-Darwaz, Eastern Hindukush and Western Pamir (e.g. species-groups of *Euxoa*, *Chersotis*, *Bryopolia*, *Bryoxena* etc.)
- Many xeromontaneous species of Nepal, W Himalaya, Transhimalaya (Ladakh) and the Karakoram region penetrate into the Pamir and Transalai ranges (*Euxoa tibetana* MOORE – *naumanni* VARGA-group, *Pamirorea eberti* RONKAY & VARGA, *Polymixis*, *Himalistra* and *Bryopolia-Bryoxena* spp., see: VARGA 1990, VARGA *et al.* 1991, HACKER & RONKAY 1993, HREBLAY & RONKAY 1995).
- A great number of relict-like monotypic or oligotypic genera occur in some parts of the Tien Shan-system (e.g. Alai Mts, Bolshoi Tshimgan) and in the Xizang-plateau (Tibet) (*Bryomixis*, *Pamirorea*, *Niaboma*, *Euxenistis* etc.)
- Numerous connections have been described between Central Asiatic xeromontane and eremic faunas (e.g. *Hadula*, *Cardiestra*, *Discestra*, *Thargelia*, *Odontelia*, VARGA & RONKAY 1989, 1991).

#### CONCLUSIONS AND HYPOTHESES ON THE ORIGIN AND EVOLUTIONARY HISTORY OF PALAEARCTIC XEROMONTANE NOCTUIDAE

It was revealed that the south-eastern part of the Palaearctic oréal biomes was especially rich in relict-like genera (*Erebophasma*, *Estimata*, *Palaeamathes*, *Perissandria*, *Hoeneidia*, *Oligarcha*, *Sinognorisma*, *Hadulipolia*, *Haderonia*, *Tricheurois*, *Niaboma*, *Euxenistis*, *Himalistra*, *Altipolia*) and in seemingly ancestral species from more widely distributed genera (*Dichagyris*, *Rhyacia*, *Xestia*, *Eu-graphe*, *Conisania*, *Sideridis*, *Polia*, *Oncocnemis*, *Lophoterges*). They often have connections to the high mountains of Central and Inner Asia and Southern Siberia and also in many cases to the continental steppe areas. The strictly stenochorous, more ancestral taxa are regularly connected to the monsoonic forested biomes, while the more derived species or species groups are partially inhabitants of the unforested, at least seasonally dry orobiomes, and in part they are zonally distributed in the boreo-continental coniferous forests of the Palaearctic (or Holarctic).

A very similar case was already described by KOSLOWA (1966) in the passerine bird family Prunellidae. The presumably most ancestral taxa are restricted to the monsoonic mountain forests of W China. Some species could penetrate into the mountain taiga and scrub formations (e.g. *Prunella atrogularis*, *P. montanella*), while others became inhabitants of xeromontane biomes (*P. ocularis* in the mountain systems of Transcaucasia and Iran, *P. fulvescens* from Transcaucasia to Transbaicalia, *P. koslowi* in the extreme cold-continental Mongolian and

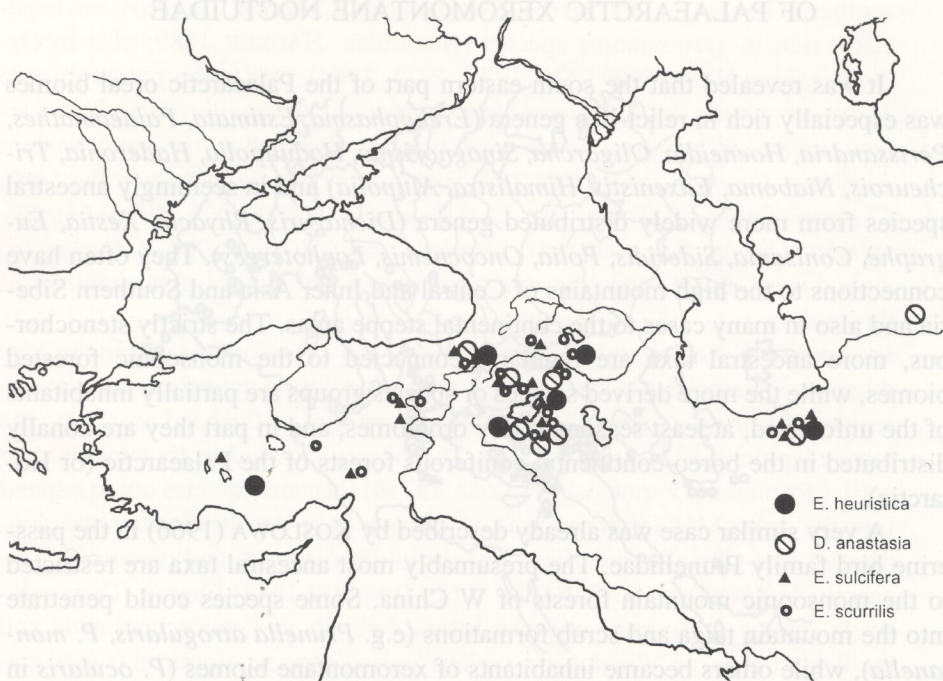


Tibetic high mountains). The members of the subgenus (related genus) *Laiscopus* could also populate alpine elevations, *P. (L.) collaris* in nearly all of the Palaearctic and *P. (L.) himalayanus* mostly in the Transhimalaya-Pamir area.

In the case of a group of four closely related, presumably monophyletic genera (*Trichoridia*, *Blepharosis*, *Bryoxena*, *Bryopolia*, see VARGA *et al.* 1990) we already described and also illustrated a stepwise "creep" from monsoonic areas into the arid central Asiatic regions, connected to the generic and subsequent specific differentiation. Based on taxonomical revision and phylogenetic survey of the genera mentioned above, we suggest some hypotheses for their possible evolutionary history.

We suppose that some basal groups of the "Trifid" Noctuidae must have evolved, jointly with some groups of Angiospermae, in the Eastern Gondwana. They could expand northwards after the earliest collision of the Gondwanian plates (e.g. Southern Tibet and some parts of southern China) with southeastern Asia (LI JI-JUN *et al.* 1981, HSÜ YEN 1981, LI XING-XUE & YAO ZHAO-QI 1981, LIU DONG-SHENG & DING MENG-LIN 1984, SHARMA 1984, etc.).

These processes of dispersal were canalised by the constraints of passing two main filter-corridors (VARGA 1995, Fig. 1).



**Fig. 12.** Distribution of four Transcaucasian-Iranian xeromontane species: *Euxoa sulcifera*, *E. scurrilis*, *Dichagyris anastasia* and *Eugnorisma heuristica*



1. The "Rhododendron-corridor", also now characteristic for several evergreen Angiospermae, e.g. *Vaccinium*, *Empetrum*, *Rhododendron* incl. *Ledum* etc., which now compose a major part of the undergrowth of the Siberian (especially southern Siberian mountain) taiga, typical for a number of "taiga-birds" (e.g. *Ficedula*, *Phylloscopus*, *Luscinia calliope*, *Tarsiger cyanurus*, *Dumeticola thoracica* etc.) and also for a great number of taiga-inhabiting Lepidoptera (Geometridae: *Dysstroma*, *Chlorochlysta*; Noctuidae: several subgenera and species-groups of *Xestia*: *Pachnobia*, *Anomogyna*; *Polia*, *Lasionycta*, some species-groups of *Apamea* etc.).

It seems to be quite typical that some stenochorous species inhabit the southern Siberian mountain taiga (e.g. *Polia vesperugo* EVERSMAAN, *P. vespertilio* DRAUDT, *P. malchani* DRAUDT, *Lasionycta hospita* BANG-HAAS, *L. alpicola* LAFONTAINE et KONONENKO, *L. buraetica* KONONENKO, *Apamea altijuga* KOZHANTSCHIKOW), while some of their relatives are widely dispersed, often having a Trans-Palaearctic or even Trans-Holarctic range of distribution (e.g. *Polia trimaculosa* ESPEY, *P. bombycina* HUFNAGEL, *P. purpurissata* GROTE, *Lasionycta leucocycla* STAUDINGER, *L. skraelingia* HERRICH-SCHAEFFER, *Apamea rubrirenna* TREITSCHKE, *A. zeta* TREITSCHKE etc.). The most recent views on the importance of Beringian refugia (KONONENKO *et al.* 1989, LAFONTAINE & WOOD 1988, MIKKOLA *et al.* 1991) do not contradict but only complement these views. The Southern Siberian mountain taiga and "goltsy" could have been the primary core areas of boreal-Holarctic Noctuidae species, while the ice-free Beringian areas could serve mainly as recent centres of survival and dispersal of these elements during the late-glacial and post-glacial phases.

2. The "xeromontane" route, leading from the Transhimalayan mountains, on one hand to the Karakoram, Pamir, Transalai or even to the Hissar, Zerawshan, Western Tien Shan and Eastern Hindukush ranges, or, on the other hand, via East-Turkestan to the Eastern Tien Shan and Altai-Sajan systems, resulting in a radiation of a rich continental xeromontane fauna. This bifurcation seems to be evident from the taxonomic division of the genera which are typical for these areas. In the xeromontane fauna of the first group of the Inner Asiatic mountains, such butterflies as *Parnassius*, *Karanasa*, *Paralasa* and many lycaenid genera, as well as some, often oligotypic genera of Noctuidae very much restricted to a few mountain ranges, e.g. *Hypsophila*, *Ferghana*, predominate. In the second group the typical butterflies belong to *Colias*, *Oeneis* and *Boloria*, which must also have a xeromontane origin but have penetrated deeply into the tundra zoniomes, as well. The typical Noctuidae genera of this second, more "Siberian", secondarily "oreotundra" group of (originally) xeromontane Noctuidae are e.g. *Trichosilia*, *Lasionycta*, *Discestra*, *Anarta*, *Oncocnemis* & *Sympistis*.

Based on these biogeographical facts, I think that the connections of the Continental, Inner Asiatic xeromontane fauna must be historically more manifold



and older than the "typical" oreotundral connections of the alpine faunal type which can be regarded mostly as a product of the Quaternary climatic fluctuations and area dislocations.

It seems very probable that the ancient groups of the Mediterranean xeromontane fauna can be derived partly from this primary bifurcation of the western continental xeromontane faunal complex and partly by the adaptation of diverse Mediterranean xerophilous arboreal groups due to the late Tertiary aridity crisis. This hypothesis is also supported by the "macro"-taxonomical duality of the Mediterranean xeromontane Noctuidae.

Those genera which belong to the Noctuinae and have "cutworm"-type larvae, have obviously originated in the continental orobiomes (e.g. *Euxoa*, *Agrotis*, *Dichagyris*, *Chersotis*, *Rhyacia*, *Standfussiana*) and their Mediterranean representatives often belong to different, divergently derived phyletic lines within these polytypic genera. The extreme taxonomic subdivision of such genera into several "new" oligo- or monotypic genera or subgenera by some "splitters" (see BECK 1991, 1992, FIBIGER & HACKER 1990), and the fruitless discussion about it, was the direct consequence of the ignorance of the high species diversity of the vast continental areas of Asia, because some authors can see only the "ends of twigs" and not the "trunks" from which these twigs originate. Other genera were probably originally connected to xerophilous scrub formations (*Eugnorisma*, *Auchmis*, *Lophoterges*) or thorny polster-scrub communities (*Xenophysa*, *Copiphana*). Their Mediterranean-Anatolian taxa also display western and central Asiatic connections, and only a marginal speciation in the Mediterranean ranges.

Other genera of the Mediterranean-xeromontane Noctuidae display an essentially autochthonous evolution which was influenced by the younger Tertiary aridisation of the Mediterranean basin. In such genera the Ponto-Mediterranean (incl. parts of Anatolia), the Atlanto-Mediterranean and Maghreb areas usually display a high level of species diversity. Examples of such genera are those of the tribe Oncocnemidini: *Calophasia* and closely related minor genera, *Ompalophana*, *Copiphana*, *Metopoceras* etc. (Cuculliinae) and some Xylenini-genera (*Eumichtis*, *Leucochlaena*, *Aporophila*, *Antitype*, *Ammoconia*, subgenera of *Mniotype*, *Polymixis*, *Agrochola*, *Conistra* etc.). This biogeographical group can be regarded as approximately equivalent to the "Palaeomediterranean-xeromontane" faunal type of some ornithologists (STEGMANN 1938, VOOUS 1960, 1963) and with the faunal type of the "ancient Mediterranean" of the Russian biogeographical school (see KRYZHANOVSKY 1965).

We can only hope that by surveying the extremely rich expedition materials mentioned above and by the intensively proceeding taxonomic and phylogenetic revision of many groups of Noctuidae, a more analytical proof of our hypotheses will be possible in the near future.



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