Centres of endemism of Noctuidae (Lepidoptera) in the Palaearctic arid mountains: biogeographical and phylogenetic implications

With 21 figures, 4 tables and 2 Appendix

ZOLTÁN VARGA

1 Dept. Evolutionary Zoology & Human Biology, Faculty of Science, University of Debrecen, H-4010 Debrecen, Hungary. – varga.zoltan@science.unideb.hu
Published on 2022–07–31
DOI: 10.3897/contrib.entomol.72.e87196

Abstract

The oreal fauna is connected with orographically limited non-arboreal habitats. Its chorological centres can be recognised by the high species-diversity of numerous typical genera, and by the accumulated occurrence of endemic species and/or subspecies of disjunct species. The oreal fauna is partitioned to the alpine type, as the faunal type of humid high-mountains with strong connections to the tundral zonobiome, and the xeromontane type, as the faunal type of arid high-mountains with close connections to the eremic zonobiomes. As the results of revisions of several Noctuinae genera, species groups and/or sister species were recognised and their distributions were mapped. The restricted areas of allopatric sister species, often described by us as new for science, fulfil the criteria of the “areas of endemism”. Core areas of the Palaearctic xeromontane Noctuidae, outlined by the distribution of endemic species, have been proven by the occurrence of allopatric subspecies of polytypic species, and/or by the presence of allopatric sister species. In the revised genera of Noctuidae several types of allopatric speciation have been identified based on the analysis of the areas of endemism and of vicariance patterns. As a result of these analyses, it is proved that allopatric sister species, as elementary monophyletic supraspecific units, are suitable for phylogenetic biogeographical surveys. Although the major part of the xeromontane fauna appears to be range-restricted, a considerable fraction of the species could have expanded into the steppic zonobiome due to adaptive changes of their life cycles. High diversity of cold-adapted species originated from the Sino-Himalayan mountains by passing two main filter-corridors. One track of this bifurcation was directed across the “Rhododendron-corridor” to the Holarctic taiga zone while the other one, across the “Xeromontane filter-corridor” to the mountain systems of Central and Inner Asia. This bifurcation becomes apparent from the taxonomic division of the genera, composing both of these main faunal types. Supposedly, the faunal movements of the xeromontanean species in the West Palaearctic had been shaped by the Messinian salinity crisis and, additionally, significantly influenced by the Mid-Pleistocene climatic transition which deeply transformed the zonality of the vegetation by cooling and aridisation of vast areas.

Key words

Noctuidae, oreal fauna, xeromontane fauna, areas of endemism, monophyletic species groups, allopatric speciation, climatic constraints, filter-corridors
Zusammenfassung

Die Orealfauna ist mit den orographisch geprägten non-arborealen Lebensräumen eng verbunden. Ihre choro-
logischen Zentren lassen sich durch die Artenmannigfaltigkeit bestimmter Genera und ein gehäuftes Vorkommen
von endemischen Arten sowie Subspezies disjunktener Arten erkennen. Die Orealfauna umfasst eine Vielzahl
von zwei wichtigen Filter-Korridoren ableiten. Ein Zweig dieser Bifurkation verläuft durch den „Rhododendron-
Korridor“ in den holarktischen Taiga-Gürteln, während ein anderer Zweig durch den xeromontanen Filter-Korridor
in die Gebirgssysteme von Zentral- und Innerasien verläuft. Diese Unterteilung lässt sich durch die unterschiedlichen
taxonomischen Einheiten bestätigen, die sich als geeignet für phylogenetisch-biogeographische Untersuchungen erwiesen. Obwohl der größte Teil der xeromontanen
Alpenengarten probe arborescentes Anteile ausweist, konnte sich ein beträchtlicher Teil der Arten weit in die zonalen
Steppengebiete der nicht arboralen biotopen verlagern. Die große Mannigfaltigkeit der im sino-himalayischen Hochgebirge entstehenden Arten in den Regionen mit kälteangepassten Arten lassen sich durch das Durchdringen von zwei wichtigen Filter-Korridoren ableiten. Ein Zweig dieser Bifurkation verläuft durch den „Rhododendron-
Korridor“ in den holarktischen Taiga-Gürteln, während ein anderer Zweig durch den xeromontanen Filter-Korridor
in die Gebirgssysteme von Zentral- und Innerasien verläuft. Diese Unterteilung lässt sich durch die unterschiedlichen
taxonomischen Einheiten bestätigen, die sich als geeignet für phylogenetisch-biogeographische Untersuchungen erwiesen. Obwohl der größte Teil der xeromontanen
Fauna an den eng begrenzten Arealen aufzuweisen scheint, konnte sich ein beträchtlicher Teil der Arten weit in die zonalen
Steppengebiete der nicht arboralen biotopen verlagern. Die große Mannigfaltigkeit der im sino-himalayischen Hochgebirge entstehenden Arten in den Regionen mit kälteangepassten Arten lassen sich durch das Durchdringen von zwei wichtigen Filter-Korridoren ableiten. Ein Zweig dieser Bifurkation verläuft durch den „Rhododendron-
Korridor“ in den holarktischen Taiga-Gürteln, während ein anderer Zweig durch den xeromontanen Filter-Korridor
in die Gebirgssysteme von Zentral- und Innerasien verläuft. Diese Unterteilung lässt sich durch die unterschiedlichen
taxonomischen Einheiten bestätigen, die sich als geeignet für phylogenetisch-biogeographische Untersuchungen erwiesen. Obwohl der größte Teil der xeromontanen
Fauna an den eng begrenzten Arealen aufzuweisen scheint, konnte sich ein beträchtlicher Teil der Arten weit in die zonalen
Steppengebiete der nicht arboralen biotopen verlagern. Die große Mannigfaltigkeit der im sino-himalayischen Hochgebirge entstehenden Arten in den Regionen mit kälteangepassten Arten lassen sich durch das Durchdringen von zwei wichtigen Filter-Korridoren ableiten. Ein Zweig dieser Bifurkation verläuft durch den „Rhododendron-
Korridor“ in den holarktischen Taiga-Gürteln, während ein anderer Zweig durch den xeromontanen Filter-Korridor
in die Gebirgssysteme von Zentral- und Innerasien verläuft. Diese Unterteilung lässt sich durch die unterschiedlichen
taxonomischen Einheiten bestätigen, die sich als geeignet für phylogenetisch-biogeographische Untersuchungen erwiesen. Obwohl der größte Teil der xeromontanen
Fauna an den eng begrenzten Arealen aufzuweisen scheint, konnte sich ein beträchtlicher Teil der Arten weit in die zonalen
Steppengebiete der nicht arboralen biotopen verlagern. Die große Mannigfaltigkeit der im sino-himalayischen Hochgebirge entstehenden Arten in den Regionen mit kälteangepassten Arten lassen sich durch das Durchdringen von zwei wichtigen Filter-Korridoren ableiten. Ein Zweig dieser Bifurkation verläuft durch den „Rhododendron-
Korridor“ in den holarktischen Taiga-Gürteln, während ein anderer Zweig durch den xeromontanen Filter-Korridor
in die Gebirgssysteme von Zentral- und Innerasien verläuft. Diese Unterteilung lässt sich durch die unterschiedlichen
taxonomischen Einheiten bestätigen, die sich als geeignet für phylogenetisch-biogeographische Untersuchungen erwiesen. Obwohl der größte Teil der xeromontanen
Fauna an den eng begrenzten Arealen aufzuweisen scheint, konnte sich ein beträchtlicher Teil der Arten weit in die zonalen
Steppengebiete der nicht arboralen biotopen verlagern. Die große Mannigfaltigkeit der im sino-himalayischen Hochgebirge entstehenden Arten in den Regionen mit kälteangepassten Arten lassen sich durch das Durchdringen von zwei wichtigen Filter-Korridoren ableiten. Ein Zweig dieser Bifurkation verläuft durch den „Rhododendron-
Korridor“ in den holarktischen Taiga-Gürteln, während ein anderer Zweig durch den xeromontanen Filter-Korridor
in die Gebirgssysteme von Zentral- und Innerasien verläuft. Diese Unterteilung lässt sich durch die unterschiedlichen
taxonomischen Einheiten bestätigen, die sich als geeignet für phylogenetisch-biogeographische Untersuchungen erwiesen. Obwohl der größte Teil der xeromontanen
Fauna an den eng begrenzten Arealen aufzuweisen scheint, konnte sich ein beträchtlicher Teil der Arten weit in die zonalen
Steppengebiete der nicht arboralen biotopen verlagern. Die große Mannigfaltigkeit der im sino-himalayischen Hochgebirge entstehenden Arten in den Regionen mit kälteangepassten Arten lassen sich durch das Durchdringen von zwei wichtigen Filter-Korridoren ableiten. Ein Zweig dieser Bifurkation verläuft durch den „Rhododendron-
Korridor“ in den holarktischen Taiga-Gürteln, während ein anderer Zweig durch den xeromontanen Filter-Korridor
in die Gebirgssysteme von Zentral- und Innerasien verläuft. Diese Unterteilung lässt sich durch die unterschiedlichen
taxonomischen Einheiten bestätigen, die sich als geeignet für phylogenetisch-biogeographische Untersuchungen erwiesen. Obwohl der größte Teil der xeromontanen
Fauna an den eng begrenzten Arealen aufzuweisen scheint, konnte sich ein beträchtlicher Teil der Arten weit in die zonalen
Steppengebiete der nicht arboralen biotopen verlagern. Die große Mannigfaltigkeit der im sino-himalayischen Hochgebirge entstehenden Arten in den Regionen mit kälteangepassten Arten lassen sich durch das Durchdringen von zwei wichtigen Filter-Korridoren ableiten. Ein Zweig dieser Bifurkation verläuft durch den „Rhododendron-
Korridor“ in den holarktischen Taiga-Gürteln, während ein anderer Zweig durch den xeromontanen Filter-Korridor
in die Gebirgssysteme von Zentral- und Innerasien verläuft. Diese Unterteilung lässt sich durch die unterschiedlichen
taxonomischen Einheiten bestätigen, die sich als geeignet für phylogenetisch-biogeographische Untersuchungen erwiesen. Obwohl der größte Teil der xeromontanen

Introduction - Oreal fauna, definition and subdivision

The composition of terrestrial animal assemblages strongly depends on the level of primary production,
limited by the available solar energy and water circulation (Beer et al. 2010, Pappas et al. 2016, Simova & Storch
2017). Satellite images clearly reveal that both the Net Primary Production (NPP) and the Gross Primary
Production (GPP) are the lowest in the tundral and desert zonobiomes. They are, however, similarly low
in orobiomes, i.e. in different high mountains, surrounded by belts with a higher level of primary production
(e.g. Rodin & Bazilevich 1966, Prince & Goward 1995, Running et al. 2004). If we simply specify the arbo-
real biomes (see de Lattin 1967) as terrestrial habitats characterised by medium or higher level of primary
production, the oreal fauna can be identified as the faunal type of humid high-mountains with prevailing glacial
weathering and morphology, and with strong connections to the tundral zonobiome, and the xeromontane type, as the
faunal type of arid high-mountains with prevailing physical weathering and manifold connections to the eremic zonobiomes. As the dynamics of the alpine faunal
type is closely connected with the Quaternary glaciations, its history is characterised by long-distance range translocactions and disjunctions, resulting in the diversifi-
cation of a great number of arctic-alpine species (Varga & Schmitt 2008, Schmitt 2009). On the contrary, the
evolutionary history of the xeromontane faunal type was supposedly less disturbed by glaciation-interglaciation
cycles. Thus, it has a high potential for speciation in several groups adapted to the seasonally arid conditions as many Noctuinae moths belonging to the genera Euxoa,
Dichagyris, Acteia s.l., Chersotis, Rhyacia, Standfussiana, Eugnorisma, Spaelotis, Xenophyia, etc. (Varga 1995,
1997, 2010b), Polyommatus blues (e.g. Polyommatus subg. Agrodiaetus, Eckweiler & Haeuser 1997, Kandul
et al. 2004, 2007, Lukhtanov et al. 2005), and also in some flightless grasshopper groups (e.g. Conophyuma,
Nocaracris, Nocarodes, see: Li et al. 2011, Uyal 2016). Considering the composition of the European alpine
Lepidoptera, high species diversity was found in several “Microlepidoptera” families and genera (Gelechiidae:
Caryocolum, Huemer et al. 2014, Huemer & Karsholt 2020; Sattleria, Huemer & Hebert 2011, Huemer & Timossi 2014; Yponomeutidae: Kessleria, Huemer & Mutanen 2015), certain genera of Geometridae (e.g. Entephrus, Psodos, Charissa, Elphos; Huemer 1998, Müller et al. 2019) and Nymphalidae (Boloria, Erebia; Varga 1996, 2003, Varga & Schmitt 2008), however, surprisingly much less in the otherwise highly diverse Noctuidae (Varga 2003). This situation is contrasting with the outstanding taxonomic diversity of the xeromontane fauna in the Central and Inner Asian1 mountain systems and these core areas were modulated regions following the emergence of the Sino-Himalayan region (Varga 2010b) where numerous genera of Noctuidae (mostly of Noctuini, Hadenini, Xylenini, Apameini, and Oncocnemidinae) feeding on grasses and herbaceous plants predominate not only in the species composition but also in the density of individuals.

Following these preliminary considerations, I developed the hypothesis that we can recognise some typically repeated patterns of vicariance in range-restricted sister species and, in parallel, essentially similar disjunct distributions in polytypic species in numerous genera of the xeromontane Noctuidae. Based on the taxonomic revisions of several diverse genera, mostly from Noctuidae, I also hypothesised that these patterns reveal important general trends of allopatric speciation which can be uncovered by phylogenetic biogeographical methods. Furthermore, I found it plausible to search for certain repeatedly appearing biogeographical and phylogenetic connections between the range-restricted xeromontane species and the zonally distributed congeneric steppe species. Finally, I hypothesised that the core areas of the Palaearctic xeromontane fauna are connected with the Central and Inner Asiatic high mountains as a consequence of the cooling and aridisation of these regions following the emergence of the Sino-Himalayan mountain systems and these core areas were modulated by the Mid-Pleistocene climatic transition.

Materials and methods

This biogeographical review is based on generic and suprageneric taxonomic revisions of several Noctuidae genera (mostly Noctuinae: Dichagyris, Actebia, Euxoa, Chersotis, Rhyacia, Standfussiana, Eugnorisma, Goniographa, Xenophysa). Most of the type specimens of the revised taxa were studied; thousands of genitalia slides were prepared, photographically and graphically documented and electronically stored. In a book series (Varga et al. 2013, 2015, 2019) and in generic revisions (Varga & Ronkay 1987, 1996, 2002; Ronkay & Varga 1999; Varga & Gulyai 1999; Varga 1998, 2011a, b, 2014; Varga et al. 1989, 2018) numerous new genera, subgenera, species and subspecies were described, subgenera and species groups were separated, pairs or triplets of sister species were stated, and new taxonomical statuses were established.

Based on the data of large European public and private collections, and of relevant literature, distribution maps of Noctuinae species were prepared, with special respect to allopatric sister species and disjunct polytypic species. Distributional data matrices of the genera Dichagyris, Chersotis, Rhyacia, Standfussiana, Eugnorisma, Goniographa, Xenophysa were prepared and the species were ordered to some types of distributions (Supplement 1), and they also grouped according to the types of geographical variations (Results 1). In the revised genera the species have been arranged into subgeneric groups, the allopatric sister species/subspecies relations were established, and based on them, area-dendrograms of species groups were constructed (Figs 4, 5, 13).

In the first step, following the principle of the “areas of endemism” (Harold & Mooi 1994), I outlined some core areas by the accumulated occurrence of strictly endemic species (e.g. Kopet-Dagh Mts, parts of Hindukush Mts, the Pamirs and the Tien Shan system, etc. (Results 2). In the next step, these core areas were confirmed by the repeated patterns of disjunct polytypic species, and pairs (eventually triplets) of allopatric sister species. These species-group taxa were considered as elementary monophyletic supraspecific units (Results 3). Principally, this procedure is followed by the analysis of monophyletic species groups within a genus, then by phylogenetic analyses of subgenera and genera etc. It is essential that the whole multi-step procedure runs from the taxonomically lower levels to the higher ones. As the last step, according to the available life cycle data (aestivation, hibernation), some eco-physiological backgrounds of restricted distribution vs expansive area dynamics were uncovered (Figs 7, 14, 15, 18; Results 3 and Discussion 1).

Results 1: Types of geographical and taxonomical subdivisions in xeromontane Noctuidae

Based on the geographical variation (in widely distributed, mostly polytypic species) and on the patterns of vicariance (in disjunct species and allopatric sister species), several types of differentiation were recognised in Palaearctic xeromontane Noctuidae.

The following types of geographical variation have been separated (Tables 1–4, Supplement 1).

- Widely distributed, often polytypic species with parallel polymorphism of distinctly marked vs. unicolorous forms in different populations2 (e.g. in some

---

1 On the meaning of the terms Central vs Inner Asia see: Fig. 1 and Discussion 2.
2 The full names of the species (with authors and years) mentioned as examples in the text are listed in the Tables 1–4 and Appendix I.
Euxoa spp.: the “huebneroides” types vs unicolorous forms, Dichagyris terminincincta, D. psammochroa, Eugnorisma (E.) insignata, E. (Metagnorisma) pontica). In these species the relative frequency of parallel marking and/or colouration variations often show some geographical trends (e.g. Euxoa christophi & f. lugens, Euxoa sigmata & f. designata, D. terminincincta f. phaetonaenia & f. capnistis; D. psammochroa & f. dichroa, E. insignata f. pallescens & f. leuconeura; E. (M.) pontica & f. consensescens), however, without any clear subspecific differentiation.

Parallel polymorphism and taxonomic differentiation are combined in the polytypic Euxoa adumbata. As an extreme case, a contrasting vs. unicolorous dark bilateral somatic mosaic male specimen (Mongolia, Govi Altai aimak, Adž Bogd Mts, leg. Peregovits & Varga, figured in Fibiger 1997:35) was found as evidence of co-specificity of infraspecific colour morphs. Incipient allopatric speciation was shown in the widely distributed, disjunct West-Central Asiatic sister species Euxoa homicida – E. transascipans (Fig. 2). These cases may be interpreted as intermediate stages of differentiation of a polytypic species into a complex of sister species.

Some further species are also polytypic (*polytypic species with disjunctions and peripheral subspeciation at the western boundary of the range, e.g.: Euxoa heringi*, Dichagyris melanura*, D. celsicola*, Chersotis capnistis*, Ch. zukovskyi*, Ch. laeta*, Rhyacia psammia* (= nyctymerides). These species are distributed in Asia Minor and/or in Western and Central Asiatic mountains. The marginal populations of most species are fragmented in high mountains of the southern part of the Balkan Peninsula by the breakdown of the Aegean Arc (Fig. 3). This process has already resulted in multiple cases of insular speciation in Crete, e.g. Euxoa melikyi (sister species of E. heringi), Dichagyris rhadamanthus (sister species of D. melanura).

Sibling species with peripatric isolation in West and/or Central Asia: These are widely distributed species with an allo- or parapatric sister species at the eastern or south-eastern periphery of the range of the more expansive, often polytypic* species, e.g. Dichagyris vallesiaca* – D. fuscashmiriana, D. vreecunda* – D. karakorealis, D. singularis* – D. melanofusca, Eugnorisma insignata* – E. conformis (see: Varga, Ronkay & Yela 1990: Figs 73, 75); Chersotis elegans – Ch. eberti (see: Dufay & Varga 1995, Varga 1997: Fig. 7), Ch. juvenis – Ch. kouros (Fig. 4), Ch. sordescens – Ch. hercizi (Fig. 5). These cases are considered as results of allopatric speciation by peripheral isolation.

Allopatric pairs of West- and Central/Inner Asiatic sibling species (Tables 1–3): Euxoa aneucta – E. subeucta, E. sigmata – E. metasignata (Fig. 6), Dichagyris striata – D. tyrannus, D. humilis – D. hypotacta, D. darius – D. argentea, D. taftana – D. guentereberti, D. streuma – D. vietteana; Hemiearnis lugumua – H. berezkii; Chersotis firdus – Ch. fidahusseini (Fig. 5); Ch. capitnis – Ch. leucostola (Fig. 7), Rhyacia gabori – R. evartianae (Fig. 8); Goniothela marcida – G. gyulaeipeteri; Xenophyes cucumen – X. anghoreana (Mikkola et al. 1987; Varga 1993, 1998, 2002, 2014; Varga & Gyulai 2000; Varga et al. 2011). In these species the populations of Asia Minor, West and North Iran are taxonomically differentiated from the populations distributed in Central Asia (Pamirs, Hindukush and Tien Shan Mts). In other cases the allopatric species occur in Iran + Transcaspia, and in Central Asia (Hissaro-Dawaz Mts, Pamirs, Hindukush Mts, Tien Shan Mts). The allopatric species are usually separated by the huge arid belt East of Transcaspia (see: Figs 5, 7, 8) as a consequence of range-restriction by aridisation of Central Asia.

Allo- or parapatric groups of species, similarly to the former groups, with long distance disjunctions between the Anatolian-Iranian and Central Asiatic massifs as Hissar Mts, Pamirs and/or Hindukush (Table 3): Chersotis vicina – Ch. peternarci; Ch. calorida – Ch. shandur (Fig. 4), Ch. delear – Ch. electrogaphra – Ch. vargai, Rhyacia diploogramma – R. orromys; Goniothela decussa – G. discusa; G. funkei – G. metafunkei – G. naumanni (Fig. 9).

Allo- or sympatric groups of species, similarly to the former groups, with long distance disjunctions between the Anatolian-Iranian and Central Asiatic mountains (Table 1, 3): Dichagyris cataleipa – D. psammochroa – D. afghana – D. kurbatskyi – D. apochora; Chersotis binaloudi – Ch. antiquaphra – Ch. argyrographa (Fig. 10); Chersotis ronkayorum – Ch. sterilis – Ch. nitens – Ch. metagrapha (Fig. 7); Chersotis sarhada – Ch. hoppei – Ch. lehmanni – Ch. lukhtanovii.

Pairs or groups of partially sympatric sibling species, evolved by former geographical isolation and secondary overlap: Chersotis andereggi – Ch. acutangula; Ch. juvenis – Ch. kouros; Ch. ocellina – Ch. alpestris – Ch. oreina – Ch. stridula – Ch. transiens; Chersotis halmi – Ch. curvispina – Ch. cryptographa; Rhyacia subdecora – R. scythepra – R. oxyethca (Fig. 8); Bryopolia virens – B. tsvetaevi – B. chamaeleon – B. chrysopora; Bryopolia monotona – B. thomasi – B. ronkayorum (Varga et al. 1990).

Species groups evolved by vicariance and, additionally, by the change of the life cycle. In these cases some allopatric endemic species are opposed to a widely distributed sister clade in which the increased dispersal capacity is the consequence of the adaptive change of the life-cycle (Chersotis capitnis-group, Varga & Ronkay 1996). Detailed description of these life-cycle changes and biogeographical consequences is provided in the Results 3.
Fig. 1: Important parts and mountain systems of Eurasia.

Fig. 2: Sister species with incipient allopatric speciation, with slight differentiation in the genitalia: *Euxoa homicida* (Asia minor and Iran, exception: Khorasan and Baluchistan) and *E. transcaspica* (Transcaspia, Afghanistan, Pakistan; subspecies are here not distinguished).

Fig. 3: Distribution of the species: *Dichagyris celsicola gracilis* (1), *Chersotis zukowskyi* (2), and *Rhyacia psammia* (3). They are distributed in Western and/or Central Asiatic mountains; some marginal populations have been fragmented in the mountains of the southern part of the Balkan Peninsula by the breakdown of the Aegean bridge. *Rhyacia psammia* is subdivided to six subspecies (Varga 2011).
Results 2: The xeromontane fauna: areas of endemism and phylogenetic implications

A major part of the xeromontane fauna appears to be range-restricted with numerous relic-like species, especially in certain mountain systems of Central and Inner Asia. The restricted areas of the endemic species and of the allopatric sister-species correspond to the criteria of the “areas of endemism” (Harold & Mooi 1994), therefore, as monophyletic species groups, they are suitable for multi-step phylogenetic-biogeographical studies (see: Methods).

As a result of taxonomic revisions, those genera proved to be most suitable for phylogenetic-biogeographical analyses in which (i) there are numerous strictly endemic species, (ii) there are also some polytypic species with disjunct ranges, and (iii) also some expansive species occur with large, seemingly continuous ranges. These highly diverse genera, as e.g. Euxoa, Dichagyris s.l., Actelis s.l. (subg.: Parexarnis, Protexarnis, Hemixarnis), Chersotis (Varga 1998), Rhynacia, Eugnorisma (Varga, Ronkay & Yela 1990), Xenophysa (Varga 1989a, 2011) etc. can often be subdivided into some subgenera and/or several groups of species with closer phylogenetic relationships (Supplement 2).

Eco-physiological responses to climatic challenges proved to be significant drivers of the ranges. The phylogenetic bifurcation of the Noctuinae genus Xenophysa (Figs 11-13) reflects a close connection with some essentially different climatic belts of the arid high mountains of Eurasia. The range of distribution of the western lineage (“X. junctimacula”-species group) reaches the central part of the Hindukush Mts, and its limitation clearly coincides with the eastern boundary of the sub-Mediterranean equinocial type of precipitation (Agakhanjants 1981, Agakhanjants & Breckle 1995). The only widespread species pair of this group, X. taeumena and X. afghanorea shows a typical long-distance disjunction (Elburs and Kopet-Dagh Mts vs. Hindukush Mts) with occurrences in the western Hindukush massif (Koh-i-Baba) and the Pamir Mts. The presence of numerous range-restricted species of this group (X. argyrogramma, X. xenogramma, X. monastica, X. poecilogramma) seems to be confined to the central and eastern-south-eastern flank of the Hindukush mountain range (Fig. 11). The range of the eastern lineage (“X. agnostica”-group: X. agnostica, X. naumannni, X. pseudopoecila and the more isolated X. sharhu) extends from the Saravshan and Hissaro-Darwaz Mts to the western part of Mongolia (Fig. 12), reaching also to the western Tien-Shan and Karakoram Mts. They have a narrow belt of overlapping with the western species group, mostly in the Hissaro-Darwaz range and in the eastern part of the Hindukush Mts. The most closely related sister species, the widespread X. agnostica and the restricted X. naumannni seem to be parapatric, while the distribution of the widespread X. pseudopoecila is partly sympatric with both species. However, X. poecilogramma, which belongs to the western group, locally co-occurs with both latter species in the eastern flank of the Hindukush range (Shandur pass, Figs 11-13).

The range of distribution of some genera or subgenera of Noctuidae, typical for xerothermic scrub-forests of western Asia (e.g. Ostheldera, see: Ronkay & Varga 1993; species groups of the large and heterogeneous genera Polyximixis, Mniotype, Anchoscelis etc.) also extends to the same eastern boundary of the sub-Mediterranean type of precipitation in the Hindukush and western Tien-Shan ranges as the western clade of Xenophysa.

The variety of allo- and sympatric distributions of sister species, combined with disjunctions of the ranges, has been observed in the Eugnorisma chaldaica – E. spodia species group. The widespread E. chaldaica occurs from Central Anatolia and the south-eastern Russian steppes to southern Siberia, with subspeciation from south-eastern Turkey to the adjacent areas of North Iran and also in the western Altai Mts (Fig. 14). Between the two major population groups of E. chaldaica a wide disjunction is gapping, from North Iran to the western Altai Mts in north-eastern part of Kazakhstan, which is “filled” by further taxa: E. kristenseni and the stenotopic E. spodia spodia in the Kopet-Dagh Mts, and the widely distributed E. kristenseni and E. spodia psamnochrea in southern Kazakhstan and Uzbekistan, respectively (Varga & Ronkay 1987; Varga & al. 1990, 2015). In the Eugnorisma ignoratum species group (Fig. 15) there are also two widespread species: Eugnorisma ignoratum and E. mikkolai occurring in the hilly and zonal steppe areas, as opposed to the montane E. puengeleri (sister species of E. mikkolai, eastern Hindukush in Afghanistan and North-West Pakistan), E. tamerlana, a Central Asiatic semi-desert species and the endemic E. cuneiferum, which only occurs in the mountains of Transcardia (Iran, Prov. Khorasan and Turkmenistan: Kopet-Dagh Mts, Varga et al. 1990, Varga & Ronkay 1994).

Results 3: Allopatric speciation and species groups in the genera Chersotis Boisdouval, 1840 and Rhynacia Hübner, [1821]

The genus Chersotis is rich in pairs and/or groups of closely related species (Tables 3–4, Appendix II). Here those allopatric species-groups are treated which are distinguished by recognised synapomorphies of genitalia. Significant characters of these species-groups are already described and illustrated in taxonomic revisions (Varga 1996b, 1998; Varga et al. 2013).

We have selected two species groups which nearly exclusively consist of range-restricted species. The sibling pair Chersotis firdusii (Elburs Mts; Kopet-Dagh Mts) and Ch. fidahusseini (West Tienshan, Hindukush, Karakoram, North-West Himalaya) are considered as sister group of the species pair consisting of the more widespread Ch. sordescens and the West Himalayan endemic
Ch. herczigi (Himalayas: Pakistan, Kaghan valley (Fig. 5)). The Ch. rectangula-andereggii species group can be regarded as outgroup of this species-group. The next "triplet" of species uniformly shows some characteristic features of genital structures. The westernmost species, Ch. binaloudi occurs in Khorasan (NE Iran), and its sister species are the "twins": Ch. antigrapha (Hindukush Mts) and Ch. argyllographa (W Pamirs range, Fig. 10). We consider the set of the Ch. vicina group and Ch. juvenis group as their sister-group (the taxonomic details and species descriptions are published by Varga 1996b, 1998; Varga & Ronkay 1996; Varga et al. 2013). Both latter species groups consist of range-restricted allopatric species.

Nearly the same pattern of allopatric distribution was observed in a species group (subg. Anchorhyacia Varga, 2011) of the closely related genus Rhyacia. The allopatric R. gabori (Kopet-Dagh Mts) and R. evartianae (Hindukush and Hissaro-Darwaz range) are forming together the sister-group of R. scythropa (Hindukush: Koh-i-Baba and Paghman Mts) and R. oxytheca (West Pamirs, East Hindukush, Karakoram, North-West Himalayas, Fig. 8). All these species share the acute process of the juxta as synapomorphy. Their probable sister-group is the widely distributed, polytypic R. subdecora. Two further species pairs also belong to this subgenus, the partly sympatric R. psammia* (polytypic, widely distributed) – R. nyctymerina (Tien Shan) and the allopatric twin species R. diplogramma (Tien Shan system) and R. oromys (Pamirs, Hindukush, West Himalayas). All of these species groups share the synapomorphies as follows: the modified clavus densely covered by small spines, the hook-shaped carina of the aedeagus, and the large subbasal and the conical, sclerotised medial diverticula of the vesica (Varga 1990, 2011).

In some other cases, there is a partial overlap in the distribution of the closely related species. These overlapping species have a fairly large extended range with subspecific subdivision (e.g. the species pairs Chersotis rectangula and Ch. andereggii, Ch. elegans* and Ch. anatolica*, Ch. fimbriola* and Ch. laeta*, Fig. 16). As all of these species are widely distributed and mostly polytypic*, their distribution patterns should be considered as cases of secondary overlaps, subsequently to the previous allopatric process of speciation.

The geographical extension of the allopatric areas of sister species may be rather different. The allopatric Chersotis andereggii and Ch. juncta, Ch. firdusii and Ch. fidahusseini, Ch. capnistis* and Ch. leucostola, Ch. sarhada and Ch. lehmanni have relatively extended ranges, while in other cases the large area of an expansive species is combined with the peripherally isolated ranges.
of some range-restricted species, obviously originating from marginal splitting: *Ch. semna* vs. *Ch. pachnosa*; *Ch. juvenis* vs. *Ch. kouros*, *Ch. elegans* vs. *Ch. kacem* and *Ch. eberti*. In some other cases both members of the allopatric pair are strictly endemic, e.g.: *Chersotis ronkayorum* – *Ch. sterilis*, *Ch. nitens* – *Ch. metagraphe*, *Ch. petermarci* – *Ch. vicina*, *Ch. calorica* – *Ch. shandar*, *Ch. binaloudi* – *Ch. antigrapha*, *Ch. gratissima* – *Ch. zagros*, *Ch. nupponenorum* – *Ch. nekrasovi* (Fig. 17).
Fig. 7: The *Chersotis capnisti* group is subdivided into four allopatric, endemic species (1. Ch. ronkayorum, 2. Ch. sterilis, 3. Ch. nitens, 4. Ch. metagrapha) and to the Ch. capnisti (5.) – Ch. leucostola (6.) pair of species. The latter have large fat-bodies and a life-cycle with aestivation of imagos with a relatively large range of distribution. Taxonomy and phylogeny: Varga 1998.

Fig. 8: Distribution of the species: *Rhyacia gabori* (1) – *Rh. evartianae* (2) – *Rh. scythropa* (3) – *Rh. oxytheca* (4) – *Rh. subdecora* (5). The range of *Rh. psammia* (6) is on Fig. 1. Taxonomy and phylogeny: Varga 2011.
However, the existence of a few, phylogenetically strongly separated species (e.g. *Ch. sjuntensis*, *Ch. glebosa*, *Ch. illauta*) supports the hypothesis, that in this genus also an older wave of speciation should have proceeded, from which most of the species became extinct. This hypothesis is strongly supported by such cases in which the species-groups consist of one strongly differentiated species, which can be regarded as outgroup of all other members of the species group, e.g. *Ch. larixia* (with extremely fragmented range of distribution) for the *Ch. elegans-kacem-eberti-anatolica* group. All these cases refer to an ancient and a subsequent, more recent wave of the allopatric speciation in the genus *Chersotis*. 

---

**Fig. 9**: Distribution of the *Goniographa funkei*-group; one more distant species, *G. marcida* (1), and three closely related ones: *G. naumanni* (1), *G. metafunkei* (2), *G. funkei* (3). The sister species (2) and (3) are strictly allopatric, (1) and (2) are overlapping in the Hissar Mts. Taxonomy and phylogeny: VARGA & RONKAY 2002.

**Fig. 10**: Distribution of the *Dichagyris psammochroa*-group: *Dichagyris cataleipa* (1) – *D. psammochroa* (2a-2b) – *D. afghana* (3) – *D. apochora* (4) – *D. kurbatskyi* (5); Distribution of the *Chersotis binaloudi*-group: *Ch. binaloudi* (6) – *Ch. antigrapha* (7) – *Ch. argyllographa* (8). Taxonomy and phylogeny: VARGA 1993, 1998; VARGA & RONKAY 1996; VARGA et al. 2021.
Discussion 1: Climatic constraints in the life cycle evolution of Noctuidae

In Noctuidae there are several types of univoltine life cycles, adapted to the seasonally cold and/or arid, temperate climate by different forms of larval and/or imago diapause (Ryabov 1956; Sukhareva 1999; Saulich et al. 2017). Such univoltine life cycles probably can be derived from ancestral polycyclic types due to the insertion of diapause periods as hibernation and/or aestivation (Fig. 19). In these cases the larvae can use some resources of short duration by the right timing of active periods, and they can also be adapted to the seasonal insufficiency of resources by the diapause. There are several, in parallel developed different combinations of life cycles, connected to the centres of species diversity, mentioned above. One of the typical responses of noctuid moths to the aridity is the aestivation of the larvae (most often in the prepupal stage, Specht et al. 2013), and/or of the adults, which has evolved in parallel in many different taxonomical groups (Fig. 19), mostly in the subfamily Noctuinae (Euxoa, Dichagyris s.l., Actebia s.l., Chersotis, Rhyacia s.l., Standfussiana, Noctua, Spaelotis etc.). The well-developed abdominal fat bodies obligatorily serve as pre-requisite of the successful aestivation and reproduction after the aestivation of the adults.

In the “capnistis”-group of the genus Chersotis there are four stenotopic endemic species (Fig. 7) in high altitudes of arid high mountains of West and Central Asia, without well-developed fat bodies, while the sister species Ch. capnistis* and Ch. leucostola have large fat-bodies and a life cycle with imaginal aestivation, combined with
a relatively large range of distribution (Varga & Ronkay 1997: 115), extending into moderate altitudes in steppe areas of the southern Ural Mts (Ch. capnistis) or the Dzhungarian Ala-Too (Ch. leucostola).

The possibility to gain a “zonal” expansion into the steppe biome seems to be linked to those noctuid moths (mostly Noctuinae) which either emerge at early summer and subsequently have a post-aestivation dispersal period in the late summer or early autumn (Fig. 19) as the above-mentioned Chersotis species, or numerous species of Noctua, Spaelotis and Standfussiana, or they have their whole, much shorter adult period in this season of the year. See examples: Euxoa basigramma*, E. christophi (Fig. 18), E. deserta*, E. diaphora, E. distinguenda*, E. fallax, E. foeda, E. hastifera*, E. sabuletorum, E. segnalis*; Agrotis bifurca, A. psammoscharis, A. ruta, A. trifurca; Chersotis elegans*, Ch. anatolica*; Eugnorisma chaldaica*; E. eminens*, E. ignoratum, E. insignata*, E. mikkolai etc. (Figs 14–15).

As one of main results of our preliminary taxonomic surveys (e.g. Ronkay & Varga 1999; Varga 1996b, 1998, 2011; Varga & Ronkay 1997; Varga et al. 2013), taxonomic groups of the Mediterranean xeromontane fauna appear to have two different main sources of origin. The bulk of genera probably can be derived from the primary bifurcation of the Palaeartic xeromontane faunal complex (Fig. 20). The other group had evolved from diverse Mediterranean xerophilous arboreal groups by adaptation to the aridity in connection with the late Tertiary Messinian Saline Crisis (Varga 1997, 2010b). This hypothesis is strongly supported by the “macro”-taxonomic duality of the Mediterranean xeromontane Noctuidae. Those genera which belong to the subfamily Noctuae and have “cutworm”-type, terricolous larvae, obviously originated in the continental, western and central Asiatic orobiomes (e.g. Euxoa, Dichagyris, Chersotis, Rhyacia, Standfussiana, etc.). Their Mediterranean representatives regularly belong to some different derived phylectic lines (subgenera) of these polytypic genera. Their East Mediterranean-Anatolian taxa often display western and Central Asiatic connections but only in a few cases a marginal speciation in the Mediterranean ranges.

This group of genera correspond to the “saxobiotic ecofaunal complex” of the Palaeartic Orthoptera, described by Bey-Bienko (1948; see also Shumakov 1963, Pavlov & Mishtschenko 1980). The diversity centres of saxobiotic Orthoptera genera (“kamenisty tip fauni”, e.g. Catantopinae: Conophyma Zubovsky, 1898; Pamphaginae: Saxetania Mishtschenko, 1951; Nocarodes Fischer-Waldheim, 1846; Nocaractis Uvarov, 1928; Paranocarodes Bolivar, 1916; Paranothorodes
Mishtshenko, 1951, etc.) are to be found in the Western- and Central Asiatic arid-semiarid high mountains (Elburs, Kopet-Dagh, Hindukush, Hissaro-Darwaz and western Tien-Shan ranges). Their ranges greatly overlap with the core areas of the Noctuidae genera mentioned above.
Another group of xeromontane genera probably has been originally connected to some xerophilous scrub formations as e.g. Eugnorisma (with its subgenus Metagnorisma), Auchmis (connected to Berberis), or Lophoterges (connected to Lonicera; Ronkay & Varga 1997; Ronkay 2000, 2005). Their Mediterranean-Anatolian taxa display western and Central Asiatic connections (Varga 2010b), and only a marginal speciation in the Mediterranean ranges. Oppositely, some other Mediterranean genera display an essen-

Fig. 16: Distribution of the species pair Chersotis fimbriola – Ch. laeta: Ch. fimbriola iminenia (1), Ch. fimbriola iberica (2), Ch. fimbriola hackeri (3), Ch. fimbriola vallensis (4), Ch. fimbriola fimbriola (5), Ch. fimbriola baloghi (6), Ch. fimbriola maravignae (7), Ch. fimbriola thurneri (8), Ch. fimbriola niculescui (9), Ch. fimbriola ssp. (10), Ch. fimbriola zernyi (11), Ch. fimbriola bohatschi (6); Ch. laeta leonhardi (a), Ch. laeta achaiana (b), Ch. laeta cretica (c), Ch. laeta macini (d), Ch. laeta laeta (e), Ch. laeta euxinia (f). Taxonomic details: Hacker & Varga 1990.

Fig. 17: Distribution of the species related to Chersotis friedeli: Ch. friedeli (1), Ch. stenographa (2), Ch. gratissima (3), Ch. zagros (4), Ch. nupponenorum (5), Ch. nekrasovi (6). (3) + (4) and (5) + (6) are allopatric sister species. Taxonomy and phylogeny: Varga et al. 2013.
tially autochthonous evolution, influenced by the younger Tertiary aridisation of the Mediterranean Basin in connection with the Messinian Saline Crisis. The Pontic-Mediterranean (including parts of Asia Minor), the Atlanto-Mediterranean and Maghreb areas usually display a high level of species diversity in these genera. Examples can be mentioned from the tribe Oncocnemini: Omphalophana, Teiomyrpha, Cleonymia, Amephana, Metopoceras, Harpgoaphana, etc. and from genera of Xylenini (Leucoclaena, Aporophila, Antitype, Artemonia, subgenera of Mniotype, Polymixis, Anchoscelis, Conistra, etc.). Due to this paleo-ecological background this biogeographical group can be considered as equivalent of the “Paleo-Mediterranean-Xeromontane” faunal type of ornithologists (Stegmann 1938, Voous 1960, 1963) and with the faunal type of the “ancient Mediterranean” of the Russian biogeographical school (Bey-Bienko 1948, Shumakov 1963, Kryzhanovsky 1965).

Discussion 2: Subdivision and history of the Palaearctic xeromontane fauna

In Europe and adjacent areas the majority of xeromontane species occur in the summer-dry Mediterranean mountain systems, from the Atlas Mts to Asia Minor (Stegmann 1938, Voous 1960, Kryzhanovsky 1965, Varga 1997). To the contrary, Central and Northern Europe just holds a few species of this faunal type and were only colonised by xeromontane species possibly during the cold-continental younger glacial and early post-glacial phases only (Mikkola et al. 1987; Varga 1996, 2010a, 2010b). A much higher diversity of xeromontane species was observed from the arid mountains of East Anatolia to the mountain systems of Central and Inner Asia, mostly due to the high species numbers of some typical genera e.g. in Noctuidae (subfamily Noctuinae), Lycenaedae: Polyommatus, Orthoptera: Catantopidae (Varga 1996, 2010a, 2010b). A much higher diversity of xeromontane species was observed from the arid mountains of East Anatolia to the mountain systems of Central and Inner Asia, mostly due to the high species numbers of some typical genera e.g. in Noctuidae (subfamily Noctuinae), Lycenaedae: Polyommatus, Orthoptera: Catantopidae (Varga 1996, 2010b; Eckweiler & Häuser 1997; Pravdin & Mishtshenko 1980; Ünal 2016).

Thus, the composition of the xeromontane fauna is subdivided into a West Palaearctic (Mediterranean-xeromontane) and a Central- and Inner-Asian (Continental) sub-type. The protracted biogeographical confusion in the use of terms Central Asia vs. Middle Asia, or Inner Asia (used historically as “Innermost Asia”, or “Died Heart of Asia”, see: M. A. Stein 1928) has been clarified by the recent paleo-ecological surveys. They have shown a deep historical split between the more western Central Asiatic and the Inner Asiatic (Mongolian-Tibetan) steppe biota, both in the composition of vegetation, and in the mammalian assemblages (Barbolini et al. 2020). This split is clearly reflected by the differentiation of the faunal composition of the more western Central Asiatic vs. the cold-continental Inner Asiatic mountain systems. While the former regions are significantly influenced by the sub-Mediterranean, equinoctial type of precipitation, the latter show an impoverished version of the continental type with scarce summer precipitation maxima (Agakanjants 1981, Agakanjants & Breckle 1995). This subdivision was also shown in the area-cladograms of the genus Xenopha (Varga 1989a, 2011). In the xeromontane fauna of the “western” Central Asiatic mountains, some butterfly genera (e.g. Parnassius, Karanasa, Paralasa, subgenera of Polyommatus) and also typical genera of Noctuidae (e.g. Euxoa, Dichagyris, Chersotis, Rhyacia, Eugnorisma, Gonioagra; and some oligotypic genera, e.g. Hypsophila, Fergana) predominate. The highest diversity of these genera mostly overlap with the core areas of the “saxobiotic” Orthoptera genera, see: Discussion 1.

Contrarily, in the eastern, Inner Asiatic group of the mountains, the typical butterflies belong to the genera Colias, Oeneis and Boloria, which also have xeromontane connections but penetrated into the tundral zonobiome. The Noctuidae of the Inner Asiatic xeromontane faunal type consist of several “Mongolian-Tibetan” cold-continental genera, e.g. Trichosia, subgenera of Xestia (Anomogyna, Pachnobia, Raddea, Estimata, Schoeyenia), subgenera of Anarta (Caloestra, Anarta s. str.), Lasiocyla, Oncocnemis and Symppis, etc. Supposedly, the connections of this faunal type with the cold steppic and tundral zonobiomes have been mostly influenced by the recently uncovered Mid-Pleistocene climatic transition (Diester-Haas et al. 2018; Sun et al. 2019; Willett et al. 2019) which had deeply transformed the general zonality of the vegetation by the global decline of the primary productivity. Hence, the connections of the xeromontane fauna must be also historically more manifold and partially more ancient than the oreotundral connections of the alpine faunal type, resulted mostly in the Quaternary climatic fluctuations and area dislocations (Varga 1995, 1996). Thus, the fauna of the subtropical, monsoonic orobiomes (e.g. in Southern China and the Himalayan region) displays a somewhat less differentiated, hypothetically more ancestral character. This regularity is clearly unfolding from the ranges of Poliina genera/subgenera Tricheurois, Haderonia and Metallolopia displaying the species diversity restricted to the Sino-Himalayan area, as opposed to the more derived genera Polia s. str. and Ctenoceras (Varga et al. 2019, Fig. 20).

We suppose that a bulk of basal groups of the fauna have evolved, jointly with some groups of Angiospermae, in the Eastern Gondwana (see: theory of Axelrod 1960). They could expand northwards after the earliest collision of the Gondwanian plates with south-eastern Asia forming an important source of the Sino-Himalayan core area of biodiversity as was also shown e.g. in the Passerine birds (Fjeldså 2013; Cai et al. 2019). A high diversity of cold-adapted ancestral species originating from the seasonally humid, monsoonic
southeastern Asiatic mountains have been constrained by passing two main filter-corridors (Fig. 21, modified from Varga 1995).

- The „Rhododendron-corridor“, being characteristic for several evergreen Angiospermae, e.g. Vaccinium, Empetrum, Rhododendron incl. Ledum, etc., which now compose a major part of the upgrowth of the Siberian (especially southern Siberian mountain) taiga, typical for a number of “taiga-birds” (e.g. Ficedula, Phylloscopus, Luscinia calliope, Tarsiger cyanurus, Dunimetica thoracica etc.) and also for numerous taiga-inhabiting Lepidoptera (Geometridae: Dysstroma, Chlorochlysta; Noctuidae: Xestia subg. Pachnobia, Anomogyna; Polia, Lasiocyna, species-groups of Apamea etc., Figs 20–21). The endemic species of these groups mostly inhabit the southern Siberian mountain taiga, while some of their relatives are widely dispersed, often having a Trans-Palaearctic or even Holarctic range of distribution.

- The “xeromontane” route, leading from the Trans-Himalayan mountains to the Karakoram, Pamir, Transalai, or to the Hissar, Seravshan, West Tien-Shan and Hindukush ranges, on one hand, or via East-Turkestian to the Eastern Tien-Shan and Altai-Sayan systems, on the other, resulting in a radiation of a rich continental xeromontane fauna. This bifurcation becomes apparent from the taxonomic division of the genera typical for these areas. In the fauna of the first group of the Inner Asiatic mountains, some butterflies (Parnassius, Karanasa, Paralasa, numerous Polyommatini genera) and oligotypic genera of Noctuidae (Hypsophila, Fergana) predominate. In the second group of the mountains the typical butterflies belong to Colias, Oeneis and Boloria, which supposedly have a xeromontane origin but penetrated into the tundral zonobiomes. The typical genera of this second, more “Siberian”, group of (originally) xeromontane Noctuidae are e.g. Trichosilia, Lasiocyna, Discestra, Anarta and some species groups of the Oncocnemis-Sympistis generic complex.

Based on these biogeographical facts, the connections of the Continental-Inner-Asiatic xeromontane fauna should be historically more manifold and ancient than the “typical” oreotundral connections of the alpine faunal type which can be mostly regarded as a consequence of the younger Quaternary climatic fluctuations and area dislocations.

Acknowledgements

Author is highly indebted to L. Ronkay, L. Rákosy and Th. Schmitt for the long-year cooperation, for critical comments and suggestions to the earlier version of the manuscript. I am especially grateful to G. Ronkay for the excellent pictures of the mapped Noctuidae species.

The research was supported by a senior fellowship in the Collegium Budapest, Institute of Advanced Study (2001), by the Re-Invitation Grant of the Alexander von Humboldt Foundation (Zoological State Collection in Munich, 2007), by the OTKA Foundation Grant No. 16465, by the Grant No. K116694 of the National Foundation of Research, Development and Innovation (NKFI-OTKA) and by the SYNTHESYS Project DE-TAF 6708.

References

Agakhanjants, O. E. 1981: The Arid High Mountains of the URSS (in Russian). – Moscow, Izd. Mysl’: pp. 170.
Agakhanjants, O. E. & Breckle, S.-W. 1995: Origin and evolution of the mountain flora in Middle Asia and neighbouring mountain regions. – In: Chapin, F. S. & Körner, C. (eds.) Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. – Springer, Berlin-New York, pp. 63–80. – https://doi.org/10.1007/978-3-642-78966-3_5.
Axelrod, D. I. 1970: Mesozoic paleogeography and early angiosperm history. – The Botanical Review 36: 277–319.
Barbolini, N.; Woutersen, A.; Dupont-Nivet, G. et al. 2020: Cenozoic evolution of the steppe-desert biome in Central Asia. – Science Advances 2020; 6: eabb8227 9 October 2020.
Beek, C.; Reichstein, M.; Tomelleri, E.; Ciais, P.; Jung, M.; Carvalhais, N.; Rödenbeck, C.; Arain, M. A.; Baldocchi, D. & Bonan, G. B. 2010: Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. – Science 329: 834–838.
Cai, T.; Shao, S.; Kennedy, J. D.; Alström, P.; Moyle, R. G.; Qu, Y.; Lei, F. & Fjeldså, J. 2020: The role of evolutionary time, diversification rates and dispersal in determining the global diversity of a large radiation of passerine birds. – Journal of Biogeography 47: 1612–1625.
Diesther-Haas, L.; Billups, K. & Lear, C. 2018: Productivity changes across the mid-Pleistocene climate transition. – Earth-Science Reviews 179 (2018): 372–391.
Dufay, C. & Varga, Z. 1995: A new noctuid species from Iran, Chersotis eberti sp. n. (Lep.: Noctuidae). – Acta Zoologica Academiae Scientiarum Hungaricae 41: 35–45.
Eckweiler, W. & Häusser, C. L. 1997: An illustrated checklist of Agrodiactus Hübner, 1822, a subgenus of Polyommatus Latreille, 1804 (Lepidoptera, Lycaenidae). – Nachrichten des entomologischen Vereins Apollo 1997: 113–166.
Enghoff, H. 1995: Historical biogeography of the Holarctic: area relationships, ancestral areas and dispersal of non-marine animals. – Cladistics 11: 223–263.
Fibiger, M. 1990: Noctuidae Europaeae. Vol. I, Noctuinae I. – Entomological Press, Soro: pp. 207.
Fibiger, M. 1993: Noctuidae Europaeae. Vol. II, Noctuinae II. – Entomological Press, Soro: pp. 230.
Fjeldså, J. 2013: The global diversification of songbirds (Oscines) and the build-up of the Sino-Himalayan diversity hotspot. – Chinese Birds 4 (2):132–143. – DOI:10.5122/cbfrd.2013.0014.
Harold, A. S. & Mooi, R. D. 1994: Areas of endemism: definition and recognition criteria. – Systematic Biology 43 (2): 261–266.
Huemer, P. 1998: Endemische Schmetterlinge der Alpen – ein Überblick (Lepidoptera). – Stapfia (2): 261–43.
Huemer, P. & Karsholt, O. 2020: Commented sequences of COI from mtDNA sequences of Hübner, 1822 (Lepidoptera: Lycaenidae) inferred & Pierce, N. E. 2004: Phylogeny of Agrodiaetus butterflies. – Nature 436: 385–389. – doi: 10.1038/nature03704.
Li, B. P.; Liu, Z. W. & Zheng Z-M. 2011: Phylogeny and classification of the Catantopidae at the tribal level (Orthoptera, Acridoidea). – ZooKeys 148: 209–255. doi:10.3897/zookeys.148.2081.
Lukhtanov, V. A.; Kandul, V. A.; Plotkin, J. B.; Dantchenko, A. V.; Haig, D. & Pierce, N. E. 2005: Reinforcement of pre-zygotic isolation and karyotype evolution in Agrodiaetus butterflies. – Nature 436: 385–389. – doi: 10.1038/nature03704.
Mikkola, K. 1992: Evidence for lock-and-key mechanisms in the internal genitalia of the Apamea moths (Lep.: Noctuidae). – Systematic Entomology 17: 145–153.
Mikkola, K.; Lafontaine, J. D. & Grotenfelt, P. 1987: A revision of the Holarctic Chersotis andereggii complex (Lep.: Noctuidae). – Nota lepidopterologica 10: 140–157.
Mikkola, K.; Lafontaine, D. J. & Kononenko, V. S. 1991: Zoogeography of the Holarctic species of the Noctuidae (Lepidoptera): importance of the Beringian refuge. – Entomologica fennica 2: 158–173.
Müller, B.; Erlacher, S.; Hausmann, A.; Rajaei, H.; Sivoven, P. & Skou, P. 2019: The Geometrid Moths of Europe. Volume 6. Subfamily Ennominae II (Boarmiini, Gnophini, additions to previous volumes). – Part 1: 1–562, part 2: 563–906. – Brill, Leiden & Boston.
Pappas, C.; Fatichi, S. & Burlando, P. 2016: Modeling terrestrial carbon and water dynamics across climatic gradients: does plant trait diversity matter? – New Phytologist 209: 137–151. – doi: 10.1111/nph.13590.
Varga, Z.: Noctuidae in Palaearctic arid mountains

Prince, S. D. & Goward, S. N. 1995: Global Primary Production: A Remote Sensing Approach. – Journal of Biogeography 22 (4/5): 815–835.

Ryabov, M. A. 1956: Types of annual life-cycles in cut-worms (Lepidoptera, Agrotidae) (in Russian). – Revue d’Entomologie de l’URSS (Entomologischeskoe Obozrenie) 35: 70–79.

Rodin, L. E. & Bazilevic, N. I. 1966: The biological productivity of the main vegetation types in the Northern Hemisphere of the Old World. – Forestry Abstracts 27: 365–375.

Ronkay, L. 2000: Revision of the genus Lophoterges. – Esperiana (Schwanfeld): 198–203.

Ronkay, L. & Varga, Z. 1999: Revision of the genus Eugnorisma Boursin, 1946, Part V. New genera and species of Eugnorisma genus group from Pakistan and China (Lepidoptera, Noctuidae). – Acta Zoologica Academiae Scientiarum Hungaricae 45 (4): 345–373.

Running, S. W.; Nemani, R. R.; Heinsch, F. A.; Zhao, M.; Reeves, M. & Hashimoto, H. 2004: A continuous satellite-derived measure of global terrestrial primary production. – BioScience 54 (6): 547–560.

Saulich, A. Kh.; Sokolova, I. V. & Musolin, D. C. 2017: Seasonal Cycles of Noctuid Moths of the Subfamily Plusiinae (Lepidoptera, Noctuidae) of the Palaearctic: Diversity and Environmental Control. – Entomological Review 97 (2): 143–157.

Shumakov, E. M. 1963: Locusts of Afghanistan and Iran. (In Russian). – Trudy Vsesoyuznogo Entomologicheskogo Obshhestva 49: 1–248.

Specht, A.; Angulo, A. O.; Olivares, T. S.; Ronza, E.; Roque-Specht, V. F.; Valduga, E.; Albrecht, F.; Peletto, G. & Barros, N. M. 2013: Life cycle of Agrotis malefida (Lepidoptera: Noctuidae): a diapausing cutworm. – Zeotologia 30 (4): 371–378.

Steegmann, B. 1938: Grundzüge der ornithogeographischen Gliederung des palaarktischen Gebietes. – Fauna SSSR, nov. ser. 19: pp. 158.

Steegmann, B. 1958: Herkunft der europäischen Steppenvögel. – Bonner zoologische Beiträge 9: 208–230.

Stein, A. M. Sir 1928: Innermost Asia: Detailed Report of Explorations in Central Asia, Kan-su and Eastern Iran, Vol. 1–5. – Oxford, Clarendon Press. (Reprint: New Delhi, Cosmo Publications, 1981).

Sukhareva, I. L. 1999: Family Noctuidae. – In: Kuznetsov, V. I. (ed.): Insects and Aracines as Agricultural Pests, Vol. 3. Lepidoptera, Part 2. (In Russian). – Nauka, St. Petersburg: pp. 332–376.

Sun, Y.; Yin, Q.; Crucifix, M. et al. & An, Zh. 2019: Diverse manifestations of the mid-Pleistocene climate transition. – Nature Communications 10: 352. – https://doi.org/10.1038/s41467-018-08257-9.

Ünal, M. 2016: Pamphagidae (Orthoptera: Acridoidea) from the Palaearctic Region: taxonomy, classification, keys to genera and a review of the tribe Nocaroedini. – Zootaxa 4206 (1): 1–223. – ISBN 978-1-77670-047-9.

Varga, Z. 1977: Das Prinzip der areal-analytischen Methode in der Zoogeographie und die Faunenelemente-Einteilung der europäischen Tagschmetterlinge (Lep.: Diurna). – Acta Biologica Debrecina 14: 223–285.

Varga, Z. 1989a: Zweiter Beitrag zur Kenntnis derGattung Xenophysa Boursin, 1969 (Lep.: Noctuidae) mit Beschreibung fünf neuer Arten. – Zeitschrift der Arbeitsgemeinschaft österreichischer Entomologen 41 (1–2): 48–77.

Varga, Z. 1989b: The origin and division of the northern-montane disjunct areas in Palaearctic Lepidoptera – Their importance in solving zoogeographical and evolutionary problems. – Acta Biologica Debrecina 21: 91–116.

Varga, Z. 1990: New species of Noctuidae from Afghanistan and adjacent territories I. The Genera Euxoa Hübner (1821) 1816, Dichagyris Lederer, 1857, Rhyacia Hübner (1821) 1816. (Lep.: Noctuidae, Noctuinae). – Esperiana (Schwanfeld) I: 167–198.

Varga, Z. 1992: Taxonomic notes on the Genus Haderonia Staudinger, 1896 with the description of a new Genus Ctenoceratoda and four new species (Lep.: Noctuidae). – Acta Zoologica Academiae Scientiarum Hungaricae 38 (1–2): 113–124.

Varga, Z. 1993: Beiträge zur Kenntnis der Gattung Dichagyris Lederer, 1857 (Lep.: Noctuidae) I. – Acta Zoologica Academiae Scientiarum Hungaricae 39 (1–4): 289–300.

Varga, Z. 1995a: Isolates of Arctic-alpine and Alpine Lepidoptera in SE Europe. – Proceedings of the EIS Colloquium, Helsinki: pp. 140–151.

Varga, Z. 1995b: Geographical Patterns of Biological Diversity in the Palaearctic Region and the Carpathian Basin. – Acta Zoologica Academiae Scientiarum Hungaricae 42 (1): 71–92.

Varga, Z. 1996a: Entomologische Aspekte der räumlichen und biotischen Diversität in einer mitteleuropäischen Mosaiklandschaft. – Verh. 14. int. Symposium für Entomofaunistik in Mitteleuropa, SIEEC, München (1994): p. 33–67.

Varga, Z. 1996b: New species and subspecies of Dichagyris Lederer 1857, Chersotis Boisdruval 1840 and Rhyacia Hübner [1821] 1816 (Noctuidae, subfam. Noctuinae) from Central Asia. – Acta Zoologica Academiae Scientiarum Hungaricae 42 (3): 195–230.
Varga, Z. 1997: Biogeography and Evolution of the orreal Lepidoptera in the Palearctic. – Acta Zoologica Hungarica Academiae Scientiarum Hungaricae 42 (4): 289–330.

Varga, Z. 1998: Sibling species and species groups in the genus Chersotis Boisduval, 1840 (Lepidoptera, Noctuidae: Noctuinae) with description of two new species. – Acta Zoologica Academiae Scientiarum Hungaricae 44 (4): 341–372.

Varga, Z. 2003: The geographical distribution of high mountain Macrolepidoptera in Europe. – In: Grabherr, G. & Nagy, L. (eds): Alpine biodiversity in Europe. – Springer-Verlag: pp. 239–257. – https://doi.org/10.1007/978-3-642-18967-8_13.

Varga, Z. 2010a: Extra-Mediterranean refugia, post-glacial vegetation history and area dynamics in Eastern Central Europe. – In: Habel, J. & Assmann, Th. (eds.): Relict species: Phylogeography and Conservation Biology. – Springer-Verlag: pp. 57–87.

Varga, Z. 2010b: Biogeography of West Palearctic Noctuidae. – In: Fibiger, M.; Ronkay, L.; Yela, J. L. & Zilli, A.: Noctuidae Europaeae 12 (incl. Suppl. 1–12): pp. 265–274. – Entomological Press, Sorø.

Varga, Z. 2011: Revision of the genus Xenophysa Boursin, 1969 (Lepidoptera, Noctuidae). – Zootaxa 3094: 1–29. – www.mapress.com/zootaxa/.

Varga, Z. 2014: New and revised Euxoa Hübner, 1821 species from Western and Central Asia (Lepidoptera, Noctuidae, Noctuinae). – Zootaxa Suppl. 2: pp. 9–30. Heterocera Press, Budapest.

Varga, Z. & Gyulai, P. 1999: Taxonomy of the genus Ctenoceratoda Varga, 1992 (Lepidoptera, Noctuidae) with the description of seven new species. – Acta Zoologica Academiae Scientiarum Hungaricae 45 (2): 169–197.

Varga, Z.; Gyulai, P.; Ronkay, G. & Ronkay, L. 2013: Noctuinae I. A Taxonomic Atlas of the Eurasian and North African Noctuoidae. – The Witt Catalogue, Vol. 6. Heterocera Press, Budapest: pp. 394.

Varga, Z.; Gyulai, P.; Ronkay, G. & Ronkay, L. 2015: Noctuinae II. A Taxonomic Atlas of the Eurasian and North African Noctuoidea. – The Witt Catalogue, Vol. 8. Heterocera Press, Budapest: pp. 394.

Varga, Z. & Ronkay, L. 1987: Revision of the Genus Euginorisma Boursin, 1946 (Lep.: Noctuidae). – Acta Zoologica Academiae Scientiarum Hungaricae 33: 187–262.

Varga, Z. & Ronkay, L. 1996: New and Revised Taxa from Genera Chersotis Boisduval, 1840 and Dichagyris Lederer, 1857 from Central Asia (Lep.: Noctuidae). – Esperiana (Schwanfeld) 5: 103–132.

Varga, Z. & Ronkay, L. 2002: A revision of the Palearctic species of the Eugraphe Hübner, [1821] 1816 generic complex. Part I. The genera Eugraphe and Goniographa (Lepidoptera, Noctuidae). – Acta Zoologica Academiae Scientiarum Hungaricae 49: 333–374.

Varga, Z.; Ronkay, L. & Hacker, H. 1990: Revision of the Genus Bryopolia Boursin, 1954 (Lep.: Noctuidae). – Esperiana (Schwanfeld) 1: 427–469.

Varga, Z.; Ronkay, L. & Yela, J. L. 1990: Revision of the Genus Eugnorisma Boursin, 1946. Part II. Taxonomic news, biogeographic and phylogenetic considerations and descriptions of two new genera: Ledereragrotis and Pseudohermonassa (Lep.: Noctuidae). – Acta Zoologica Academiae Scientiarum Hungaricae 36 (3–4): 331–360.

Voous, K. H. 1960: Atlas of European birds. – Nelson, London: pp. 284.

Voous, K. H. 1963: The concept of faunal elements or faunal types. – Proceedings of the 13 international Congress of Ornithology: pp. 1104–1108.

Willeit, M.; Ganopolski, A.; Calov, R. & Brovkin, V. 2019: Mid-Pleistocene transition in glacial cycles explained by declining CO₂ and regolith removal. – Science Advances 2019, 5: eaav7337.
Tab. 1: Allopatric pairs and groups of *Dichagyris* (subg. *Dichagyris*) species (†with peripatric overlap, *polytypic species*).

| Western species                                                                 | Eastern species                                                                 |
|---------------------------------------------------------------------------------|----------------------------------------------------------------------------------|
| *Dichagyris* (*Dichagyris*) *vallesiaca* (Boisdouval, 1837)*; SW and Central Alps, Crimea, South Russia, South Urals, Asia Shan, Zagros, Elburs, Binaloud Mts, Kopet-Dagh, Tien Shan, Pamirs, Altai, Khangai, Sayan Mts. | *Dichagyris* (*Dichagyris*) *fuscashmiriana* Varga, Ronkay & Ronkay, 2020: Hindukush East, Karakoram, W Himalayas |
| *Dichagyris* (*Dichagyris*) *striata* Kozhantschikov*, 1930*: Zagros, Elburs, Binaloud Mts, Kopet-Dagh | *Dichagyris* (*Dichagyris*) *tyrannus* (A. Bang-Haas, 1912)*: Tien Shan, Hissaro-Darwaz, Pamirs, Hindukush, Karakoram, W Himalayas |
| *Dichagyris* (*Dichagyris*) *squalidior* (Staudinger, 1901)*; Asia Minor, Zagros, Elburs, Binaloud Mts, Kopet-Dagh | *Dichagyris* (*Dichagyris*) *payotiorum* Varga, Ronkay & Ronkay: Hissaro-Darwaz, Hindukush, Paghman Mts. Karakoram, W Himalayas |
| *Dichagyris* (*Dichagyris*) *clara* (Staudinger, 1888)*; Tien Shan, Mongol Altai, Gobi Altai | *Dichagyris* (*Dichagyris*) *leucographa* Varga, 1990: Pamirs *Dichagyris* (*Dichagyris*) *scotographa* Varga, 1990: Pamirs, Karakoram, W Himalayas (Kashmir) *Dichagyris* (*Dichagyris*) *kautti* Varga, 1996: W Himalayas (Ladakh) |
| *Dichagyris* (*Dichagyris*) *jacobsoni* Kozhanchikov, 1930: Kopet-Dagh | *Dichagyris* (*Dichagyris*) *umbrifera* (Alphéraky, 1882): Tien Shan |
| *Dichagyris* (*Dichagyris*) *naumannii* Varga, 1996: Kugitang-Tau, Hindukush | *Dichagyris* (*Dichagyris*) *kasabri* Varga, 1973: Mongol & Gobi Altai |
| *Dichagyris* (*Dichagyris*) *catalepa* Varga, 1993: Eastern Asia Minor | *Dichagyris* (*Dichagyris*) *afghana* Boursin, 1963: Central Hindukush |
| *Dichagyris* (*Dichagyris*) *psammochroa* (Boursin, 1940)*; Zagros, Elburs, Kopet-Dagh | *Dichagyris* (*Dichagyris*) *kuratskyi* Varga, Ronkay & Ronkay, 2021: W Tien Shan *Dichagyris* (*Dichagyris*) *apochora* Gyulai & Varga, 2001: Pamirs |
| *Dichagyris* (*Dichagyris*) *taftana* Brandt, 1941*: Elburs, Zagros | *Dichagyris* (*Dichagyris*) *guentereberti* Varga, Ronkay & Ronkay, 2021: Central Hindukush |
| *Dichagyris* (*Dichagyris*) *humilis* (Boursin, 1940): Zagros, Elburs, Kopet-Dagh | *Dichagyris* (*Dichagyris*) *hypotacta* Varga, Ronkay & Ronkay 2021: East Tien Shan, Pamirs, Hindukush |
| *Dichagyris* (*Dichagyris*) *verecunda* (Püngeler, 1898)*; Tien Shan system, Pamirs, Mongol Altai, Gobi Altai | *Dichagyris* (*Dichagyris*) *karakorealis* Varga, Ronkay & Ronkay, 2020: West Himalayas |

* Sympatric endemic species: *Dichagyris* (*Dichagyris*) *griseotincta* (Wagner, 1931) – Central Anatolia.
* Northern sister species (?subspecies): *Dichagyris lux* Fibiger & Nupponen, 2002 – South Urals.
Tab. 2: Allopatric pairs of *Euxoa* species (exceptionally with peripatric overlap).

| Western species                        | Eastern species                        |
|----------------------------------------|----------------------------------------|
| *Euxoa homicida* (Staudinger, 1900)*: Asia Minor, Transcaucasia, Zagros, Elburs | *Euxoa transcaspica* Kozhantshikov, 1928*: Kopet-Dagh, Binaloud Mts (ssp.); Hindukush, Karakoram, W. Himalayas (ssp.) |
| *Euxoa decora* ([Denis & Schiffermüller], 1775): Pyrenees, Alps, Carpathians, Europa Centr., Apennines, Balkans | *Euxoa kurushensis* Boursin, 1940: Daghestan (NE Caucasus) |
| *Euxoa heringi* (Staudinger, 1877): Asia Minor, Elburs, Kopet-Dagh | *Euxoa cretaporos* Varga, G. Ronkay & L. Ronkay, 2020: Daghestan (NE Caucasus) |
| *Euxoa aneucta* Brandt, 1938*: Zagros Mts, Binaloud Mts (ssp.) | *Euxoa subeucta* Varga, 2014: Hissar Mts., Transalai Mts, Hindukush Central & East |
| *Euxoa perierga* Brandt, 1938*: Zagros Mts, Elburs (ssp.) | *Euxoa dichagyroides* Varga, 1979: Darwaz Mts., Pamirs, Transalai Mts, Hindukush Central & East |
| *Euxoa sigmata* Kozhantshikov, 1928: Kopet-Dagh, Binaloud Mts | *Euxoa metasigmata* Varga, 2014: Hissar Mts, Hindukush Central & East |
| *Euxoa conifera* Christoph, 1885*: Daghestan, Transcaucasia, Asia Minor (East), Elburs, Kopet-Dagh | *Euxoa bactriana* Varga, 2014: Tien Shan (Seravshan), Transalai, Hissar Mts, Pamirs, Hindukush Central & East, Karakoram, West Himalayas |
| *Euxoa bogdanovi* (Erschoff, 1873): Tien Shan | *Euxoa xanthophylla* Varga, 1990: Darwaz Mts, Pamirs |

Fig. 18: Early autumnal steppic *Euxoa* species: *E. distinguenda* (1), *E. christophi* (2).

---

* Senior synonym of *E. difficillima* Draut, 1937.
| Western species | Eastern species |
|----------------|----------------|
| *Ch. firdusii* Schwingenschuss, 1937: East Anatolia, Zaghros, Elburs, Binaloud Mts, Kopet-Dagh | *Ch. fidahusseini* Varga, Gyulai, Ronkay & Ronkay, 2013: E Tien Shan, Hissar and Darwaz range, Central and East Hindukush, Karakoram, West Himalayas |
| *Ch. sordescens* (Staudinger, 1900): Tien-Shan range, Hindukush, Hissar and Darwaz range | *Ch. herczigi* Varga, 1996: West Himalayas |
| *Ch. ronkayorum* Fibiger, Hacker & Varga, 1993: Central and East Anatolia | *Chersotis sterilis* Brandt, 1938: Zaghros Mts |
| *Ch. nitens* Brandt, 1941: Binaloud Mts, Kopet-Dagh | *Ch. metagrapha* Varga, 1975: Afghanistan, Hindukush Mts, Badakhshan |
| *Ch. capnisitis* (Lederer, [1870]): South Russia, Caucasus, Transcaucasia, Asia Minor, South Balkans | *Ch. leucostola* Varga & Ronkay, 1996: Tien-Shan Mts, Dzhungarian Ala-too |
| *Ch. semna* (Püngeler, 1906): Asia Minor, Trans-caucasia, Elburs, Binaloud Mts, Kopet-Dagh | *Ch. pachnosa* Varga, 1975: Afghanistan, Badakhshan |
| *Ch. juvenis* (Staudinger, 1901): Asia Minor, Transcaucasia, Elburs Mts, Zaghros Mts. | *Ch. kouros* Varga & Ronkay, 1996: Kopet-Dagh, Hindukush |
| *Ch. calorica* (Corti, 1930): North & East Tien-Shan Mts | *Ch. shandur* Varga, 1998: Pakistan, Karakoram Mts, Afghanistan, Paghman Mts |
| *Ch. petermarci* Varga, 1998: Seravshan Mts, W Tien-Shan Mts | *Ch. vicina* (Corti, 1930): N and E Tien-Shan Mts |
| *Chersotis delear* Boursin, 1970*: Central Afghanistan, Nimla | *Ch. electrographa* Varga, 1990: Afghanistan, Darwaz Mts. *Ch. vagai* Hacker, 1992 Hindukush Mts, Karakoram |
| *Ch. binaloudi* Brandt, 1941*: Khorassan, Binaloud Mts | *Ch. antigrapha* Boursin, 1961: Hindukush Mts *Ch. argyllographa* Varga & Gyulai, 2001: W Pamirs |
| *Ch. elegans* (Eversmann, 1837): Iberian Mts, Pyrenees, Alps, Balkans, Asia Minor, Transcaucasia, S Russia, W Tien-Shan and W Altai Mts | *Ch. eberti* Dufay & Varga, 1995: Elburs Mts, Zaghros Mts |
| *Ch. sarhada* Brandt, 1941*: Asia Minor, Transcaucasia, Elburs and Kopet-Dagh Mts | *Ch. lehmanni* Varga, Gyulai, Ronkay, Ronkay, 2010: Hindukush, Hissar and Darwaz Mts *Ch. lukhtanovi* Varga & Gyulai, 2001: S Tadjikistan |
| *Ch. rungsi* Boursin, 1944: Atlas Mts | *Ch. stenographa* Varga, 1979: Asia Minor East, Transcaucasia |
| *Ch. gratissima* (Corti, 1932) | *Ch. zagroica* Gyulai & Varga, 2006: Zaghros Mts |
| *Ch. suppionenorum* Varga, Gyulai, Ronkay & Ronkay, 2013: W Transcasperia | *Ch. nekrasovi* Varga, 1996: Pamir Mts |

* A „triplet” of species.
+ A „triplet” of species.
*+ A „triplet” of species.
Tab. 4: Partly sympatric pairs and groups of *Chersotis* species.

| Species | Distribution |
|---------|--------------|
| *Ch. rectangula* ([Denis & Schiffermüller], 1775): | Central and Southern Europe, Caucasus, Asia Minor |
| *Ch. andereggi* (Boisduval, [1837]): | N Europe, Alps, Balkans, Asia Minor, Caucasus, Transcaucasia, Iran, Mts of Southern Siberia |
| *Ch. acutangula* (Staudinger, 1892) | Transalai and Hindukush Mts |
| *Ch. hahni* (Christoph, 1885): | Transcaucasia, Elburs, Kopet-Dagh Mts |
| *Ch. curvispina* Boursin, 1961: | Kopet-Dagh Mts, Hindukush Mts |
| *Ch. elegans* (Eversmann, 1837): | Iberian Mts, Pyrenees, Alps, Balkans, Asia Minor, Caucasus, Transcaucasia, S Russia, W Tien-Shan and W Altai Mts |
| *Ch. eberti* Dufay & Varga, 1995: | Elburs Mts, Zaghros Mts |
| *Ch. anatolica* (Draudt, 1936): | Iberian Mts, Pyrenees, SW Alps, Central Apennines, Balkans, Asia Minor, Caucasus, Transcaucasia, S Russia (Europa + Siberia), Kopet-Dagh, W Tien-Shan Mts |
| *Ch. fimbriola* (Esper, [1803]): | Atlas, Iberian Mts, Pyrenees, Sicily, W Alps, Pannonian Basin, Balkans, Asia Minor, Crimea, Transcaucasia, Zaghros, Elburs Mts, Kopet-Dagh Mts |
| *Ch. laeta* (Rebel, 1904): | Balkans, W coastal area of Black Sea, Asia Minor, Caucasus, Transcaucasia, Elburs Mts |

Tab. 4: Partly sympatric pairs and groups of *Chersotis* species.

- **Autumnal imagos**
  - **Oviposition**
  - **Aestivating pupae**
  - **Feeding larvae at the spring**
  - **Hatching of larvae at the spring**

Case 1: Autumnal imagos (*Euxoa part.*, *Eugnorisma*, etc.)

- **Hibernation in the egg-shell**

Case 2: Aestivating imagos (*Chersotis part.*, *Standfussiana*, etc.)

- **Hibernation in the egg-shell**

Fig. 19: Adaptation to the arid environment in Noctuinae genera: two types of univoltine life-cycles with autumnal period of oviposition and dispersal. Type I. (e.g. *Euxoa*, *Eugnorisma* – aestivating pupae, late summer, early autumn imagos), type II. (e.g. *Chersotis*, *Spaelotis*, *Standfussiana*, aestivating imagos).

---

10 Latter species is strictly localised in the Tien-Shan and Hindukush mountain systems.
11 These species are not sibling species, because they are strongly differentiated from each other (see: Dufay & Varga 1995).
Fig. 20: General distribution of Poliina (Noctuidae) genera with primary centre of diversity (light blue) in the monsoonic mountainous areas of South-Eastern Asia (Himalayan – Sino-Tibetan faunal type, *Tricheurois, Haderonia, Metallopolia*) and secondary core area (light green) in the South Siberian mountains (*Polia* spp.). The main faunal corridor is extended from the Himalaya to the South Siberian mountain systems (arrows).
Appendix I

Biogeographical types of xeromontane Noctuidae (with special regard to Noctuidae genera: Actebia s.l., Dichagyris s.l., Euxoa s.l., Rhyacia s.l., Chersotis, Eugnorisma s.l., and Xenophysa) with taxonomic notes

1. Mediterranean- (Western Palearctic-) xeromontane species

(= „Mediterranean-Asiatic” p.p. in most publications, e.g. Boursin 1964, Dufay 1981, Fibiger 1990, etc.). Species marked with * are polytypic species.

1.1. Holo-Mediterranean-xeromontane: Dichagyris (Dichagyris) candelisca (Denis & Schiffermüller, 1775)*, D. (D.) renigera (Hübner, [1808])*, D. (Yigoga) forcipula (Denis & Schiffermüller, 1775)*, Euxoa (Euxoa) decoria (Denis & Schiffermüller, 1775)*, E. (E.) birvia (Denis & Schiffermüller, 1775)*, E. (E.) hastifera (Donzel, 1847)*, E. (E.) cos (Hübner, 1827)*, Chersotis alpestris (Boisduval, 1834)*, Ch. elegans (Eversmann, 1837)*, Ch. anatolica (Drault, 1936)*, Ch. larixia (Guenée, 1852)*, Ch. fimbriola (Esper, [1803])*, Rhyacia (Lafontainea) helvetina (Boisduval, 1833)*, Hadena clara (Staudinger, 1901)*, H. tephroleuca (Staudinger, 1901)*, Hadena vulcanica, Calophasia (Turati, 1907) (Reisser, 1958)*, Dichagyris (Pleonec-)
Pleonectopoda 1925).
2. West-and West-Central Asiatic xeromontane species

(„Mediterranean-Asiatic“ species p. p. in Boursin 1964, Dufay 1981, Fibiger 1990, 1993)

2.1. Anatolian–xeromontane: Actebia (Protocarnis) squamidiformis (Corti & Draudt, 1933), Dichagyris (D.) griseotincta (F. Wagner, 1931), D. (D.) cataleipa Varga, 1993, Euxoa (E.) luteomixta F. Wagner, 1930, E. (E.) anatolica Draudt, 1936, E. (E.) robingiosa (Staudinger, 1894), Agrotis scruposa (Draudt, 1934), Pachyagrotis ankarensis (Rebel, 1930), Chersotis ronkayorum Fibiger, Hacker & Varga, 1992, Eugnoria (Phacognorisma) enargiars (Draudt, 1934), Hadena cappadocia Hacker, 1987, H. cavalla Pinker, 1980, Osthledera gracilis (Osthelder, 1933), Victrix gracilis (F. Wagner, 1931), V. hackeri Varga & Ronkay, 1991 (maps: Varga 1997).

2.2. Anatolian–Transcaucasian–xeromontane: Dichagyris (D.) armeniaca Kozhantshikov, 1930*, D. (D.) romanovi (Christoph, 1885), Stenosomides carthalinus (Christoph, 1893), Euxoa (E.) herciana (Staudinger, 1900)*, E. (E.) pleonectopoda) rjabovi Kozhantshikov, 1929, Chersotis stenographa Varga, 1979, Ch. gratissima Corti, 1932, Ch. friedeli Pinker, 1974, Polymixis (Mysymma) csorbagi Ronkay, Varga & Hreblay, 1998, Dasyypolia transcaucasica Ronkay & Varga, 1985, Luperina diversa (Staudinger, 1892), Victrix karsiana Staudinger, 1879*, V. artaxias Varga & Ronkay, 1989 (maps: Varga 1997).

2.3. Transcaucasian–Kurdestanian–xeromontane: Dichagyris (Yigoga) willshirei (Boursin, 1936), Xenophysa xanthomaculata huberi Varga, 1989, Eicomorpha kurdestanica de Freina & Hacker, 1985, Ammonoconia anonyma Ronkay & Varga, 1984, Osthledera arne Ronkay & Varga, 1994, Resapaema vaskeni Varga, 1979*.

2.4. Anatolian–Transcaucasian–N-Iranian–xeromontane: Actebia (Protocarnis) opisoleuca (Staudinger, 1881), Dichagyris (D.) pfeifferi Corti & Draudt, 1933 (= D. fredi Brandt, 1938), D. (D.) forficula (Eversmann, 1851)*, Dichagyris (D.) erubescens (Staudinger, 1892), Dichagyris (D.) anastasia (Draudt, 1936), D. (Yigoga) weigerti Hacker & Varga, 1992, Euxoa (E.) heringi Christoph, 1877*, E. (E.) adjemi Brandt, 1941, E. (E.) dseiron Brandt, 1938, E. (E.) magicar Christoph, 1877* (= E. difficilima Draudt), Euxoa (E.) sulcifera (Christoph, 1893), E. (E.) saccillaris Draudt, 1937, Chersotis semia (Püngeler, 1906), Ch. sarhadu Brandt, 1941, Chersotis obnubila (Corti, 1926)*, Ch. illauta (Draudt, 1936)*, Eugnoria (Metagnorisma) heuristica Varga & Ronkay, 1987, Polymixis (P) rosinae (Bohatsch, 1908) (= P. para-diesiacu Boursin, 1944), Eremohadena (Megahadena) rjabovi (Boursin, 1970), Osthledera persa Ronkay & Varga, 1994 (maps: Varga 1997).

2.5. Daghestanian–Transcaucasian–xeromontane: Dichagyris (D.) achtalensis (Kozhantshikov, 1929)*, Euxoa (E.) kuruschenisi Boursin, 1940, E. (E.) cretaporos Varga, G. Ronkay & L. Ronkay, 2020, E. (E.) pleonectopoda) uncarpa Kozhantshikov, 1929, Agrotis fratercula Pekarsky, Varga, G. Ronkay & L. Ronkay, 2020.

2.6. Iranian–Farsian–xeromontane: Dichagyris (D.) taftana Brandt, 1941*, D. (D.) zargoica Hacker & Ebert, 2002, D. (D.) gyulaivani Gyulai & Varga, D. (D.) strena Corti, 1926), Euxoa (E.) charlesboursini Varga, 2014, Chersotis fridsiisi Schwingenschuss, 1937, Ch. sterili Brandt, 1938, Ch. eberti Dufay & Varga, 1995, Ch. zargoica Gyulai & Varga, 2006, Xenophysa acacuma (Brandt, 1938), Polymixis (Brandticola) dubiosa (Brandt, 1938).

2.7. Iranian–Turcomanian–xeromontane: Dichagyris (D.) psammochroa Boursin, 1940*, D. (D.) darius Boursin, 1940, D. (D.) hubilis Boursin, 1940*, Euxoa (E.) subdecora Hampson, 1903 (= E. clauda Püngeler, 1906), E. (E.) aneucta Brandt, 1938*, Rhyacia (Anchorhyacia) gabiort Varga, 1996, Xenophysa xanthomaculata (Christoph, 1887)*, Catoceratoda lupa (Christoph, 1893), Polymixis (Boursinxius) periscapus Ronkay, Varga & Hreblay, 1998, Anchoscelsis oropetamica (Wiltshire, 1941)*.

2.8. Turcomanian–xeromontane: Actebia (Hemiearnis) iuguma (Brandt, 1938), Dichagyris (D.) korshunovi Varga, 1996, D. (D.) devota (Christoph, 1884), D. (D.) herzi Kozhantshikov, 1930, D. (D.) spintherops Varga & Ronkay, 1996, D. (D.) thylacina Varga, 1996, D. (D.) exornata Varga, 1990, D. (Yigoga) glaucescens (Christoph, 1887), Euxoa (E.) sigmata Kozhantshikov, 1928, Pachyagrotis benigna (Corti, 1926), Chersotis nitens Brandt, 1941, Ch. kouros Varga & Ronkay, 1996, Ch. binalaudi Brandt, 1941, Eugnoria (Holognorisma) cuneiform Varga & Ronkay, 1994, Osthledera minna Ronkay & Varga, 1994, Polymixis (Mysymma) schistochlora Ronkay, Varga & Hreblay, 1998.

2.9. Transcaucasian–Turcomanian–Iranian–xeromontane: Chersotis hahnii (Christoph, 1885), Ch. cuneiform Kusnetzov, 1958, Polymixis (M.) philippii (Püngeler, 1911), (P. (M.) achrysa Ronkay, Varga & Hreblay, 1998, P. (E. colluta (Staudinger, 1888) (= E. apotheina (Brandt, 1938), P. (Lophotyna) crinomima (Wiltshire, 1946)*, Rhiza (Graphantha) gnorima (Püngeler, 1907)*.
2.10. N-Iranian–Turcomanian–Turkestanian-xeromontane: *Dichagyris (D.) grisescens* Staudinger, 1878*, D. (D.) leucomelas* Brandt, 1841*, D. (D.) terminicina* Corti, 1933*, D. (D.) squalidior* (Staudinger, 1901), D. (D.) celebrata* (Alphéraky, 1897)*, D. (D.) elbursica* Draudt, 1937*, D. (D.) singularis* (Staudinger, 1877)*, D. (D.) eureteoces* (Boursin, 1940)*, D. (D.) amoena* (Staudinger, 1891)*, D. (Yigoga) disturbans* (Püngeler, 1914), D. (Y.) improba* (Staudinger, 1888)*, *Euxoa (E.) transcupisca* Közhantshikov, 1928 (= *E. catervaria* Corti, 1929, E. lugubris* Brandt, 1941)*, E. (E.) perierga* Brandt, 1938*, E. (E.) mustelina* (Christoph, 1877)*, E. (E.) cespitis* (Swinhoe, 1885)* (= *E. praestigiosa* Brandt, 1941), *Agritis bifurca* Staudinger, 1881, A. psammocharis* Boursin, 1948, *Chersotis curvispina* Boursin, 1961, *Rhyacia (Anchorhyacia) psammina* (Püngeler, 1899)* (= *R. nyctymerides* (Bang-Haas, 1922), *Eugnorisma* (Holognorisma) spodia* (Püngeler, 1899)*, E. (H.) kristsenii* Varga, G. Ronkay & L. Ronkay, 2015, E. (H.) atrabraeblops* Varga, 1975*, Eugraphe maricida* (Christoph, 1887)*, Rhiza (G.) laciniosa* (Christoph, 1887)*, *Heptapotamia* (= *Guselderia* eustratii* Alphéraky, 1882 (= G. lutea Hacker, 1987)*.

2.11. Anatolian–N-Iranian–Tien-Shan–Altai-xeromontane: *Dichagyris (D.) truculenta* (Lederer, 1853)*, *Eugnorisma* (H.) eminens* (Lederer, 1855)*, *E. insignata* (Lederer, 1853)*.

3. Central- and Inner-Asiatic xeromontane species

3.1. Turkestanian–(Tien-Shan)–Mongolian-xeromontane: *Actebia (Purexarnis) pocelia* (Staudinger, 1895), A. (P) laetifica* (Staudinger, 1889), A. (P) candida* (Staudinger, 1888), A. (Protexarnis) confusa* (Alphéraky, 1882)*, *Dichagyris (D.) verecunda* (Staudinger, 1898)*, D. clara* (Staudinger, 1888)*, D. (D.) pudica* (Staudinger, 1895)*, D. (subg. ?) plumbea* (Alphéraky, 1887), *Xestia (Pachnobia) senescens* (Staudinger, 1881)*, Ammogrotis suavis* (Staudinger, 1888)*, *Chersotera zetina* (Staudinger, 1900)*, Polia lama* (Staudinger, 1886) (= *P. enoda* Bang-Haas, 1912)*, *Auchmis detersina* (Staudinger, 1889), A. curva* (Staudinger, 1889)*, *Aedophron eos* Varga & Ronkay, 1991.

3.2. W-Mongolian-xeromontane species: *Xenophysa sharhu* Varga, 1989, *Chersotera sukharevae* (Varga, 1973)*, C. oxytera* Varga, 1992, C. juliannae* Varga, 1992, C. argyrea* Varga, 1992, C. persephone* Varga, Ronkay & Ronkay, 2017, C. scotosparsa* Varga, Ronkay & Ronkay, 2017, C. cyanochrea* Varga, Ronkay & Ronkay, 2017, Rhiza (Grapbantha) calligrapha* (Ronkay & Varga, 1989), *Orohadenula clementissima* (Ronkay & Varga, 1993), *Auchmis mongolica* (Staudinger, 1896)*.

3.3. Mongolian–S-Siberian-xeromontane species: *Actebia (Ledereragrotis) difficilis* (Ershov, 1877), *Dichagyris (D.) kaszabi* Varga, 1973, D. (D.) ignara* (Staudinger, 1896), D. (Stenomides) spisslinea* (Staudinger, 1896), *Trichosilis nigrita* (Graeser, 1896), T. honesta* (Staudinger, 1892) (= T. pulchrella* Bang-Haas, 1912), Euxoa (E.) decorans* (Staudinger, 1896), E. (E.) fissa* (Staudinger, 1895), E. (Orosagrotis) trisitis* (Staudinger, 1897), *Chersotis transiens* (Staudinger, 1896), Prognorisma albisurca* (Ershov, 1877), *Pseudohermonassa melanholica* (Lederer, 1857), P ononensis* (Bremer, 1861), Versutorographa versuta* (Püngeler, 1901), Estimata herichschaefferi* (Alphéraky, 1898), *Chersotera peregovelii* Varga & Gyulai, 1999, *Onocnemis senica* (Eversmann, 1857), *Palaeagrotis inops* (Lederer, 1857).

3.4. W-Tien-shan–Alai-xeromontane: *Dichagyris (Yigoga) subturbans* (Boursin, 1948), *Euxoa (E.) enixa* Püngeler, 1906, E. (E.) bogadanovi (Ershov, 1873), *Chersotis petermari* Varga, 1988, *Rhyacia (Dichorhyacia) ignobilis* (Staudinger, 1888), *Eugnorisma (E.) jubilans* Varga, Ronkay & Gyulai, 1995, *Ctenoceratoda tancrei* (Graeser, 1892), *Bryomixis lichenosa* Ronkay & Varga, 1990.

3.5. Turkestanian–E. Tienshan-xeromontane: *Actebia (Purexarnis) violeta* (Staudinger, 1895), *Dichagyris (D.) stellans* Corti & Draudt, 1933, D. (D.) umbrifera* (Alphéraky, 1882)*, D. (Albocosta) juldusii* (Alphéraky, 1882), *Euxoa (subg. ?) cuprina* (Staudinger, 1899), *Chersotis vicina* (Corti, 1930), C. calorica* (Corti, 1930), Rhyacia (Anchorhyacia) nyctymerina* (Staudinger, 1888), R. (A.) diplogramma* (Hampson, 1903), R. (Orophryacia) hampsoni* (Bang-Haas, 1910), Rh. (Standfussryacia) junonia* (Staudinger, 1881)*, *Xenophysa agnostica* Varga, 1989, *Chersotera khorgossi* (Alphéraky, 1882), *Bryopolia chrysospora* Boursin, 1944.

3.6. Tienshan–(Alai)–Hissarro-Darwaz-xeromontane: *Dichagyris (Albocosta) lasciva* (Staudinger, 1888)*, *Chersotis leucostola* Varga & Ronkay, 1996, C. sordescens* (Staudinger, 1899), *Eugnorisma* (Eugnorisma) gaunax* (Püngeler, 1899), E. (E.) variago* (Staudinger, 1882), *Xestia ornata* (Staudinger, 1891), *Bryoxena tenuicorns* (Alphéraky, 1887).
3.7. **Hissaro-Darwaz–(Shugnan)-xeromontane**: *Euxoa (E.) hissarica* Varga, 1990, *E. (E.) xanthophylla* Varga, 1990, *Chersotis electrographa* Varga, 1990, *Eugnorisma (E.) deleasma* Boursin, 1970, *Xenophysa paradoxa* Varga, 1989, *Ostheldera kondara* Ronkay & Varga, 1994.

3.8. **Tienshan–W-Pamir-xeromontane**: *Euxoa (E.) flavisignata* Corti, 1931, *E. (E.) plumbina* (E Wagner, 1913), *Rhyacia (Stenorhynacia) electra* (Staudinger, 1888)* (= R. griseoalba* Kozhantshikov, 1937), *Rh. (Anarchorhynacia) subdecora* Staudinger, 1887*, Rh. (A.) similis* Staudinger, 1881, *Xenophysa agnostica* Varga, 1990, *Ctenoceratoda turpis* (Staudinger, 1900), *Bryopolia chamaeleon* (Alphéraky, 1887).

3.9. **W-Pamir-xeromontane**: *Dichagyris (D.) apochora* Varga & Gyulai, 2001, *Dichagyris (Yigoga) nekrosovi* Varga & Gyulai, 2001, *Euxoa (E.) melanochroa* Varga, 1990, *E. (E.) psammospora* Varga & Gyulai, 2001, *Chersotis argyropogon* Varga & Gyulai, 2001, *Ch. lukhtanovi* Varga & Gyulai, 1999, *Ch. nekrosovi* Varga, 1998, *Dasypolia shugnana* Varga, 1982, *Polymixis (Boursinixis) pamiridia* Boursin, 1970.

3.10. **Transalai–E. Pamir-xeromontane**: *Euxoa (Pleoneuctopoda) murzini* Varga, 1990, *E. (P.) puengeleri* (F. Wagner, 1913), *Ctenoceratoda longicornis* (Graesser, 1892), *Lukhtanovi Varga & Gyulai, 1999, C. psychrogena* Varga & Gyulai, 1999, *C. aksakal* Varga & Gyulai, 1999, *Apamea nekrosovi* Mikkola, Varga & Gyulai, 1995.

3.11. **Tienshan–Hissar–Hindukush-xeromontane**: *Eugnorisma (E.) trigonica* Alphéraky, 1872*, Goniographa funkei* Püngeler, 1901, *G. decussa* Staudinger, 1896.

3.12 **W-Pamir–Hindukush-xeromontane**: *Actebia (Hemixarnis) berezkii* (Kozhantshikov, 1937), *Dichagyris (D.) chrysopyga* Boursin, 1963, *D. (Yigoga) unifica* (Kozhantshikov, 1937), *Euxoa (E.) submelanochroa* Gyulai & Varga, 2006, *E. (Pleoneuctopoda) kotschii* Draudt, 1937 (*= E. plumbeascens* Kozhantshikov, 1937).

3.13 **(Hissaro-Darwaz)–Pamirs–West-Himalayan-xeromontane**: *Actebia (Protexarnis) monogramma* (Hampson, 1903), *Actebia (Hemixarnis) peperida* (Hampson, 1903), *Dichagyris (D.) leucographa* Varga, 1990, *D. (D.) scotothina* Varga, 1990, *D. (D.) hypotacta* Varga, 1990, *Euxoa (E.) naumanni* Varga, 1990, *E. (E.) hypochlora* Boursin, 1964*, Agrotis semivirens* Kozhantshikov, 1937, *Rhyacia (A.) oxytheca* Boursin, 1957, *Rh. (A.) oromys* Varga, 1990, *Xenophysa pocilogramma* Varga, 1985, *Bryopolia monotona* Varga & Ronkay, 1990, *B. tsveaevi* Varga & Ronkay, 1990*, Bryoxena plantei* Varga, 1975, *V. lichenodes* Varga & Ronkay, 1991.

3.14. **Hindukush-xeromontane**: *Dichagyris (D.) euteles* (Boursin, 1940), *D. (D.) stenoptera* Boursin, 1961, *D. (D.) ammoxanthoides* Varga, 1975, *Euxoa (E.) subeucta* Varga, 2014, *E. (E.) metasignata* Varga, 2014, *E. (E.) eremo-realis* Varga, 1975, *E. (Orosargotis) triumregium* Varga, 1979, *Chersotis pachnosa* Varga, 1975, *Ch. antigrapha* Boursin, 1961, *Ch. metagraphe* Varga, 1975, *Ch. delear* Boursin, 1970, *Rhyacia (A.) evartiana* Varga, 1990, *Rh. (A.) scythropa* Boursin, 1961, *Standfussiana socors Corti, 1925, Xenophysa bournsi* Varga, 1985, *X. argyrogramma* Varga, 1985, *X. xenogramma* Boursin, 1969, *X. monastica* Boursin, 1969, *Eicomorpha episcilloidea* Boursin, 1969, *Ctenoceratoda septemlacinistris* Gaal-Hasler, Lödl, G. Ronkay, L. Ronkay & Varga, *Polymixis (Bourssinixis) zophodes* (Boursin, 1960), *P. (B.) polymorph* (Boursin, 1960), *P. (B.) stictineura* (Boursin, 1960), *P. (Eremophysa) roehrei* Boursin, 1961, *Bryopolia holoserica* Boursin, 1960, *Bryoxena bournsi* (Plante, 1983), *B. tribulis* (Plante, 1983), *Victrix chloroxantha* Boursin, 1957, *V. lichenodes* Varga & Ronkay, 1969, *V. illusiris* Varga & Ronkay, 1991.

3.15. **Hindukush–West-Himalayan-xeromontane**: *Actebia (Hemixarnis) peperida* (Hampson, 1903), *Dichagyris (D.) payottorum* Varga, G. Ronkay & L. Ronkay, 2020, *D. (Yigoga) acutijuxta* Boursin, 1957, *D. (subg.?) poliogramma* (Hampson, 1903), *D. (subg.?) chersotoideus* Hacker, 1990, *Euxoa (E.) vartianica* Boursin, 1963, *E. (E.) hactriana* Varga, 2014, *Chersotis fidahusseini* Varga, Gyulai, G. Ronkay & L. Ronkay, 2014, *Eugnorisma (E.) asad* Boursin, 1963*, E. (E.) conformis* (Swinhoe, 1885), *Anagorismus eucratides* (Boursin, 1957), *A. glareomima* (Varga & Ronkay, 1991), *Xenophysa pocilogramma* Varga, 1985, *X. naumannii* Varga, 1990, *Polymixis (subg.?) vartianorum* (Varga, 1979), *P. (Bourssinixis) fabiani* Ronkay, Varga & Hreblay, 1998, *P. (Eremophysa) acharis* (Püngeler, 1903), *P. (E.) argyllosa* Boursin, 1970, *Bryopolia virescens* (Hampson, 1894)*.
3.16. West-Himalayan–(Karakoram)-xeromontane: *Dichagyris* (subg. ?) *nivisparsa* (Butler, 1889), *D. (subg. ?) draesekei* (Corti, 1928), *Euxoa* (*E.*) *hyperythra* Boursin, 1964, *E. dimorpha* (Hampson, 1919), *E. (E.) amorpha* Boursin, 1964*, E. (E.) vargai* Hacker, 1996, *Standfussiana herbuloti* Plante, 1987*, Rhyacia* (*Standfussryhacia*) *chimaera* Hacker & Varga, 1993, *R. (S.) peksi* Hacker, 1990, *R. (S.) karakoreas* Hacker & Varga, 1990, *R. (S.) horroreas* Varga, 2011, *Anagromysia goniothorax* (Varga, Ronkay & Hacker, 1990), *Ctenoceratoda gandhara* Varga, Gyulai, Ronkay & Ronkay, 2018, *Hacker, 1990, & Varga, 1990, B. ronkayorum* Hacker, 1996, *Polyzonix* (*E.*) *calamistis* (Hampson, 1894).

3.17. Trans-Himalayan–Tibetan-xeromontane species: *Actetia* (*Hemixemaris*) *mocchilla* (Püngeler, 1906), *A. (H.) epiphan* (Boursin, 1940), *Dichagyris* (*Albocosta*) *dulcis* (Alphéraky, 1892), *D. (A.) musivula* (Staudinger, 1895), *D. (subg. ?) subplumbea* (Staudinger, 1895), *D. (subg. ?) geochroides* Boursin, 1940, *D. (subg. ?) astignata* (Hampson, 1906), *D. (subg. ?) vargasoli* Gyulai & Ronkay, 2001, *D. (subg. ?) kormos* Gyulai & Ronkay, 2001, *D. (subg. ?) minuta* Gyulai & Ronkay, 2001, *Euxoa* (*E.*) *polytela* Boursin, 1940, *E. (E.) hypobscura* Hreblay & Ronkay, 1998, *E. (E.) ratna* Hreblay & Ronkay, 1998, *E. (E.) trividia* Hreblay & Ronkay, 1998, *Euxoa* (*E.*) *zugmayeri* Boursin, 1948, *Agrotis lamprosericea* Hreblay & Ronkay, 1998, *A. macrobscura* Hreblay & Ronkay, 1998, *Rhyacia* (*Standfussryhacia*) *oreas* (Püngeler, 1904); *R. (S.) mirabilis* Boursin, 1954, *R. (S.) admiranda* Gyulai & Ronkay, 2001.

4. Xeromontane (mostly polycentric) species with expansion into the zonal steppe areas (expansive species of different faunal types!)

*Dichagyris* (*D.*) *nigroleane* Kozhantshikov, 1930* (syn: *D. squarulum* Auct. nec Eversmann, 1856)*, *D. (D.) celebretia* (Alphéraky, 1897)*, *Dichagyris* (*D.*) *triculenta* (Lederer, 1853)*, *D. (D.) lutescens* (Eversmann, 1844), *D. (Yigoga) flavina* (Herrich-Schäffer, 1852, *D. (Yigoga) orientis* (Alphéraky, 1882)*, *Euxoa* (*E.*) *basigramma* (Staudinger, 1870)*, E. (E.) christophi* (Staudinger, 1870), E. (E.) *distinguenda* (Lederer, 1857)*, *E. (E.) phanto* Kozhantshikov, 1928, *E. (E.) mustelina* (Christoph, 1876)*, *E. (E.) deserta* (Staudinger, 1870)*, *E. (E.) foeda* (Lederer, 1885), *E. (E.) fallax* (Eversmann, 1854), *E. (E.) triaena* Kozhantshikov, 1929 (= *E. sagittata* Hübnner, 1827), *E. (E.) acuminifera* (Eversmann, 1854), *E. (Orosagrotis) tristis* (Staudinger, 1897), *Chersotis capnistis* (Lederer, 1871)*, Ch. *andereggii* (Boisdual, 1837), *Ch. alpestris* (Boisdual, 1834)*, *Ch. transiens* (Staudinger, 1896), *Eugonorismia* (*Holognorismia*) *puengeleri* Varga & Ronkay, 1987, *E. (H.) ignotatum* Varga & Ronkay, 1994, *E. (H.) chadoraica* (Boisdual, 1840)*, *Xestia sareptana* (Herrich-Schäffer, 1851) (= *Amathes iobaphes* Boursin, 1940), *Polia serratlinea* (Treitschke, 1825)*, *Apamea leucodon* (Eversmann, 1837)*, *Rhiza* (*Rh.*) *commoda* (Staudinger, 1889), G. *ignida* (Christoph, 1887), *Rhiza* (*Rh.*) *minuta* (Püngeler, 1900), *Eremohadena siri* (Ershov, 1874), *E. adscripta* (Püngeler, 1914), *Oncocnemis confusa* (Freyer, 1842), *O. strioligera* (Lederer, 1853), *O. nigricula* (Eversmann, 1847), etc.
Appendix II

Allopatric and parapatric sister species in Palaearctic Noctuinae

2.1. Species groups in the genus Dichagyris
Lederer, 1857 (subg. Dichagyris)

Subg. Dichagyris (type species Agrotis melanura Kollar, 1846)

Dichagyris melanura group
Dichagyris melanura (Kollar, 1846)
Dichagyris melanura melanura (Kollar, 1846)
Dichagyris melanura albida (Caradja, 1931)
Dichagyris melanura dufayi Moberg & Fibiger, 1990
Dichagyris melanura hyrcanica Boursin, 1963
Dichagyris rhadamanthys Reisser, 1958
Dichagyris korshunovi Varga, 1996

Dichagyris leucomelas group
Dichagyris leucomelas Brandt, 1941
Dichagyris leucomelas leucomelas Brandt, 1941
Dichagyris leucomelas endemica Fibiger, Svendson & Nilsson, 1999
Dichagyris leucomelas ladakhensis Hacker & Peks, 1990
Dichagyris stellans (Corti & Draudt, 1933)
Dichagyris duskei Moberg & Fibiger, 1990

Dichagyris imperator group
Dichagyris imperator (Bang-Haas, 1912)

Dichagyris pfeifferi group
Dichagyris pfeifferi (Corti & Draudt, 1933) (= fredi Brandt, 1941)

Dichagyris vallesiaca group
Dichagyris vallesiaca Boisdouval, 1932
Dichagyris vallesiaca vallesiaca Boisdouval, 1932
Dichagyris vallesiaca squarulorum (Eversmann, 1856)
Dichagyris vallesiaca subsquarulorum Kozhantshikov, 1930
Dichagyris vallesiaca crymaea Kozhantshikov, 1930
Dichagyris vallesiaca inexpectata Kozhantshikov, 1925
Dichagyris vallesiaca venosa Kozhantshikov, 1930
Dichagyris vallesiaca opulenta Brandt, 1941 (species?)
Dichagyris fuscashmiriana Varga, G. Ronkay & L. Ronkay, 2020 (subspecies?)
Dichagyris griseotincta Wagner, 1931

Dichagyris nigrolineata group
Dichagyris nigrolineata Kozhantshikov, 1930
Dichagyris nigrolineata nigrolineata Kozhantshikov, 1930 (= squalorum sensu Boursin et Auctorum, nec Eversmann, 1856)
Dichagyris nigrolineata rubidior Corti, 1933
Dichagyris tyrannus (Bang-Haas, 1912)
Dichagyris striata Kozhantshikov, 1930
Dichagyris striata striata Kozhantshikov, 1930
Dichagyris striata beluchus Brandt, 1941
Dichagyris striata kalastriata Varga, G. Ronkay & L. Ronkay, 2020

Dichagyris eremicola group
Dichagyris eremicola (Standfuss, 1888)
Dichagyris wilsoni Fibiger, 2002 (subspecies ?!)

Dichagyris squalidior group
Dichagyris squalidior (Staudinger, 1901)
Dichagyris lux Fibiger & Nupponen, 2002 (subspecies of D. squalidior?!)
Dichagyris payotiorum Varga, G. Ronkay & L. Ronkay, 2020

Dichagyris taftana group
Dichagyris taftana Brandt, 1941
Dichagyris taftana taftana Brandt, 1941
Dichagyris taftana elborsasta Varga, G. Ronkay & L. Ronkay, 2021
Dichagyris taftana safavida Varga, G. Ronkay & L. Ronkay, 2021
Dichagyris guentereberti Varga, G. Ronkay & L. Ronkay, 2021

Dichagyris kirghisa group
Dichagyris kirghisa (Eversmann, 1856)

Dichagyris terminicincta group
Dichagyris terminicincta (Corti & Draudt, 1933)
Dichagyris terminicincta terminicincta (Corti & Draudt, 1933)
Dichagyris terminicincta maraschi Corti & Draudt, 1933 (= phaeotenia (Boursin, 1940)
Dichagyris terminicincta sps. from the Kopet-Dagh Mts
Dichagyris terminicincta capnista (Boursin, 1963)
Dichagyris ilseae Stangelmaier, Wieser & Fibiger, 2003
Dichagyris euteles (Boursin, 1963)

Dichagyris psammochroa group
Dichagyris psammochroa Boursin, 1940
Dichagyris psammochroa psammochroa Boursin, 1940
Dichagyris psammochroa dichroa Boursin, 1940
Dichagyris psammochroa kopetdaghimena Varga, G. Ronkay & L. Ronkay, 2021
Dichagyris cataleipa Varga, 1993
Dichagyris afghana Boursin, 1963
Dichagyris kurbatskyi Varga, G. Ronkay & L. Ronkay, 2021
Dichagyris apochora Varga & Gyulai 2001
Dichagyris humilis group
Dichagyris humilis Boursin, 1940
Dichagyris hypotacta Varga, G. Ronkay & L. Ronkay, 2021

Dichagyris clara group
Dichagyris clara Staudinger, 1888
  Dichagyris clara clara Staudinger, 1888
  Dichagyris clara gobialtaica Varga, 1996
Dichagyris leucographa Varga, 1990
Dichagyris scotographa Varga, 1990
Dichagyris kautti Varga & Ronkay, 1991

Dichagyris hymalayensis group
Dichagyris hymalayensis Turati, 1933 (= despecta Corti & Draudt, 1933, subsp.?)
  Dichagyris chrysopyga (Boursin, 1963)
Dichagyris celebrata group
Dichagyris armeniaca Kozhantshikov, 1930
  Dichagyris armeniaca armeniaca Kozhantshikov, 1930
  Dichagyris armeniaca centranatolica Varga, Gyulai & Miatleuski, 2002
Dichagyris kongur Varga, 1996
Dichagyris umbrifera group
Dichagyris umbrifera (Alphéraky, 1882)
  Dichagyris umbrifera inumbrata Varga, Gyulai & Miatleuski, 2002
Dichagyris kaszabi Varga, 1973
Dichagyris naumanni Varga, 1996
Dichagyris herzi Kozhantshikov, 1930
Dichagyris jacobsoni Kozhantshikov, 1930
Dichagyris boursini Brandt, 1941
Dichagyris achtalensis Kozhantshikov, 1929
Dichagyris korsak Varga, Gyulai & Miatleuski, 2002

Dichagyris pudica group
Dichagyris pudica (Staudinger, 1895)
  Dichagyris pudica pudica (Staudinger, 1895)
  Dichagyris pudica griseola (Staudinger, 1895)

Dichagyris singularis group
Dichagyris singularis (Staudinger, 1877)
  Dichagyris singularis singularis (Staudinger, 1877)
  Dichagyris singularis mesopotamica Hacker & Weigert, 1986
Dichagyris melanofusca Varga, G. Ronkay & L. Ronkay, 2020

Dichagyris amoena group
Dichagyris amoena (Staudinger, [1892])
  Dichagyris amoena amoena (Staudinger, [1892])
  Dichagyris amoena diffuentior Varga, G. Ronkay & L. Ronkay, 2020
  Dichagyris amoena fuscarenosa Varga, G. Ronkay & L. Ronkay, 2020
Dichagyris anosasia (Draudt, 1936)

Dichagyris constanti group
Dichagyris constanti (Millière, 1860)
  Dichagyris constanti constanti (Millière, 1860)
  Dichagyris constanti eos (Oberthür, 1913)

Dichagyris candelisequa group
Dichagyris candelisequa [(Denis & Schiffermüller], 1775)
  Dichagyris candelisequa candelisequa ([Denis & Schiffermüller], 1775)
  Dichagyris candelisequa zernyi (Rungs, 1952)
  Dichagyris candelisequa cyrnos (Schawerda, 1928)
  Dichagyris candelisequa achaemenidica Hacker, 1990
  Dichagyris candelisequa rana (Kindermann, 1853)
  Dichagyris candelisequa serpens Varga, G. Ronkay & L. Ronkay, 2020
Dichagyris elbursica Draudt, 1937

Dichagyris verecunda group
Dichagyris verecunda (Püngeler, 1898)
  Dichagyris verecunda verecunda (Püngeler, 1898)
  Dichagyris verecunda psammodis Varga, 1993
Dichagyris karakorealis Varga, G. Ronkay & L. Ronkay, 2020

Dichagyris renigera group
Dichagyris renigera (Hübner, [1808])
  Dichagyris renigera renigera (Hübner, [1808])
  Dichagyris renigera funestissima (Bubacek, 1926)
  Dichagyris renigera argentina (Caradja, 1930)
  Dichagyris renigera funebris (Staudinger, 1892)
  Dichagyris renigera subsp. (from Lebanon)
Dichagyris poecilopetala Varga, 1979

Dichagyris forficula group
Dichagyris forficula (Eversmann, 1851)
  Dichagyris forficula forficula (Eversmann, 1851)
  Dichagyris forficula hadjina (Staudinger, 1892)
  Dichagyris forficula adelfi Fibiger, Svendson & Nilsson, 1999
  Dichagyris forficula devota (Christoph, 1884)
Dichagyris turana (Staudinger, 1892)
  Dichagyris turana turana (Staudinger, 1892)
  Dichagyris turana furiosa (Bang-Haas, 1912)
Dichagyris contermina (Corti, 1930) (= D. wolfi Hacker, 1985)
Dichagyris erubescens (Staudinger, 1892)

Dichagyris argentea group
Dichagyris argentea Kozhantshikov 1929
Dichagyris darius Boursin, 1940
  Dichagyris darius darius Boursin, 1940
  Dichagyris darius acrpieta Varga, 1996
Dichagyris gyulaiivani Gyulai & Varga, 2002
Dichagyris eureteocles group
Dichagyris eureteocles Boursin, 1940
Dichagyris eureteocles kappadotis Varga, G. Ronkay & L. Ronkay, 2020
Dichagyris eureteocles karayalchis Varga, G. Ronkay & L. Ronkay, 2020
Dichagyris danilevskyi (Shtshetkin, 1965)
Dichagyris zagroica Hacker & Ebert, 2002
Dichagyris nekrasovi Varga & Gyulai, 2001
Dichagyris multicuspis group
Dichagyris multicuspis (Eversmann, 1852)
Dichagyris aequicuspis (Staudinger, 1900)
Dichagyris spintheropis group
Dichagyris spintheropis Varga & Ronkay, 1996

2.2. Species groups in the genus Chersotis
Boisduval, 1840

Chersotis rectangula group
Chersotis rectangula ([Denis & Schiffermüller], 1775)
Chersotis andereggii (Boisduval, [1837])
Chersotis andereggii andereggii (Boisduval, [1837])
Chersotis andereggii saricana Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis acutangula (Staudinger, 1892)
Chersotis acutangula acutangula (Staudinger, 1892)
Chersotis acutangula klapperichi Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis acutangula subtilis Hacker & Peks, 1990
Chersotis juncta (Grote, 1878)

Chersotis sordescens group
Chersotis sordescens (Staudinger, 1900)
Chersotis herczigi Varga, 1996
Chersotis firdasii Schwingenschuss, 1937
Chersotis fidahusseini Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis fidahusseini fidahusseini Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis fidahusseini heptalimna Varga, Gyulai, L. Ronkay & G. Ronkay, 2013

Chersotis ocellina group
Chersotis ocellina ([Denis & Schiffermüller], 1775)
Chersotis alpestris (Boisduval, [1837])
Chersotis alpestris alpestris (Boisduval, [1837])
Chersotis alpestris pontica (Draudt, 1936)
Chersotis alpestris caucasia Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis oreina Dufay, 1984

Chersotis transiens (Staudinger, 1896)
Chersotis stridula (Hampson, 1903)
Chersotis stridula stridula (Hampson, 1903)
Chersotis stridula chimana Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis cortifera Rêzbányai-Reser, 1997 (species status questioned)

Chersotis capnitis group
Chersotis capnitis (Lederer, 1871)
Chersotis capnitis capnitis (Lederer, 1871)
Chersotis capnitis glabripennis (Corti, 1926)
Chersotis capnitis schnacki Fibiger & Moberg, 1993
Chersotis leucostola Varga & Ronkay, 1996
Chersotis nitis Brandt, 1941
Chersotis metagraphe Varga, 1975
Chersotis sterilis (Brandt, 1938)
Chersotis ronkayorum Fibiger, Hacker & Varga, 1993

Chersotis multangula group
Chersotis multangula (Hübner, [1803])
Chersotis andreae Dufay, 1973
Chersotis semna (Püngeler, 1906)
Chersotis pachnosa Varga, 1975

Chersotis griseivena group
Chersotis griseivena (Hampson, 1894)
Chersotis harutai Ronkay & Varga, 1998
Chersotis delear Boursin, 1970
Chersotis vargai Hacker, 1992
Chersotis electographa Varga, 1990

Chersotis juvenis group
Chersotis juvenis (Staudinger, 1901)
Chersotis kouros Varga & Ronkay, 1996
Chersotis kouros kouros Varga & Ronkay, 1996
Chersotis kouros zahlirshahi Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis shandur Varga, 1998
Chersotis calorica (Corti, 1930)

Chersotis vicina group
Chersotis vicina (Corti, 1930)
Chersotis semnica (Püngeler, 1906)

Chersotis binaloudi group
Chersotis binaloudi Brandt, 1941
Chersotis antennaphera Boursin, 1961
Chersotis argyllographa Varga & Gyulai, 2001

Chersotis deplanata group
Chersotis deplanata (Eversmann, 1843)

Chersotis halni group
Chersotis halni (Christoph, 1885)
Chersotis curvispina Boursin, 1961
Chersotis cryptographa Varga & Gyulai, 2002
Chersotis zukowskyi (Draudt, 1936)

1 Coloured letters: allo-(para-)patric sister species
Chersotis obnubila group
Chersotis obnubila (Corti, 1926)
Chersotis sjuntensis group
Chersotis sjuntensis (Kuznetsov, 1958)

Chersotis elegans group
Chersotis elegans (Eversmann, 1837)
Chersotis eberti Dufay & Varga, 1995
Chersotis kacem (Le Cerf, 1933)
Chersotis anatolica (Draudt, 1936)
Chersotis larixia (Guenée, 1852)
Chersotis fimbriola group
Chersotis fimbriola (Esper, [1803]) (several subspecies, see Fig. 16)
Chersotis laeta (Rebel, 1904) (several subspecies, see Fig. 16)
Chersotis cuprea ([Denis & Schiffermüller], 1775)
Chersotis cryptocuprea Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis rungsi Boursin, 1944
Chersotis stenographa Varga, 1979
Chersotis gratissima (Corti, 1932)
Chersotis zagros Gyulai & Varga, 2006
Chersotis nekrasovi Varga, 1996
Chersotis nupponenorum Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis friedeli Pinker, 1974

Chersotis illauta group
Chersotis illauta (Draudt, 1936)

Chersotis glebosa group
Chersotis glebosa (Staudinger, 1900)

Chersotis sarhada group
Chersotis sarhada Brandt, 1941
Chersotis hoppei Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis lehmanni Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis lukhtanovi Varga & Gyulai, 2001

Chersotis margaritacea group
Chersotis margaritacea (de Villers, 1789)
Chersotis orophila Rungs, 1967

Chersotis anachoreta group (subg. Cyrebia)
Chersotis anachoreta (Herrich-Schäffer, 1851)
Chersotis sogani Matov, Gyulai, Varga, Ronkay & Ronkay, 2013
Chersotis adili (Koçak, 1987)
Chersotis tsheverikovi Matov, Gyulai, Varga, Ronkay & Ronkay, 2013
Chersotis shaposhnikovi Matov, Gyulai, Varga, Ronkay & Ronkay, 2013

Chersotis rungsi Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis friedeli Pinker, 1974

Chersotis luperinoides (Guenée, 1852)

Chersotis romanovi Matov, Gyulai, Varga, Ronkay & Ronkay, 2013

Chersotis luperinoides (Guenée, 1852)

Chersotis shaposhnikovi Matov, Gyulai, Varga, Ronkay & Ronkay, 2013

Chersotis laeta (Rebel, 1904) (several subspecies, see Fig. 16)
Chersotis cuprea ([Denis & Schiffermüller], 1775)
Chersotis cryptocuprea Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis rungsi Boursin, 1944
Chersotis stenographa Varga, 1979
Chersotis gratissima (Corti, 1932)
Chersotis zagros Gyulai & Varga, 2006
Chersotis nekrasovi Varga, 1996
Chersotis nupponenorum Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis friedeli Pinker, 1974

Chersotis illauta group
Chersotis illauta (Draudt, 1936)

Chersotis glebosa group
Chersotis glebosa (Staudinger, 1900)

Chersotis sarhada group
Chersotis sarhada Brandt, 1941
Chersotis hoppei Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis lehmanni Varga, Gyulai, L. Ronkay & G. Ronkay, 2013
Chersotis lukhtanovi Varga & Gyulai, 2001

Chersotis margaritacea group
Chersotis margaritacea (de Villers, 1789)
Chersotis orophila Rungs, 1967

Chersotis anachoreta group (subg. Cyrebia)
Chersotis anachoreta (Herrich-Schäffer, 1851)
Chersotis sogani Matov, Gyulai, Varga, Ronkay & Ronkay, 2013
Chersotis adili (Koçak, 1987)
Chersotis tsheverikovi Matov, Gyulai, Varga, Ronkay & Ronkay, 2013
Chersotis shaposhnikovi Matov, Gyulai, Varga, Ronkay & Ronkay, 2013

2.3. Species groups in the genus Rhyacia
Hübner [1821] 1816

Rhyacia subg. Rhyacia Hübner [1821] 1816
Rhyacia (subg. Rhyacia) lucipeta group:
Rhyacia (Rhyacia) lucipeta ([Denis & Schiffermüller], 1775) – type species of the genus.

Rhyacia (subg. Rhyacia) ledereri group
Rhyacia (Rhyacia) ledereri (Erschoff, 1870)
Rhyacia (Rhyacia) quadrangula (Zetterstedt, 1839)
Rhyacia (Rhyacia) elemens (Smith, 1890)

Rhyacia (subg. Rhyacia) simulans group
Rhyacia (Rhyacia) simulans (Hufnagel, 1766)
Rhyacia (Rhyacia) arenacea (Hampson, 1907) – probably a complex of closely related species.
Rhyacia (Rhyacia) afghanidia Boursin, 1968

Rhyacia subg. Stenorhyacia Varga 2011

Rhyacia (subg. Stenorhyacia) electra group
Rhyacia (Stenorhyacia) electra (Staudinger, 1888)
(= R. griseoalba Kozhantshikov, 1937)
Rhyacia (Stenorhyacia) caradrinoides (Staudinger, 1896).

Rhyacia subg. Dichorhyacia Varga 2011
Rhyacia (Dichorhyacia) ignobilis Staudinger, 1888
Rhyacia (Dichorhyacia) fabiani Varga, 1996

Rhyacia subg. Ororhyacia Varga 2011

Rhyacia (Ororhyacia) hampsoni (Bang-Haas, 1910)

Rhyacia subg. Anchorhyacia Varga 2011

Rhyacia (Anchorhyacia) psammia group
Rhyacia (Anchorhyacia) psammia (Püngeler, 1906)
(= nyctymerides (Bang-Haas, 1922)
Rhyacia (Anchorhyacia) psammia psammia (Püngeler, 1906)
Rhyacia (Anchorhyacia) psammia stavoitiacus Toulskhoff, 1951
Rhyacia (Anchorhyacia) psammia alagesica Boursin, 1962
Rhyacia (Anchorhyacia) psammia rehnensis (F. Wagner, 1937)
**Rhyacia** (Anchorhyacia) psammia roseoflava (Corti, 1933)  
**Rhyacia** (Anchorhyacia) psammia nghtymerides (Bang-Haas, 1922)  
**Rhyacia** (Anchorhyacia) latebrosa Gyulai, 2021 (Pakistan, Hindukush) (syn. or sp.??)  
**Rhyacia** (Anchorhyacia) nyctymerina (Staudinger, 1888)  
**Rhyacia** (Anchorhyacia) gabori Varga, 1996  
**Rhyacia** (Anchorhyacia) evartianae Varga, 1990  
**Rhyacia** (Anchorhyacia) oxythea Boursin, 1957  
**Rhyacia** (Anchorhyacia) sp. from Iran, Khorasan  
**Rhyacia** (Anchorhyacia) subdecora (Staudinger, 1887)  
**Rhyacia** (Anchorhyacia) scytho Boursin, 1961

**Rhyacia** (Anchorhyacia) diplogramma group  
**Rhyacia** (Anchorhyacia) diplogramma (Hampson, 1903)  
**Rhyacia** (Anchorhyacia) oromys Varga, 1990

**Rhyacia** (Anchorhyacia) similis group:  
**Rhyacia** (Anchorhyacia) similis (Staudinger, 1888) (= decorata Staudinger, 1881, praeocc.)  
**Rhyacia** subg. Standfussrhyacia Hacker & Varga, 1990

**Rhyacia** (Standfussrhyacia) chimaera group:  
**Rhyacia** (Standfussrhyacia) chimaera (Hacker & Varga, 1990)

**Rhyacia** (Standfussrhyacia) mirabilis group:  
**Rhyacia** (Standfussrhyacia) mirabilis Boursin, 1954  
**Rhyacia** (Standfussrhyacia) mirabilis mirabilis Boursin, 1954  
**Rhyacia** (Standfussrhyacia) mirabilis nepalensis Boursin, 1954  
**Rhyacia** (Standfussrhyacia) admiranda Gyulai & Ronkay, 2001  
**Rhyacia** (Standfussrhyacia) miranda Gyulai & Ronkay, 2021

**Rhyacia** (Standfussrhyacia) junonia group:  
**Rhyacia** (Standfussrhyacia) junonia (Staudinger, 1881)  
**Rhyacia** (Standfussrhyacia) junonia junonia (Staudinger, 1881)  
**Rhyacia** (Standfussrhyacia) junonia alaina (Staudinger, 1888)  
**Rhyacia** (Standfussrhyacia) junonia alexandrina Corti & Draudt, 1933  
**Rhyacia** (Standfussrhyacia) junonia calamocho Varga, 1973)

**Rhyacia** (Standfussrhyacia) schistocroha Varga, 1973  
**Rhyacia** (Standfussrhyacia) kunluna Gyulai, 2021  
**Rhyacia** (Standfussrhyacia) ilustris Hacker & Kautt, 1996  
**Rhyacia** (Standfussrhyacia) horroreas Varga, 2011  
**Rhyacia** (Standfussrhyacia) oreas (Püngeler, 1904)  
**Rhyacia** (Standfussrhyacia) unicornis Varga 2011  
**Rhyacia** (Standfussrhyacia) karakoreas Hacker & Varga, 1990  
**Rhyacia** (Standfussrhyacia) peksi Hacker, 1990

---

2.4. Species groups in the genus **Eugnorisma**  
Boursin, 1846

**Eugnorisma**, subg. **Holognorisma** Varga, Gyulai, Ronkay & Ronkay, 2014

**Eugnorisma** (Holognorisma) chaldaica group  
**Eugnorisma** (Holognorisma) chaldaica (Boisdulav, 1840)  
**Eugnorisma** (Holognorisma) chaldaica chaldaica (Boisduval, 1840)  
**Eugnorisma** (Holognorisma) chaldaica kurdistana Hacker, 1986  
**Eugnorisma** (Holognorisma) chaldaica rubicunda Varga & Ronkay, 1990  
**Eugnorisma** (Holognorisma) kristenseni Varga, Gyulai, Ronkay & Ronkay, 2014  
**Eugnorisma** (Holognorisma) spodia (Püngeler, 1900)  
**Eugnorisma** (Holognorisma) spodia spodia (Püngeler, 1900)  
**Eugnorisma** (Holognorisma) spodia psammochrea Varga & Ronkay, 1987

**Eugnorisma** (Holognorisma) ignoratum group  
**Eugnorisma** (Holognorisma) ignoratum Varga & Ronkay, 1994  
**Eugnorisma** (Holognorisma) cuneiferum Varga & Ronkay, 1994  
**Eugnorisma** (Holognorisma) puengeleri Varga & Ronkay, 1987  
**Eugnorisma** (Holognorisma) mikkolai Varga, Gyulai, Ronkay & Ronkay, 2014  
**Eugnorisma** (Holognorisma) tamerlana (Hampson, 1903)

**Eugnorisma** (Holognorisma) eminens group  
**Eugnorisma** (Holognorisma) eminens (Lederer, 1855)  
**Eugnorisma** (Holognorisma) eminens eminens (Lederer, 1855)  
**Eugnorisma** (Holognorisma) eminens clairor Varga, 1975  
**Eugnorisma** (Holognorisma) atrabaelbops Varga, 1975  
**Eugnorisma** (Holognorisma) atrabaelbops atrabaelbops Varga, 1975  
**Eugnorisma** (Holognorisma) atrabaelbops firyuza Varga, Gyulai, Ronkay & Ronkay, 2014  
**Eugnorisma** (Holognorisma) atrabaelbops scotophaia Varga, Gyulai, Ronkay & Ronkay, 2014

**Eugnorisma**, subg. **Eugnorisma** Boursin, 1946

**Eugnorisma** (Eugnorisma) trigonica group  
**Eugnorisma** (Eugnorisma) trigonica (Alphéraky, 1882)  
**Eugnorisma** (Eugnorisma) trigonica trigonica (Alphéry, 1882)

**Eugnorisma** (Eugnorisma) trigonica gauracoides Hacker & Peks, 1990
**Eugnorisma** (Eugnorisma) gaurax (Püngeler, 1900) (= funebris Varga & Ronkay, 1990)

**Eugnorisma** (Eugnorisma) deleasma Boursin, 1967

**Eugnorisma** (Eugnorisma) deleasma deleasma Boursin, 1967

**Eugnorisma** (Eugnorisma) deleasma reducta Boursin, 1968

**Eugnorisma** (Eugnorisma) deleasma hissarica Varga & Ronkay, 1987

**Eugnorisma** (Eugnorisma) jubilans Varga, Ronkay & Gyulai, 1995

**Eugnorisma** (Eugnorisma) insignata group

- **Eugnorisma** (Eugnorisma) insignata (Lederer, 1853) – Polytypic species, subspp. not clarified
- **Eugnorisma** (Eugnorisma) conformis (Swinhoe, 1885)
- **Eugnorisma** (Eugnorisma) rafidain (Boursin, 1936) (= semiramis (Boursin, 1940))
- **Eugnorisma** (Eugnorisma) asad Boursin, 1963
- **Eugnorisma** (Eugnorisma) asad asad Boursin, 1963
- **Eugnorisma** (Eugnorisma) asad plantei Varga, Ronkay & Hacker, 1990
- **Eugnorisma** (Eugnorisma) asad eva Varga, Gyulai, Ronkay & Ronkay, 2014
- **Eugnorisma** (Eugnorisma) variago (Staudinger, 1882)
- **Eugnorisma** (Eugnorisma) variago variago (Staudinger, 1882)
- **Eugnorisma** (Eugnorisma) variago xanthiago Varga & Ronkay, 1987

**Subgenus Metagnorisma** Varga & Ronkay, 1987

**Eugnorisma** (Metagnorisma) depuncta group

- **Eugnorisma** (Metagnorisma) depuncta (Linnaeus, 1761)
- **Eugnorisma** (Metagnorisma) depuncta depuncta (Linnaeus, 1761)
- **Eugnorisma** (Metagnorisma) depuncta transcaucasica Varga, Gyulai, Ronkay & Ronkay, 2014

**Eugnorisma** (Metagnorisma) arenoflava Varga & Ronkay, 2014

**Eugnorisma** (Metagnorisma) janhabeli Varga, Gyulai, Ronkay & Ronkay, 2014

**Eugnorisma** (Metagnorisma) pontica group

- **Eugnorisma** (Metagnorisma) pontica (Staudinger, 1891)
- **Eugnorisma** (Metagnorisma) pontica pontica (Staudinger, 1891)
- **Eugnorisma** (Metagnorisma) pontica anis Varga & Ronkay, 1987
- **Eugnorisma** (Metagnorisma) pontica zagros Varga & Ronkay, 1987

2.5. Species groups in the genus *Goniographa*

**Goniographa decussa** group

- **Goniographa decussa** (Staudinger, 1897)
- **Goniographa discussa** Varga & Ronkay, 2002
- **Goniographa shchetkini** Varga & Ronkay, 2002

**Goniographa funkei** group

- **Goniographa funkei** (Püngeler, 1901)
- **Goniographa metafunkei** Varga & Ronkay, 2002
- **Goniographa naumanni** Varga & Ronkay, 2002

**Goniographa marcida** group

- **Goniographa marcida** (Christoph, 1893)
- **Goniographa gyulaipeteri** Varga & Ronkay, 2002