

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

With 21 figures, 4 tables and 2 Appendix

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Published on 2022-07-31

DOI: 10.3897/contrib.entomol.72.e87196

## Abstract

The orear 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 orear fauna is partitioned to the alpine type, as the faunal type of humid high-mountains with strong connections to the tundra zoniobiome, and the xeromontane type, as the faunal type of arid high-mountains with close connections to the eremic zoniobiomes. As the results of revisions of several Noctuidae 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 Palaeartic 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 zoniobiome 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 xeromontane species in the West Palaeartic 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, orear 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 chorologischen Zentren lassen sich durch die Artenmannigfaltigkeit bestimmter Genera und ein gehäuftes Vorkommen von endemischen Arten bzw. Subspezies disjunkter Arten erkennen. Die Orealfauna unterteilt sich einerseits in den alpinen Faunentyp, d. h. den Faunentyp der humiden Hochgebirge, mit engen Beziehungen zum tundralen Zonobiom, andererseits in den xeromontanen Faunentyp, d. h. den Faunentyp der ariden Hochgebirge, mit engen Beziehungen zum eremialen Zonobiom. Als ein Ergebnis der Revisionen mehrerer Noctuiden-Genera, Artengruppen bzw. Geschwisterarten konnte dies nachgewiesen werden; ihre Verbreitungen wurden kartiert. Die engbegrenzten Areale der allopatrischen Geschwisterarten, die oft als neu für die Wissenschaft beschrieben wurden, entsprechen den Kriterien der „*areas of endemism*“. Die Kerngebiete der paläarktischen xeromontanen Noctuidae, die aufgrund der Verbreitung der endemischen Arten postuliert wurden, wurden durch das Vorkommen der allopatrischen Subspezies der polytypischen Arten, bzw. der allopatrischen Geschwisterarten bestätigt. In den revidierten Noctuidengattungen wurden mehrere Typen der allopatrischen Artbildung durch die Analyse von Endemismusarealen bzw. Vikarianzmustern nachgewiesen. Als Ergebnis dieser Untersuchungen wurden die allopatrischen Geschwisterarten als elementare monophyletische supraspezifische Einheiten bestätigt, die sich als geeignet für phylogenetisch-biogeographische Untersuchungen erwiesen. Obwohl der größte Teil der xeromontanen Fauna engbegrenzte Areale aufzuweisen scheint, konnte sich ein beträchtlicher Anteil der Arten weit in die zonalen Steppengebiete durch die adaptiven Veränderungen der Lebenszyklen ausbreiten. Die große Mannigfaltigkeit der im sino-himalayanischen Hochgebirge entstandenen kälteangepassten Arten lässt sich durch das Durchdringen von zwei wichtigen Filter-Korridoren ableiten. Ein Zweig dieser Bifurkation verläuft durch den „Rhododendron-Korridor“ in den holarktischen Taiga-Gürtel, während ein anderer Zweig durch den xeromontanen Filter-Korridor in die Gebirgssysteme von Zentral- und Innerasien verläuft. Diese Unterteilung lässt sich durch die unterschiedliche taxonomische Verteilung jener Genera verstehen, aus denen diese beiden grundsätzlichen Faunentypen bestehen. Es ist wahrscheinlich, dass die Ausbreitungsvorgänge der xeromontanen Elemente in der Westpaläarktis durch die Messinischen Salinitätskrise geformt wurden; einen weiteren wichtigen Einfluss besaß die mittelpaläozäne klimatische Transition, während derer durch großräumige Abkühlung und Austrocknung die zonale Anordnung der Vegetation umgeordnet wurde.

## 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, SIMOVÁ & 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 arboreal biomes (see: DE LATTIN 1967) as terrestrial habitats characterised by medium or higher level of primary production, the orreal fauna can be identified as the faunal type of the orographically defined non-arboreal biomes (VARGA 1997). Its members, as a rule, have insular, endemic or disjunct areas in the Eurasiatic high mountains (Fig. 1). Their core areas can be recognised by the high species-diversity of numerous typical genera and, thereby, the accumulated occurrence of endemic species and/or subspecies of disjunct species.

Parallel with the non-arboreal zonobiomes, the orreal fauna can be subdivided into the *alpine* type, 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 translocations and disjunctions, resulting in the diversification 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*, *Actebia* s.l., *Chersotis*, *Rhyacia*, *Standfussiana*, *Eugnorisma*, *Spaelotis*, *Xenophysa*, etc. (VARGA 1995, 1997, 2010b), Polyommata blues (e.g. *Polyommatus* subg. *Agrodiaetus*, ECKWEILER & HÄUSER 1997, KANDUL et al. 2004, 2007, LUKHTANOV et al. 2005), and also in some flightless grasshopper groups (e.g. *Conophyma*, *Nocaracris*, *Nocarodes*, see: LI et al. 2011, ÚNAL 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 & TIMOSSO 2014; Yponomeutidae: *Kessleria*, HUEMER & MUTANEN 2015), certain genera of Geometridae (e.g. *Entephria*, *Psodos*, *Charissa*, *Elophos*; 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 faunal assemblages in the Central and Inner Asiatic<sup>1</sup> mountain systems (Fig. 1, 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 Noctuinae, 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 steppic species. Finally, I hypothesised that the core areas of the Palearctic 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*, *Spaelotis*, *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 & GYULAI 1999; VARGA 1998, 2011a, b, 2014; VARGA et al. 1989, 2018) numerous

<sup>1</sup> On the meaning of the terms Central vs Inner Asia see: Fig. 1 and Discussion 2.

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 Palearctic xeromontane Noctuidae.

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

- Widely distributed, often polytypic species with parallel polymorphism of distinctly marked vs. unicolorous forms in different populations<sup>2</sup> (e.g. in some

<sup>2</sup> 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 terminicincta*, *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. terminicincta* f. *phaeotaenia* & f. *capnista*; *D. psammochroa* & f. *dichroa*, *E. insignata* f. *pallescens* & f. *leuconaura*; *E.* (*M.*) *pontica* & f. *consenescens*), however, without any clear subspecific differentiation.

- Parallel polymorphism and taxonomic differentiation are combined in the polytypic *Euxoa adumbrata*. 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. transcaspica* (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*<sup>\*</sup>, *Dichagyris melanura*<sup>\*3</sup>, *D. celsicola*<sup>\*</sup>, *Chersotis capnistis*<sup>\*</sup>, *Ch. zukowskyi*<sup>\*</sup>, *Ch. laeta*<sup>\*</sup>, *Rhyacia psammia*<sup>\*</sup> (= *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 malickyi* (sister species of *E. heringi*), *Dichagyris rhadamanthys* (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<sup>\*</sup> species, e.g. *Dichagyris vallesiaca*<sup>\*</sup> – *D. fuscashmiriana*, *D. verecunda*<sup>\*</sup> – *D. karakorealis*, *D. singularis*<sup>\*</sup> – *D. melanofusca*, *Eugnorisma insignata*<sup>\*</sup> – *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. herczigi* (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. metasigmata*

(Fig. 6), *Dichagyris striata* – *D. tyrannus*, *D. humilis* – *D. hypotacta*, *D. darius* – *D. argentea*, *D. taftana* – *D. guentereberti*, *D. strenua* – *D. vietteana*; *Hemiexarnis iuguma* – *H. berezskii*; *Chersotis firdusii* – *Ch. fidahusseini* (Fig. 5); *Ch. capnistis* – *Ch. leucostola* (Fig. 7), *Rhyacia gabori* – *R. evartiana* (Fig. 8); *Goniographa marcida* – *G. gyulaipeteri*; *Xenophysa cacumena* – *X. afghanorea* (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-Darwaz 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.

- Allopatric pairs (or triplets) of Central Asiatic sibling species, differentiated either between different parts of the Tien Shan system, or between the Tien Shan system and other Central Asiatic massifs as Hissar Mts, Pamirs and/or Hindukush (Table 3): *Chersotis vicina* – *Ch. petermarci*; *Ch. calorica* – *Ch. shandur* (Fig. 4), *Ch. delear* – *Ch. electrographa* – *Ch. vargai*, *Rhyacia diplogramma* – *R. oromys*; *Goniographa decussa* – *G. discussa*; *G. funkei* – *G. metafunkei* – *G. naumanni* (Fig. 9).
- Allo- or parapatric 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. antigrapha* – *Ch. argyllographa* (Fig. 10); *Chersotis ronkayorum* – *Ch. sterilis* – *Ch. nitens* – *Ch. metagrapha* (Fig. 7); *Chersotis sarhada* – *Ch. hoppei* – *Ch. lehmanni* – *Ch. lukhtanovi*.
- Pairs or groups of partially sympatric sibling species, evolved by former geographical isolation and secondary overlap: *Chersotis andereggii* – *Ch. acutangula*; *Ch. juvenis* – *Ch. kouros*; *Ch. ocellina* – *Ch. alpestris* – *Ch. oreina* – *Ch. stridula* – *Ch. transiens*; *Chersotis hahni* – *Ch. curvispina* – *Ch. cryptographa*; *Rhyacia subdecora* – *R. scythropa* – *R. oxytheca* (Fig. 8); *Bryopolia virescens* – *B. tsvetaevi* – *B. chamaeleon* – *B. chrysozona*; *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 capnistis*-group, VARGA & RONKAY 1996). Detailed description of these life-cycle changes and biogeographical consequences is provided in the Results 3.

<sup>3</sup> The western isolated populations represent the nominotypical subspecies.





Fig. 1: Important parts and mountain systems of Eurasia.

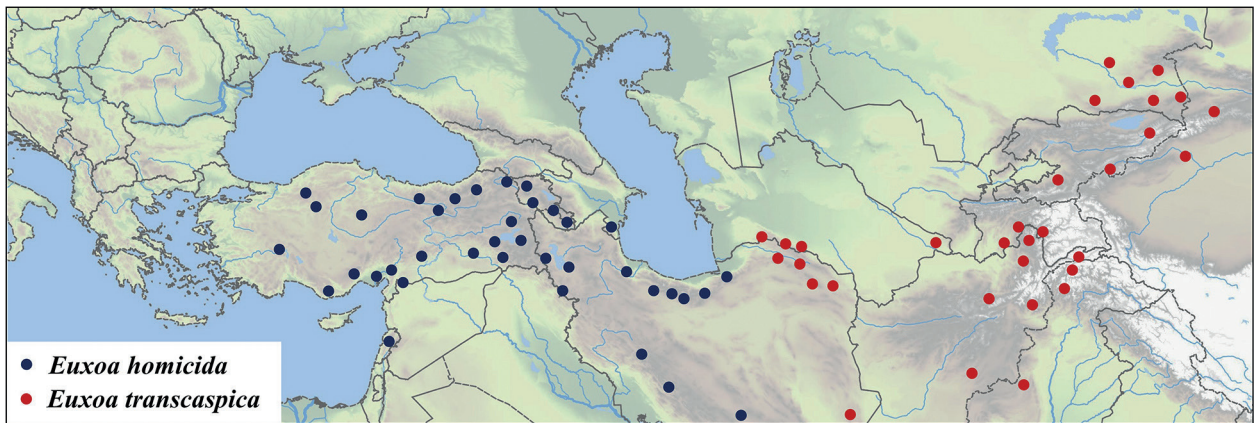


Fig. 2: Sister species with incipient allopatric speciation, with slight differentiation in the genitalia: *Euxoa homocida* (Asia minor and Iran, exception: Khorasan and Baluchistan) and *E. transcaspica* (Transcaspia, Afghanistan, Pakistan; subspecies are here not distinguished).

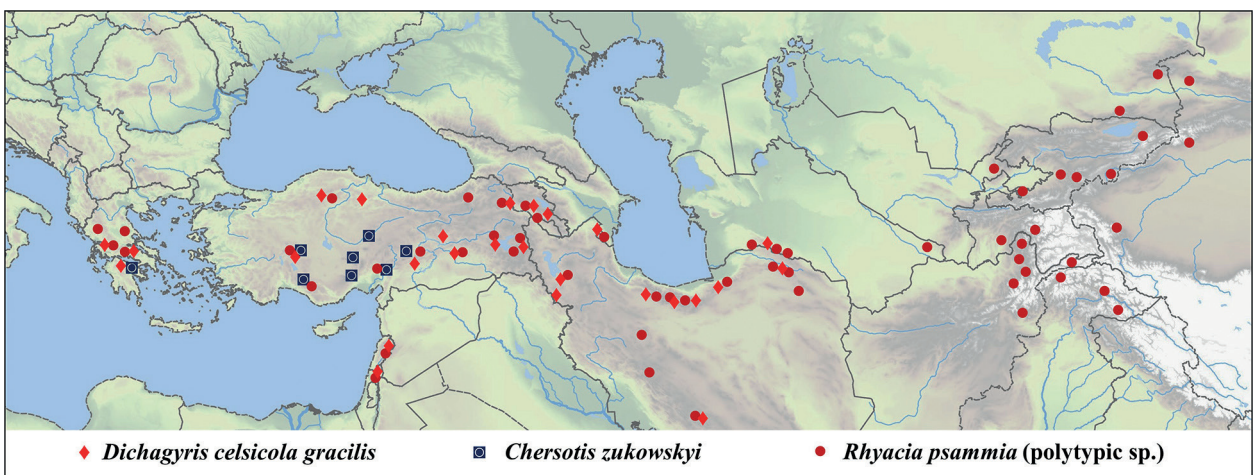


Fig. 3: Distribution of the species: *Dichagyris celsicola gracilis* (1), *Chersotis zukowskyi* (2), and *Rhyacia psammia* (3). They are distributed in Western and/or Central Asiatic mountains; some marginal populations have been fragmented in the mountains of the southern part of the Balkan Peninsula 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., *Actebia* s.l. (subg.: *Parexarnis*, *Protexarnis*, *Hemiexarnis*), *Chersotis* (VARGA 1998), *Rhyacia*, *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 Noctuidae 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 equinoctial type of precipitation (AGAKHANJANTS 1981, AGAKHANJANTS & BRECKLE 1995). The only widespread species pair of this group, *X. cacumena* 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 Paghman 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. naumanni*, *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. naumanni* 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 *Polymixis*, *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 psammochrea* in southern Kazakhstan and Uzbekistan, respectively (VARGA & RONKAY 1987; Varga & et 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 Transcaspia (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* BOISDUVAL, 1840 and *Rhyacia* 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 Tianshan, 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



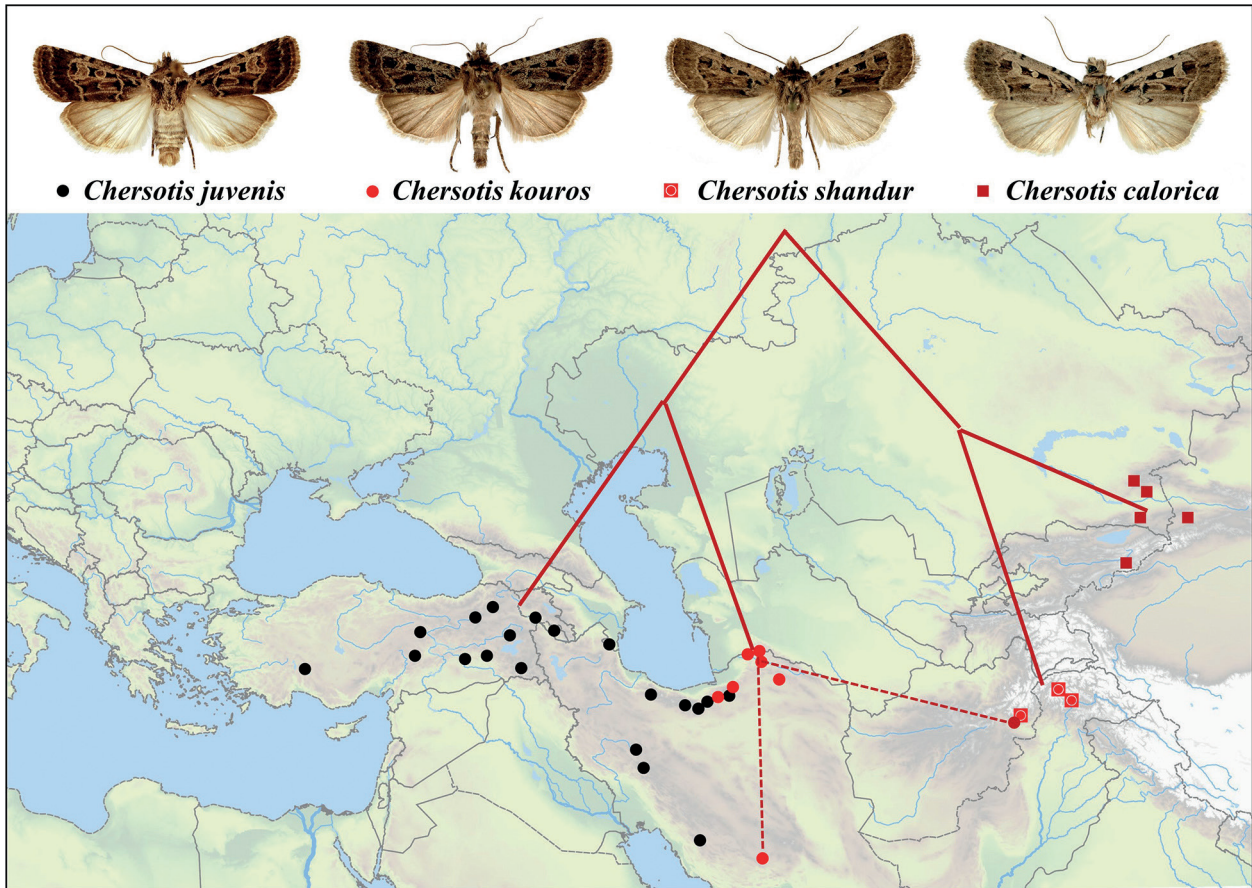


Fig. 4: Distribution of the pairs of sister species: *Ch. juvenis* (1. Asia Minor, Iran, exception: Khorasan) – *Ch. kouros* (2. Iran: Khorasan, Turkmenistan) and *Ch. calorica* (3. Kazakhstan, China: Xinjiang) – *Ch. shandur* (4. Afghanistan, Pakistan). Taxonomic details: VARGA et al. 2013.

*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 Khorassan (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. evar-tianae* (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



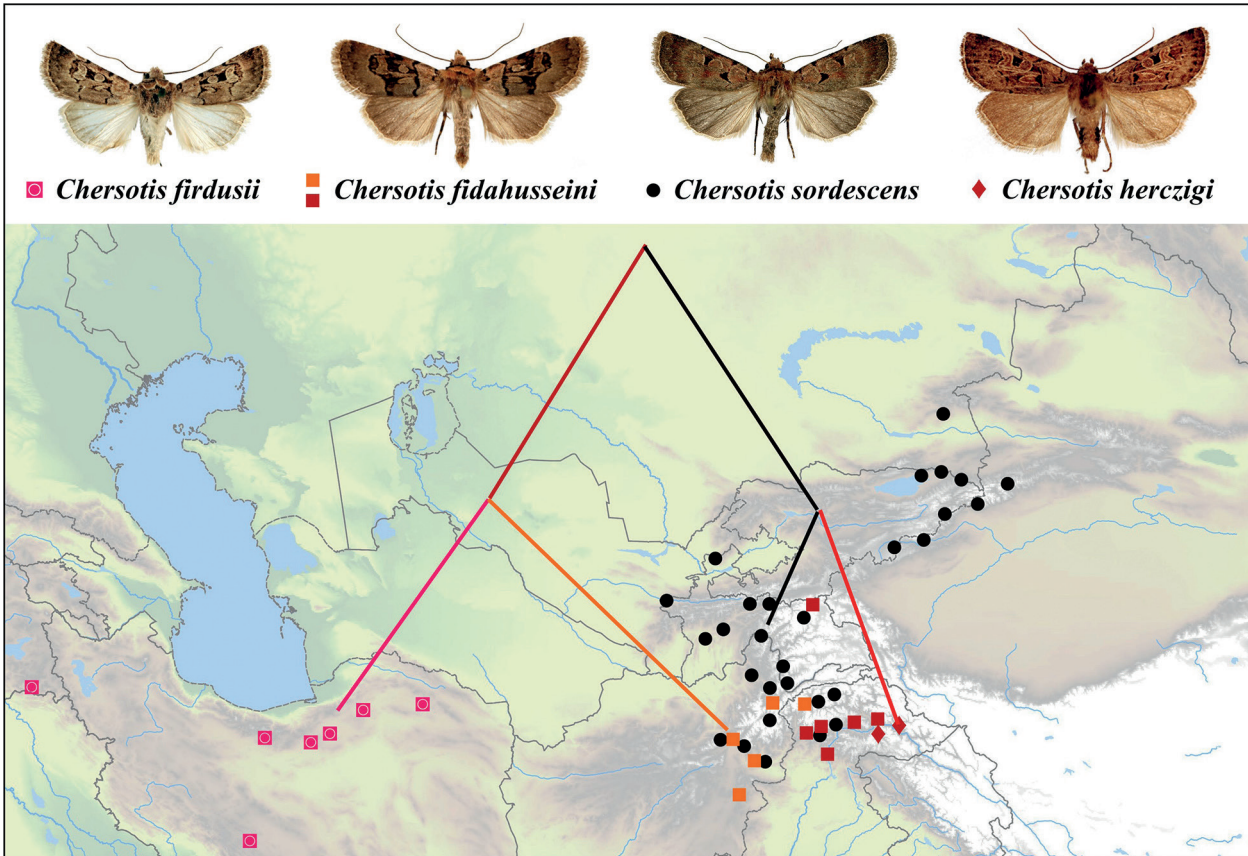


Fig. 5: Distribution of the pairs of sister species: *Chersotis firdusii* (1. Iran) – *Ch. fidahusseini* (2. Kirghisia, Tadjikistan, Afghanistan, Pakistan, two subspecies) and *Ch. herczigi* (3. Pakistan: Kashmir) – *Ch. sordescens* (4. Central Asia). Taxonomic details: VARGA et al. 2013.

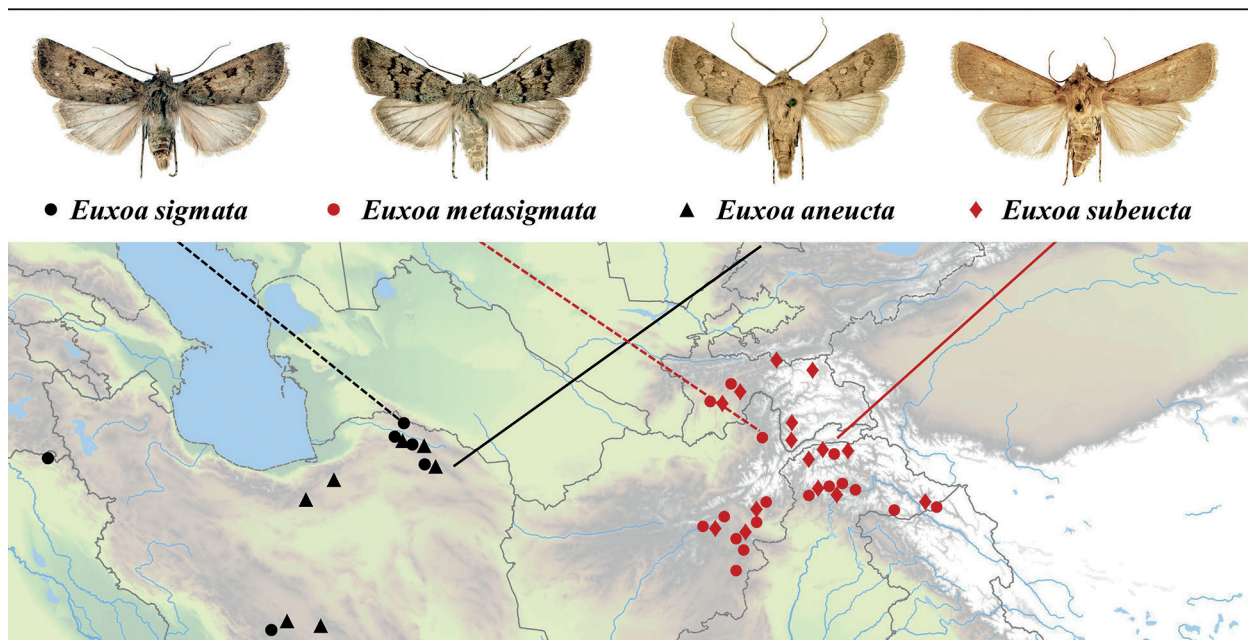


Fig. 6: Distribution of the pairs of sister species: *Euxoa sigmata* (1. Iran: Khorasan, Turkmenistan) – *E. metasigmata* (2. Afghanistan, Pakistan) and *E. aneucta* (3. Iran: Khorasan) – *E. subeucta* (4. Afghanistan, Pakistan). Taxonomic details: VARGA 2014.

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. metagrapha*, *Ch. petermarci* – *Ch. vicina*, *Ch. calorica* – *Ch. shandur*, *Ch. binaloudi* – *Ch. antigrapha*, *Ch. gratissima* – *Ch. zaghros*, *Ch. nupponenorum* – *Ch. nekrasovi* (Fig. 17).



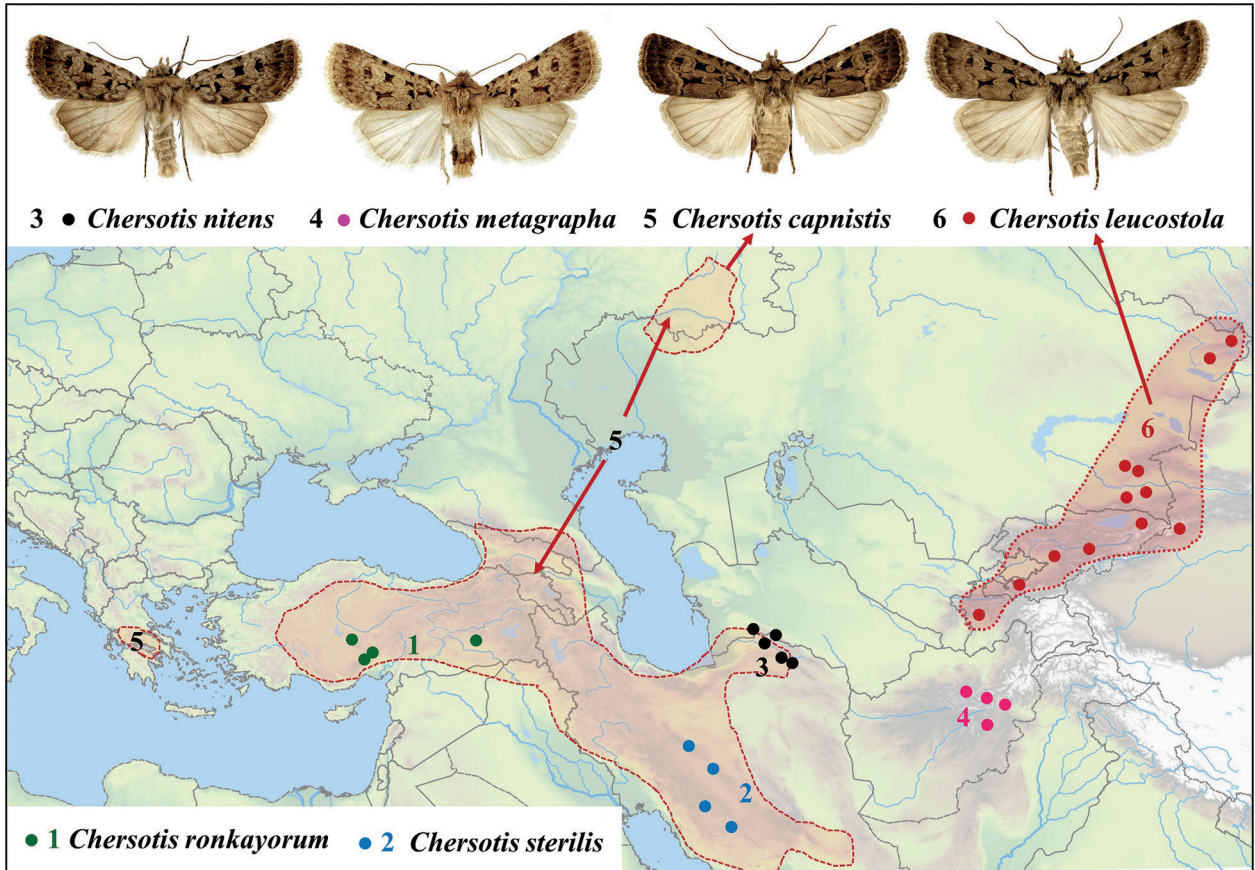


Fig. 7: The *Chersotis capnistis* group is subdivided into four allopatric, endemic species (1. *Ch. ronkayorum*, 2. *Ch. sterilis*, 3. *Ch. nitens*, 4. *Ch. metagrapha*) and to the *Ch. capnistis* (5.) – *Ch. leucostola* (6.) pair of species. The latter have large fat-bodies and a life-cycle with aestivation of imagos with a relatively large range of distribution. Taxonomy and phylogeny: VARGA 1998.

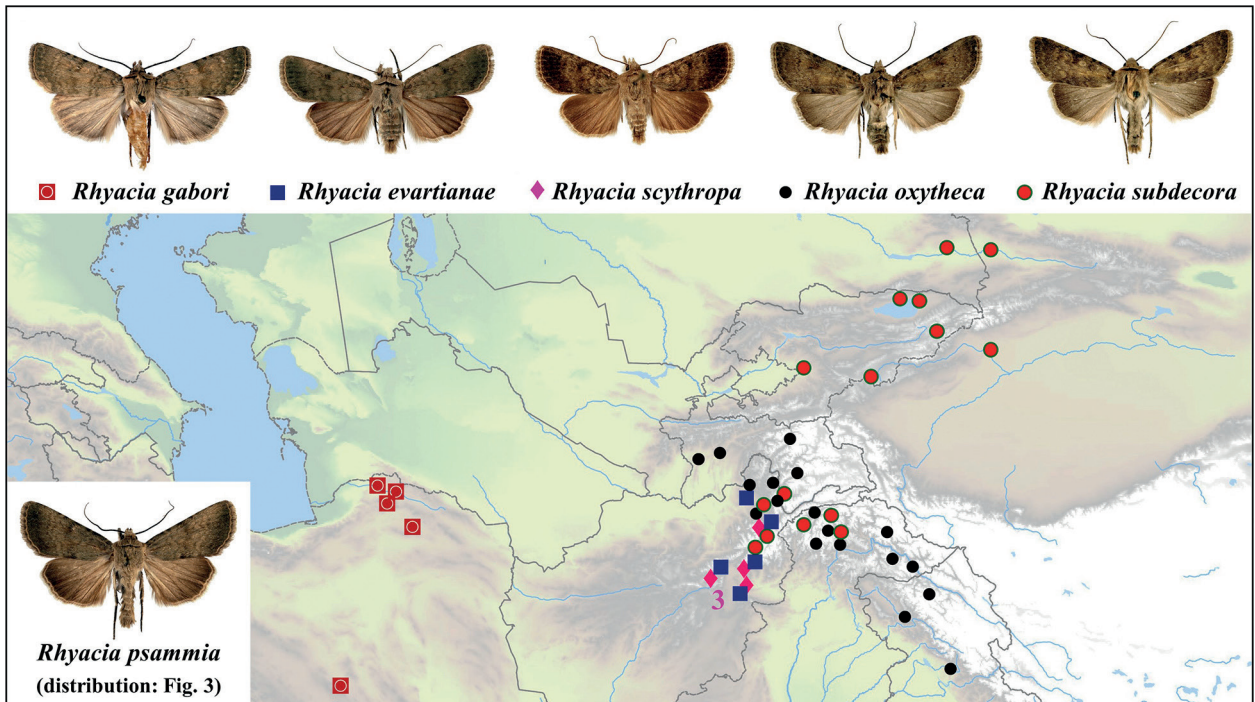


Fig. 8: Distribution of the species: *Rhyacia gabori* (1) – *Rh. evartianae* (2) – *Rh. scythropa* (3) – *Rh. oxytheca* (4) – *Rh. subdecora* (5). The range of *Rh. psammia* (6) is on Fig. 1. Taxonomy and phylogeny: VARGA 2011.



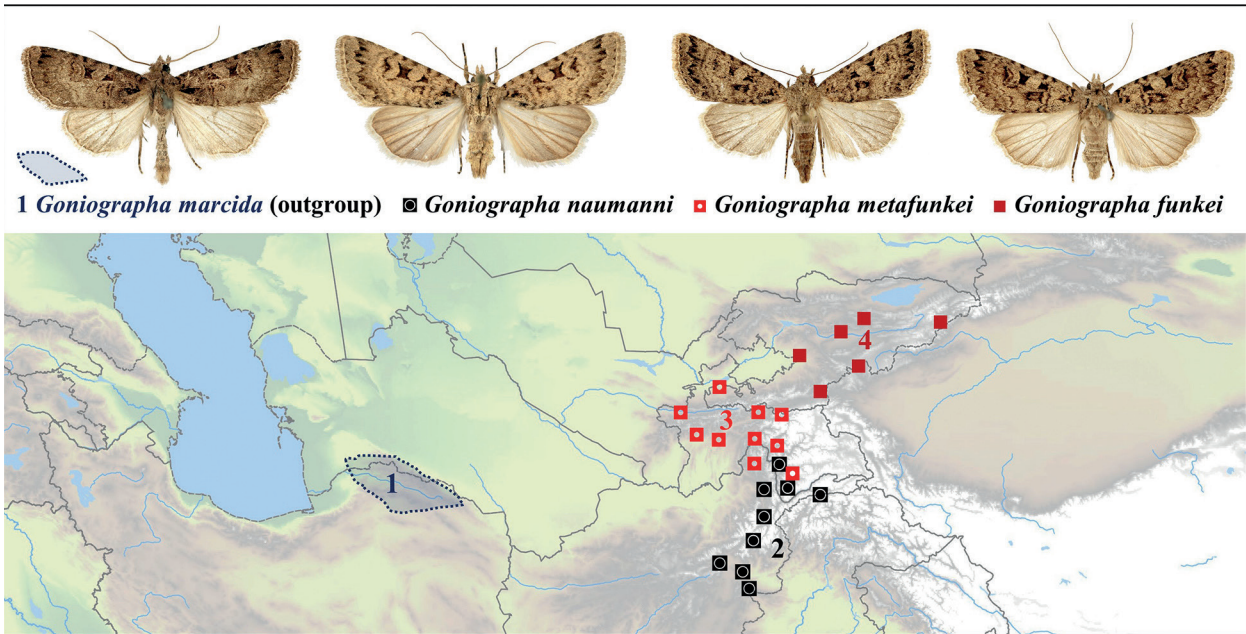


Fig. 9: Distribution of the *Goniographa funkei*-group; one more distant species, *G. marcida* (1), and three closely related ones: *G. naumanni* (1), *G. metafunkei* (2), *G. funkei* (3). The sister species (2) and (3) are strictly allopatric, (1) and (2) are overlapping in the Hissar Mts. Taxonomy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

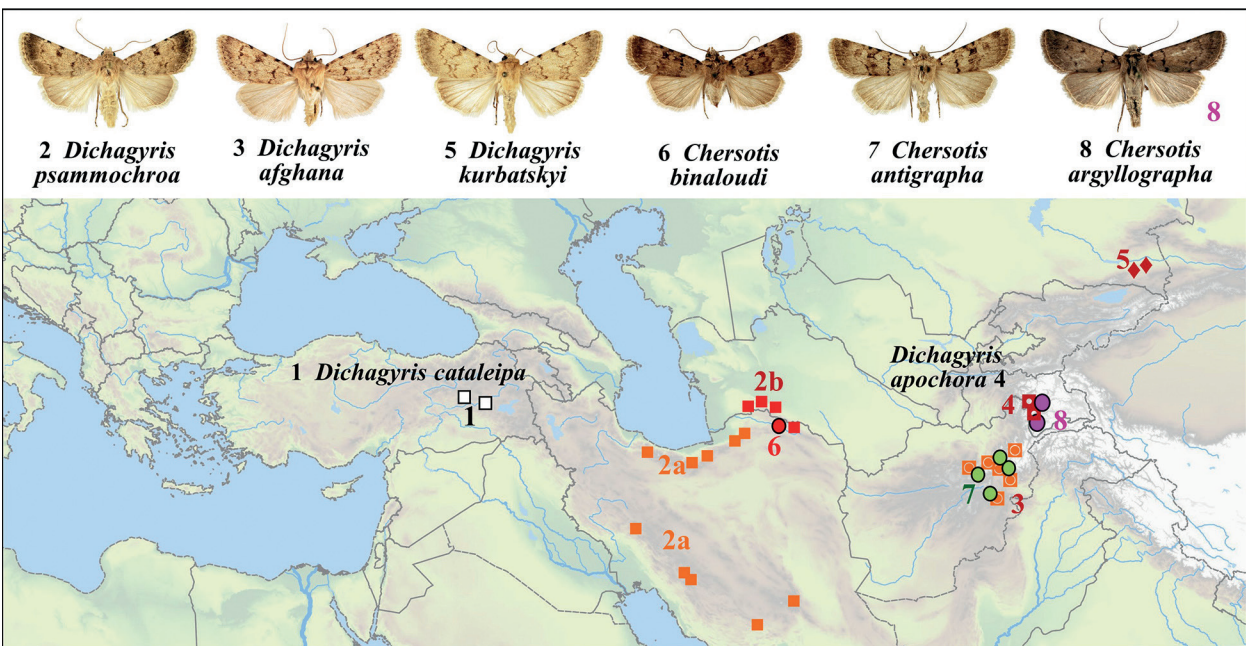


Fig. 10: Distribution of the *Dichagyris psammochroa*-group: *Dichagyris cataleipa* (1) – *D. psammochroa* (2a-2b) – *D. afghana* (3) – *D. apochora* (4) – *D. kurbatskyi* (5); Distribution of the *Chersotis binaloudi*-group: *Ch. binaloudi* (6) – *Ch. antigraha* (7) – *Ch. argyllographa* (8). Taxonomy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

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*.

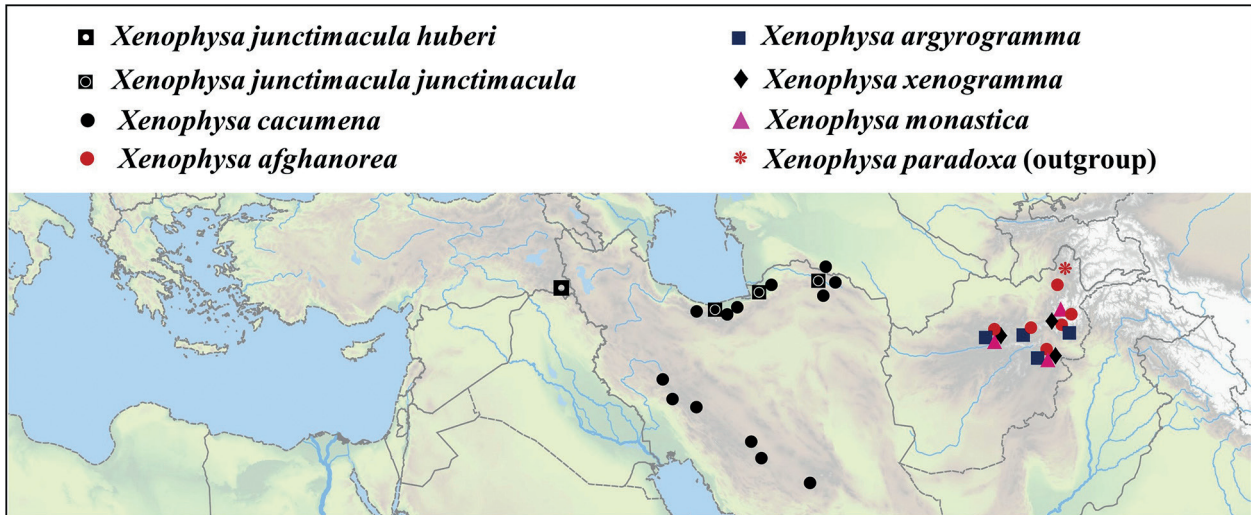


Fig. 11: The West Asiatic species group of the genus *Xenophysa*: *X. junctimacula huberi* (1) – *X. junctimacula junctimacula* (2) – *X. cacumena* (3) – *X. afghanorea* (4) – *X. argyrogramma* (5) – *X. xenogramma* (6) – *X. monastica* (7). Outgroup: *X. paradoxa* (8). Taxonomy and phylogeny: VARGA 2011.

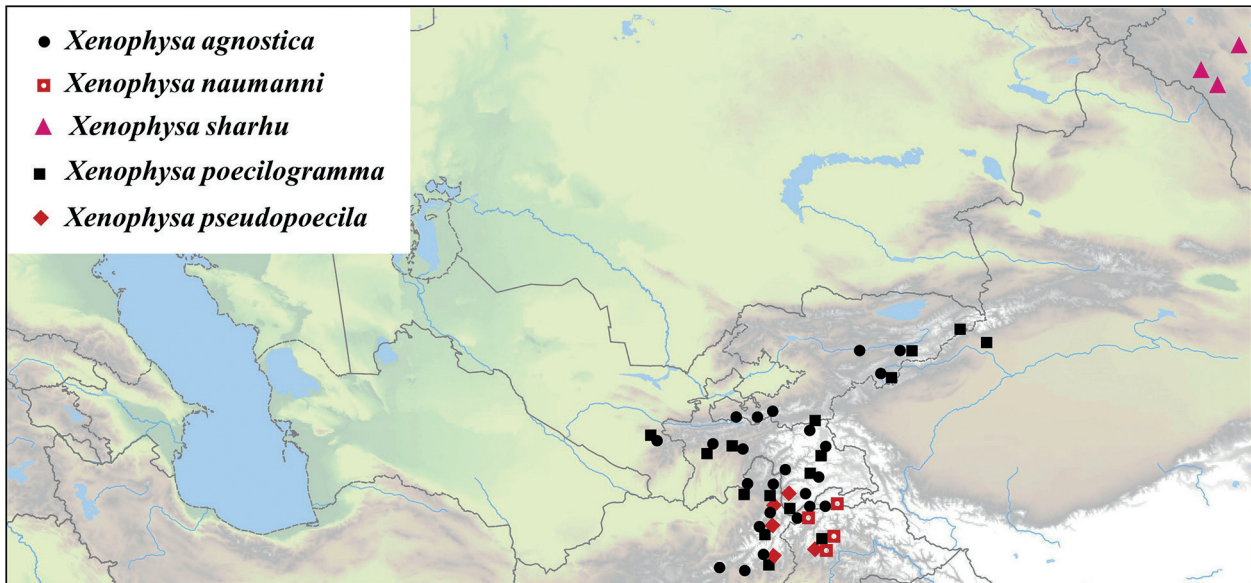


Fig. 12: The Inner Asiatic species of the genus *Xenophysa*: *X. agnostica* (1) – *X. naumanni* (2) – *X. pseudopoecila* (3) – *X. poecilogramma* (4) – *X. sharhu* (5). Taxonomy and phylogeny: VARGA 2011.

### 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, SPЕCHT 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



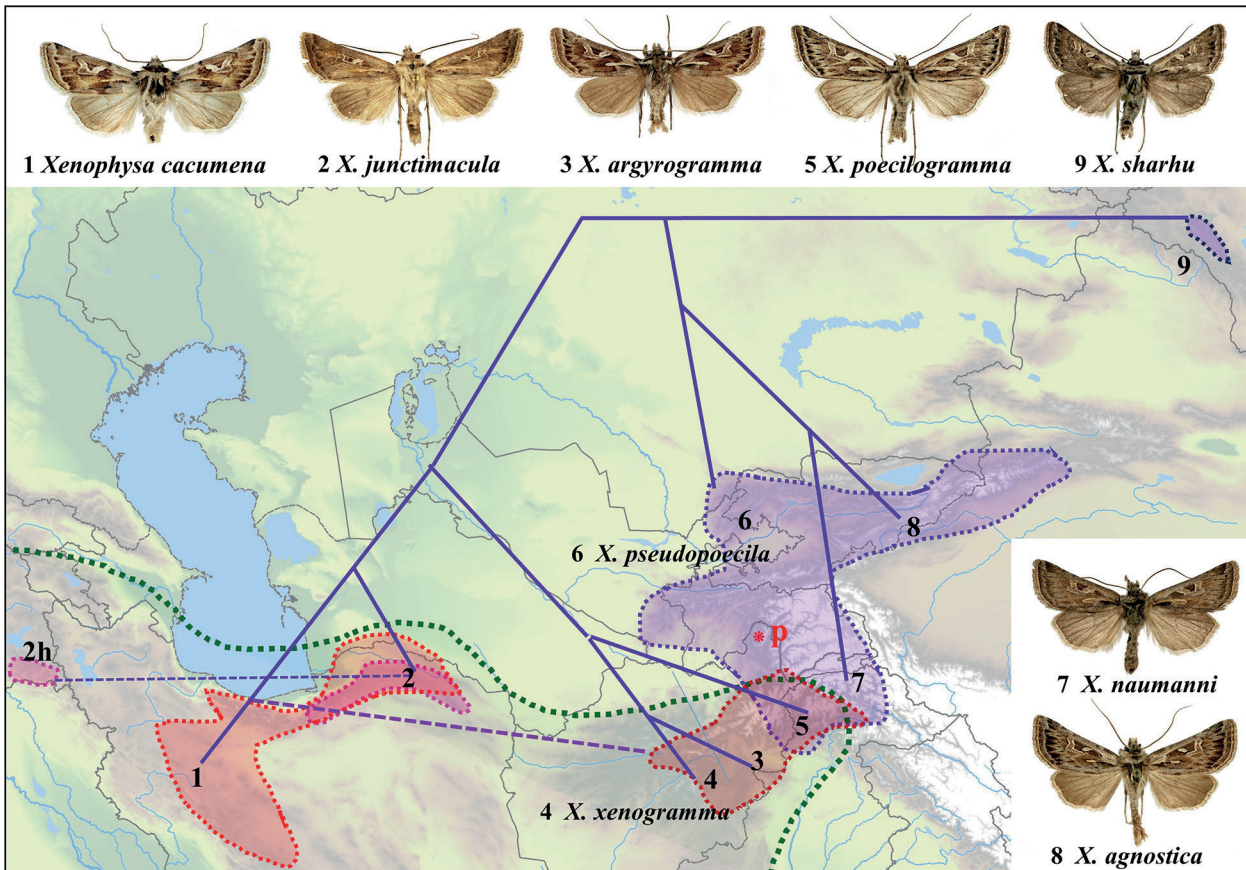


Fig. 13: The phylogenetic bifurcation of the Noctuidae genus *Xenophysa* clearly shows a close connection to the two main different climatic provinces of the arid high mountains of Eurasia. 1. *X. cacumena*, 1a. *X. afghanorea*, 2h. *X. junctimacula huberi*, 2. *X. junctimacula*, 3. *X. argyrogramma*, 4. *X. xenogramma*, 5. *X. poecilogramma*, 6. *X. pseudopoecila*, 7. *X. naumanni*, 8. *X. agnostica*, 9. *X. sharhu*. p *X. paradoxa* (outgroup). Taxonomy and phylogeny: VARGA 2011.

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 Noctuidae) 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. segnilis*\*; *Agrotis bifurca*, *A. psammocharis*, *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 Noctuidae 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 phyletic 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, PRAVDIN & MISHTSHENKO 1980). The diversity centres of saxobiotic Orthoptera genera (“kamenistiy tip fauni”; e.g. Catantopinae: *Conophyma* ZUBOVSKY, 1898; Pamphaginae: *Saxetania* MISHTSHENKO, 1951; *Nocarodes* FISCHER-WALDHEIM, 1846; *Nocaracris* UVAROV, 1928; *Paranocarodes* BOLIVAR, 1916; *Paranothrotres*



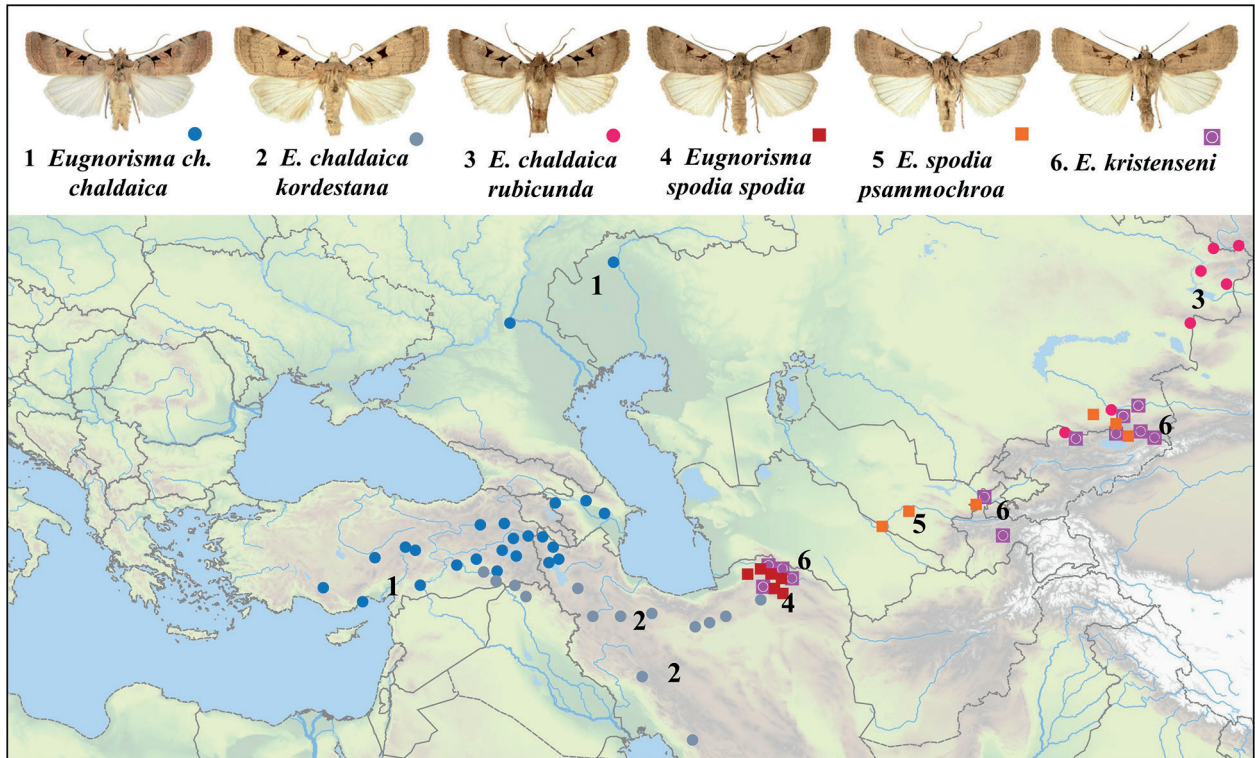


Fig. 14: Distribution of the species of the *Eugnorisma chaldaica* group: *E. chaldaica chaldaica* (1), *E. chaldaica kordestana* (2), *E. chaldaica rubicunda* (3), *E. spodia spodia* (4), *E. spodia psammochroa* (5), *E. kristenseni* (6). Taxonomy and phylogeny: VARGA et al. 2015.

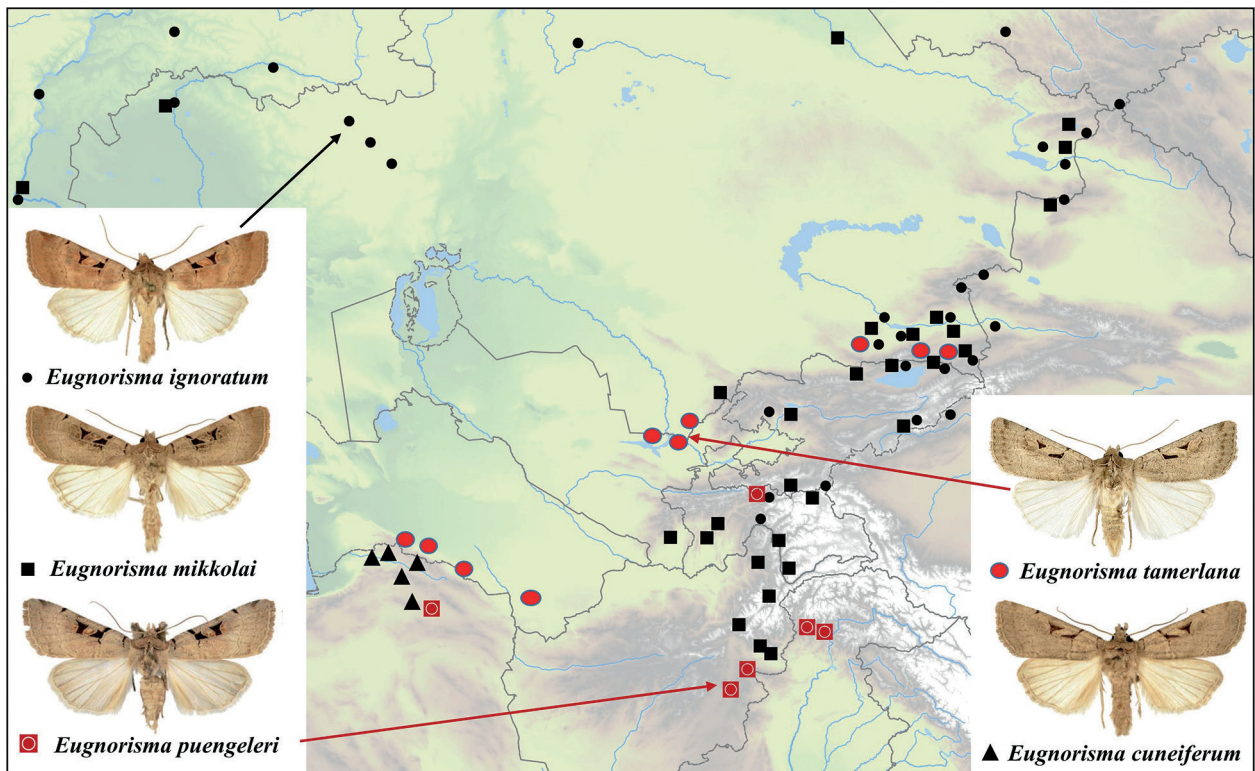


Fig. 15: Distribution of the species: *Eugnorisma ignoratum* (1), *E. mikkolai* (2), *E. puengeleri* (3), *E. tamerlana* (4), and *E. cuneiferum* (5). Taxonomy and phylogeny: VARGA et al. 2015.

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.



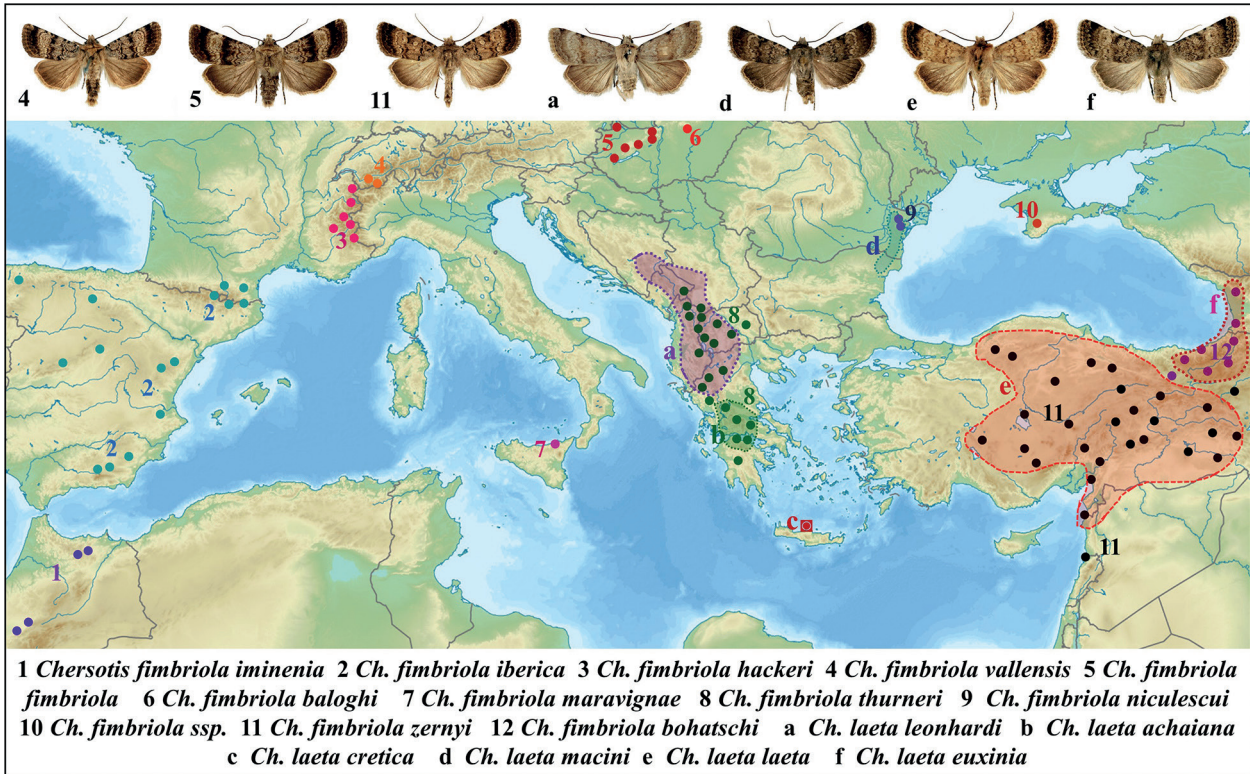


Fig. 16: Distribution of the species pair *Chersotis fimbriola* – *Ch. laeta*: *Ch. fimbriola iminenia* (1), *Ch. fimbriola iberica* (2), *Ch. fimbriola hackeri* (3), *Ch. fimbriola vallensis* (4), *Ch. fimbriola fimbriola* (5), *Ch. fimbriola baloghi* (6), *Ch. fimbriola maravignae* (7), *Ch. fimbriola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

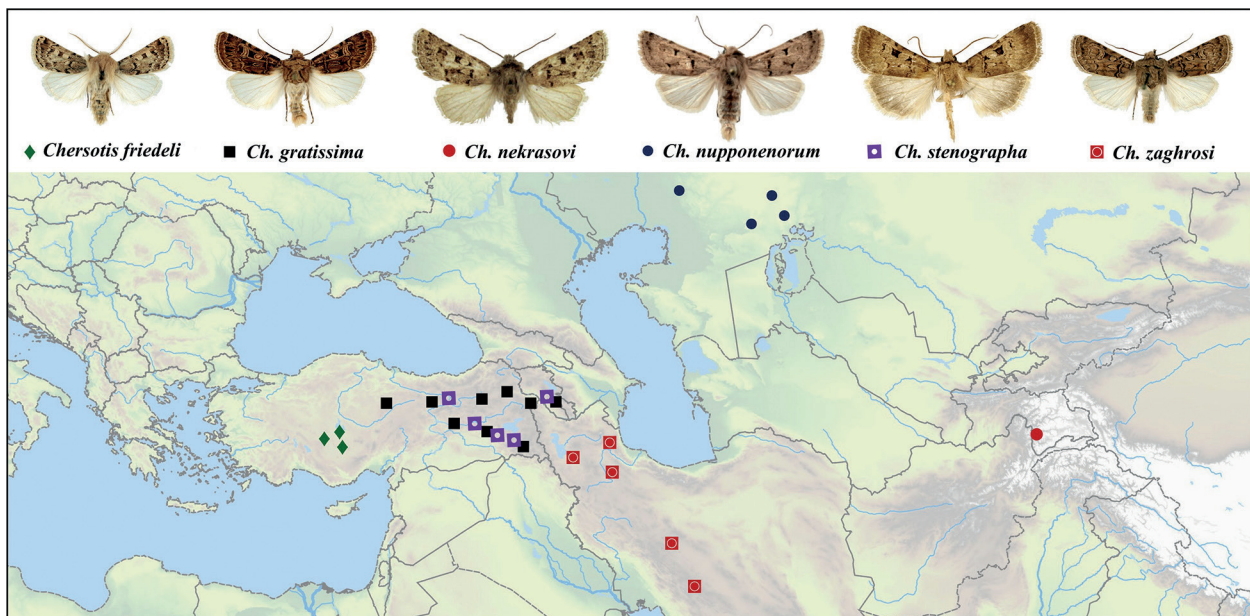


Fig. 17: Distribution of the species related to *Chersotis friedeli*: *Ch. friedeli* (1), *Ch. stenographa* (2), *Ch. gratissima* (3), *Ch. zaghrosi* (4), *Ch. nupponenorum* (5), *Ch. nekrasovi* (6). (3) + (4) and (5) + (6) are allopatric sister species. Taxonomy and phylogeny: VARGA et al. 2013.

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-

tially autochthonous evolution, influenced by the younger Tertiary aridisation of the Mediterranean Basin in connection with the Messinian Saline Crisis. The Ponto-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 Oncocnemidini: *Omphalophana*, *Teinoptera*, *Cleonymia*, *Amephana*, *Metopoceras*, *Harpagophana*, etc. and from genera of Xylenini (*Leucochlaena*, *Aporophila*, *Antitype*, *Ammoconia*, 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, KRZYZHANOVSKY 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, KRZYZHANOVSKY 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 high 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), Lycaenidae: Polyommataini, 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-Asiatic (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 (AGAKHANJANTS 1981, AGAKHANJANTS & BRECKLE 1995). This subdivision was also shown in the area-cladograms of the genus *Xenophysa* (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*, *Goniographa*; 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 tundra zonobiome. The Noctuidae of the Inner Asiatic xeromontane faunal type consist of several “Mongolian-Tibetan” cold-continental genera, e.g. *Trichosilia*, subgenera of *Xestia* (*Anomogyna*, *Pachnobia*, *Raddea*, *Estimata*, *Schoeyenia*), subgenera of *Anarta* (*Calocestra*, *Anarta* s. str.), *Lasionycta*, *Oncocnemis* and *Sympistis*, etc. Supposedly, the connections of this faunal type with the cold steppic and tundra zonobiomes have been mostly influenced by the recently uncovered Mid-Pleistocene climatic transition (DIESTER-HAAS et al. 2018; SUN et al. 2019; WILLEIT 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 oreotundra 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 *Metallopolia* displaying the species diversity restricted to the Sino-Himalayan area, as opposed to the more derived genera *Polia* s. str. and *Ctenoceratoda* (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 (e.g. Southern Tibet and parts of south-western China) 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 undergrowth of the Siberian (especially southern Siberian mountain) taiga, typical for a number of “taiga-birds” (e.g. *Ficedula*, *Phylloscopus*, *Luscinia calliope*, *Tarsiger cyanurus*, *Dumeticola thoracica* etc.) and also for numerous taiga-inhabiting Lepidoptera (Geometridae: *Dysstroma*, *Chlorochlysta*; Noctuidae: *Xestia* subg. *Pachnobia*, *Anomogyna*; *Polia*, *Lasionycta*, 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-Turkestan 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 *Polyommata* 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 tundra zoniobiomes. The typical genera of this second, more “Siberian”, group of (originally) xeromontane Noctuidae are e.g. *Trichosilia*, *Lasionycta*, *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” orotundal 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. Rákósy 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.

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**Tab. 1:** Allopatric pairs and groups of *Dichagyris* (subg. *Dichagyris*) species (\*with peripatric overlap, \*polytypic species).

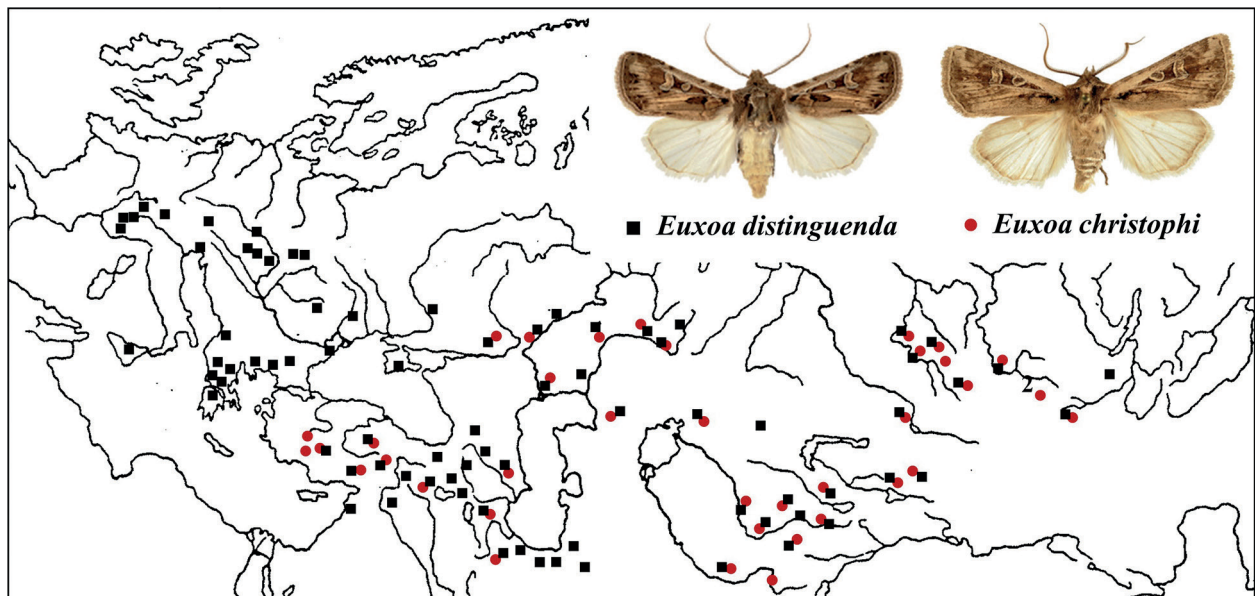
Western species	Eastern species
<i>Dichagyris (Dichagyris) vallesiaca</i> (Boisduval, 1837)* <sup>4</sup> : SW and Central Alps, Crimea, South Russia, South Urals, Asia Minor, Zaghros, Elburs, Binaloud Mts, Kopet-Dagh, Tien Shan, Pamirs, Altai, Khangai, Sayan Mts.	<i>Dichagyris (Dichagyris) fuscashmiriana</i> Varga, Ronkay & Ronkay, 2020: Hindukush East, Karakoram, W Himalayas
<i>Dichagyris (Dichagyris) striata</i> Kozhantschikov*, 1930: Zaghros, Elburs, Binaloud Mts, Kopet-Dagh	<i>Dichagyris (Dichagyris) tyrannus</i> (A. Bang-Haas, 1912)*: Tien Shan, Hissaro-Darwaz, Pamirs, Hindukush, Karakoram, W Himalayas
<i>Dichagyris (Dichagyris) squalidior</i> (Staudinger, 1901) <sup>5</sup> : Asia Minor, Zaghros, Elburs, Binaloud Mts, Kopet-Dagh	<i>Dichagyris (Dichagyris) payotiorum</i> Varga, Ronkay & Ronkay: Hissaro-Darwaz, Hindukush, Paghman Mts. Karakoram, W Himalayas
<i>Dichagyris (Dichagyris) clara</i> (Staudinger, 1888)* Tien Shan, Mongol Altai, Gobi Altai	<i>Dichagyris (Dichagyris) leucographa</i> Varga, 1990: Pamirs <i>Dichagyris (Dichagyris) scotographa</i> Varga, 1990: Pamirs, Karakoram, W Himalayas (Kashmir) <i>Dichagyris (Dichagyris) kautti</i> Varga, 1996: W Himalayas (Ladakh)
<i>Dichagyris (Dichagyris) jacobsoni</i> Kozhanchikov, 1930: Kopet-Dagh <i>Dichagyris (Dichagyris) naumanni</i> Varga, 1996: Kugitang-Tau, Hindukush	<i>Dichagyris (Dichagyris) umbrifera</i> (Alphéraky, 1882): Tien Shan <i>Dichagyris (Dichagyris) kaszabi</i> Varga, 1973: Mongol & Gobi Altai
<i>Dichagyris (Dichagyris) cataleipa</i> Varga, 1993: Eastern Asia Minor <i>Dichagyris (Dichagyris) psammochroa</i> (Boursin, 1940)*: Zaghros, Elburs, Kopet-Dagh	<i>Dichagyris (Dichagyris) afghana</i> Boursin, 1963: Central Hindukush <i>Dichagyris (Dichagyris) kurbatskyi</i> Varga, Ronkay & Ronkay, 2021: W Tien Shan <i>Dichagyris (Dichagyris) apochora</i> Gyulai & Varga, 2001: Pamirs
<i>Dichagyris (Dichagyris) taftana</i> Brandt, 1941*: Elburs, Zaghros	<i>Dichagyris (Dichagyris) guentereberti</i> Varga, Ronkay & Ronkay, 2021: Central Hindukush
<i>Dichagyris (Dichagyris) humilis</i> (Boursin, 1940): Zaghros, Elburs, Kopet-Dagh	<i>Dichagyris (Dichagyris) hypotacta</i> Varga, Ronkay & Ronkay 2021: East Tien Shan, Pamirs, Hindukush
<i>Dichagyris (Dichagyris) verecunda</i> (Püngeler, 1898)*: Tien Shan system, Pamirs, Mongol Altai, Gobi Altai	<i>Dichagyris (Dichagyris) karakorealis</i> Varga, Ronkay & Ronkay, 2020: West Himalayas

<sup>4</sup> Sympatric endemic species: *Dichagyris (Dichagyris) griseotincta* (Wagner, 1931) – Central Anatolia.<sup>5</sup> 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
<i>Euxoa homicida</i> (Staudinger, 1900)*: Asia Minor, Transcaucasia, Zagros, Elburs	<i>Euxoa transcaspica</i> Kozhantshikov, 1928*: Kopet-Dagh, Binaloud Mts (ssp.); Hindukush, Karakoram, W. Himalayas (ssp.)
<i>Euxoa decora</i> ([Denis & Schiffermüller], 1775): Pyrenees, Alps, Carpathians, Europa Centr., Apennines, Balkans	<i>Euxoa kurushensis</i> Boursin, 1940: Daghestan (NE Caucasus)
<i>Euxoa heringi</i> (Staudinger, 1877): Asia Minor, Elburs, Kopet-Dagh	<i>Euxoa cretaporos</i> Varga, G. Ronkay & L. Ronkay, 2020: Daghestan (NE Caucasus)
<i>Euxoa aneucta</i> Brandt, 1938*: Zagros Mts, Binaloud Mts (ssp.)	<i>Euxoa subeucta</i> Varga, 2014: Hissar Mts., Transalai Mts, Hindukush Central & East
<i>Euxoa perierga</i> Brandt, 1938*: Zagros Mts, Elburs (ssp.)	<i>Euxoa dichagyroides</i> Varga, 1979: Darwaz Mts., Pamirs, Transalai Mts, Hindukush Central & East
<i>Euxoa sigmata</i> Kozhantshikov, 1928: Kopet-Dagh, Binaloud Mts	<i>Euxoa metasigmata</i> Varga, 2014: Hissar Mts, Hindukush Central & East
<i>Euxoa conifera</i> Christoph, 1885* <sup>6</sup> : Daghestan, Transcaucasia, Asia Minor (East), Elburs, Kopet-Dagh	<i>Euxoa bactriana</i> Varga, 2014: Tien Shan (Seravshan), Transalai, Hissar Mts, Pamirs, Hindukush Central & East, Karakoram, West Himalayas
<i>Euxoa bogdanovi</i> (Erschoff, 1873): Tien Shan	<i>Euxoa xanthophylla</i> Varga, 1990: Darwaz Mts, Pamirs

Fig. 18: Early autumnal steppic *Euxoa* species: *E. distinguenda* (1), *E. christophi* (2).<sup>6</sup> Senior synonym of *E. difficillima* Draudt, 1937.

Tab. 3: Allopatric pairs of *Chersotis* species (exceptionally with peripatric overlap).

Western species	Eastern species
<i>Ch. firdusii</i> Schwingenschuss, 1937: East Anatolia, Zagros, Elburs, Binaloud Mts, Kopet-Dagh	<i>Ch. fidahusseini</i> Varga, Gyulai, Ronkay & Ronkay, 2013: E Tien Shan, Hissar and Darwaz range, Central and East Hindukush, Karakoram, West Himalayas
<i>Ch. sordescens</i> (Staudinger, 1900): Tien-Shan range, Hindukush, Hissar and Darwaz range	<i>Ch. herczigi</i> Varga, 1996: West Himalayas
<i>Ch. ronkayorum</i> Fibiger, Hacker & Varga, 1993: Central and East Anatolia	<i>Chersotis sterilis</i> Brandt, 1938: Zagros Mts
<i>Ch. nitens</i> Brandt, 1941: Binaloud Mts, Kopet-Dagh	<i>Ch. metagrapha</i> Varga, 1975: Afghanistan, Hindukush Mts, Badakhshan
<i>Ch. capnistis</i> (Lederer, [1870]): South Russia, Caucasus, Transcaucasia, Asia Minor, South Balkans	<i>Ch. leucostola</i> Varga & Ronkay, 1996: Tien-Shan Mts, Dzhungarian Ala-too
<i>Ch. semna</i> (Püngeler, 1906): Asia Minor, Trans-caucasia, Elburs, Binaloud Mts, Kopet-Dagh	<i>Ch. pachnosa</i> Varga, 1975: Afghanistan, Badakhshan
<i>Ch. juvenis</i> (Staudinger, 1901): Asia Minor, Transcaucasia, Elburs Mts, Zagros Mts.	<i>Ch. kouros</i> Varga & Ronkay, 1996: Kopet-Dagh, Hindukush
<i>Ch. calorica</i> (Corti, 1930): North & East Tien-Shan Mts	<i>Ch. shandur</i> Varga, 1998: Pakistan, Karakoram Mts, Afghanistan, Paghman Mts
<i>Ch. petermarci</i> Varga, 1998: Seravshan Mts, W Tien-Shan Mts	<i>Ch. vicina</i> (Corti, 1930): N and E Tien-Shan Mts
<i>Chersotis delear</i> Boursin, 1970 <sup>7</sup> : Central Afghanistan, Nimla	<i>Ch. electrographa</i> Varga, 1990: Afghanistan, Darwaz Mts. <i>Ch. vargai</i> Hacker, 1992 Hindukush Mts, Karakoram
<i>Ch. binaloudi</i> Brandt, 1941 <sup>8</sup> : Khorassan, Binaloud Mts	<i>Ch. antigrapha</i> Boursin, 1961: Hindukush Mts <i>Ch. argyllographa</i> Varga & Gyulai, 2001: W Pamirs
<i>Ch. elegans</i> (Eversmann, 1837): Iberian Mts, Pyrenees, Alps, Balkans, Asia Minor, Transcaucasia, S Russia, W Tien-Shan and W Altai Mts	<i>Ch. eberti</i> Dufay & Varga, 1995: Elburs Mts, Zagros Mts
<i>Ch. sarhada</i> Brandt, 1941 <sup>9</sup> : Asia Minor, Transcaucasia, Elburs and Kopet-Dagh Mts	<i>Ch. lehmanni</i> Varga, Gyulai, Ronkay, Ronkay, 2010: Hindukush, Hissar and Darwaz Mts <i>Ch. lukhtanovi</i> Varga & Gyulai, 2001: S Tadjikistan
<i>Ch. rungsi</i> Boursin, 1944: Atlas Mts	<i>Ch. stenographa</i> Varga, 1979: Asia Minor East, Transcaucasia
<i>Ch. gratissima</i> (Corti, 1932)	<i>Ch. zagroica</i> Gyulai & Varga, 2006: Zagros Mts
<i>Ch. nupponenorum</i> Varga, Gyulai, Ronkay & Ronkay, 2013: W. Transcaspia	<i>Ch. nekrasovi</i> Varga, 1996: Pamir Mts

<sup>7</sup> A „triplet” of species.<sup>8</sup> A „triplet” of species.<sup>9</sup> A „triplet” of species.



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

<i>Ch. rectangulara</i> ([Denis & Schiffermüller], 1775): Central and Southern Europe, Caucasus, Asia Minor	<i>Ch. andereggii</i> (Boisduval, [1837]): N Europe, Alps, Balkans, Asia Minor, Caucasus, Transcaucasia, Iran, Mts of Southern Siberia <i>Ch. acutangula</i> (Staudinger, 1892) <sup>10</sup> : Transalai and Hindukush Mts
<i>Ch. hahni</i> (Christoph, 1885): Transcaucasia, Elburs, Kopet-Dagh Mts	<i>Ch. curvispina</i> Boursin, 1961: Kopet-Dagh Mts, Hindukush Mts
<i>Ch. elegans</i> (Eversmann, 1837): Iberian Mts, Pyrenees Alps, Balkans, Asia Minor, Caucasus, Transcaucasia, S Russia, W Tien-Shan and W Altai Mts <i>Ch. eberti</i> Dufay & Varga, 1995: Elburs Mts, Zaghros Mts	<i>Ch. anatolica</i> (Draudt, 1936) <sup>11</sup> : Iberian Mts, Pyrenees, SW Alps, Central Apennines, Balkans, Asia Minor, Caucasus, Transcaucasia, S Russia (Europa + Siberia), Kopet-Dagh, W Tien-Shan Mts
<i>Ch. fimbriola</i> (Esper, [1803]): Atlas, Iberian Mts, Pyrenees, Sicily, W Alps, Pannonian Basin, Balkans Asia Minor, Crimea, Transcaucasia, Zaghros, Elburs Mts, Kopet-Dagh Mts	<i>Ch. laeta</i> (Rebel, 1904): Balkans, W coastal area of Black Sea, Asia Minor, Caucasus, Transcaucasia, Elburs Mts

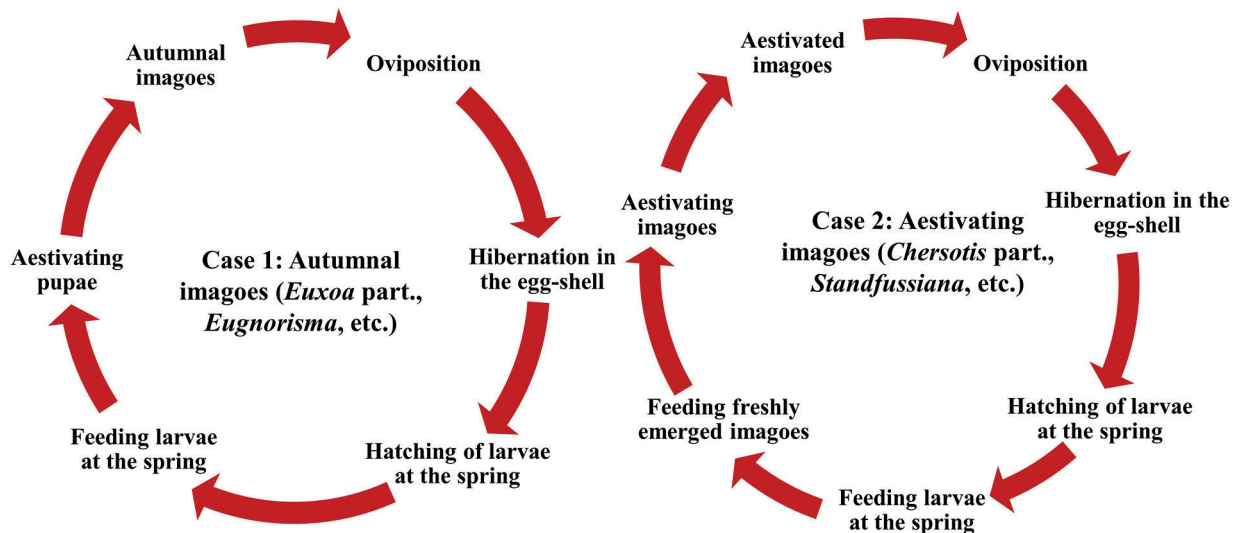


Fig. 19: Adaptation to the arid environment in Noctuidae genera: two types of univoltine life-cycles with autumnal period of oviposition and dispersal. Type I. (e.g. *Euxoa*, *Eugnorisma* – aestivating pupae, late summer, early autumn imagoes), type II. (e.g. *Chersotis*, *Spaelotis*, *Standfussiana*,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

<sup>10</sup> Latter species is strictly localised in the Tien-Shan and Hindukush mountain systems.

<sup>11</sup> These species are not sibling species, because they are strongly differentiated from each other (see: Dufay & Varga 1995).

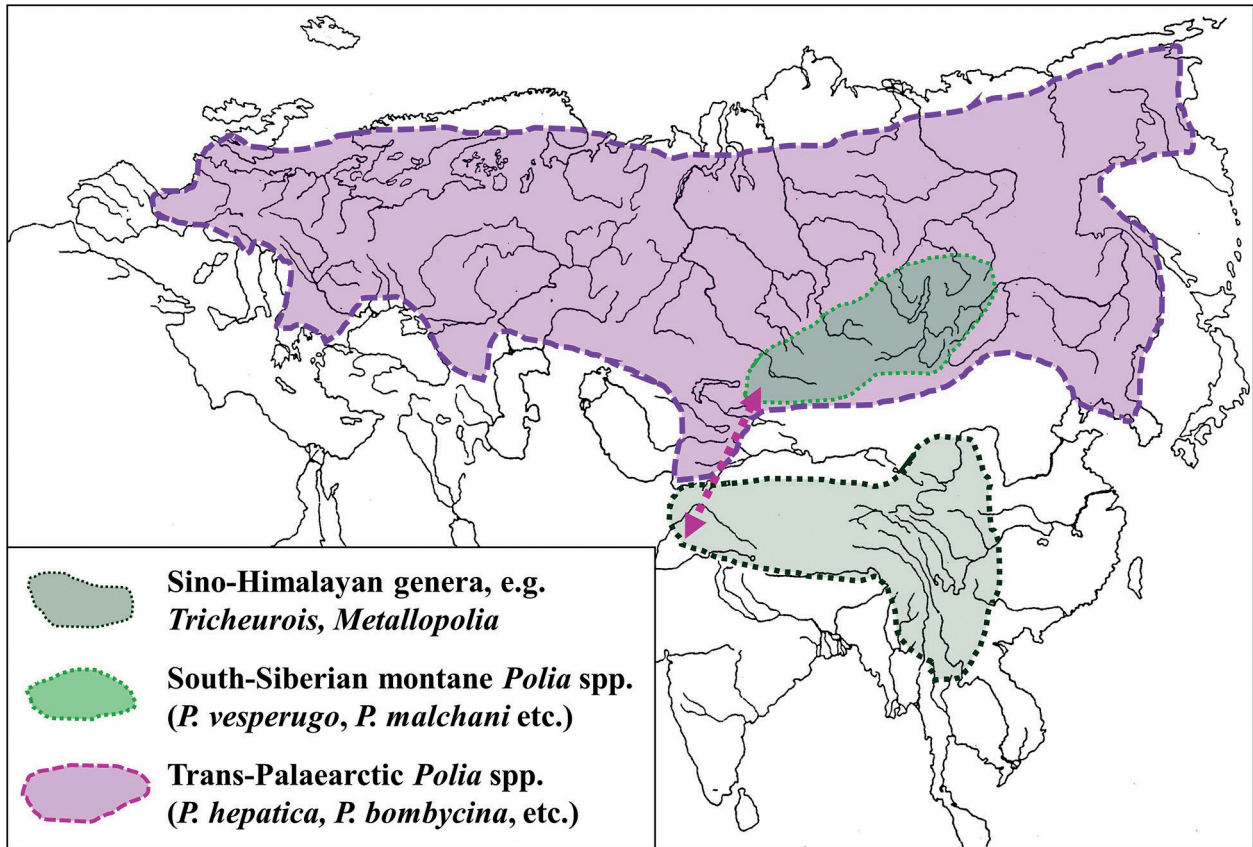
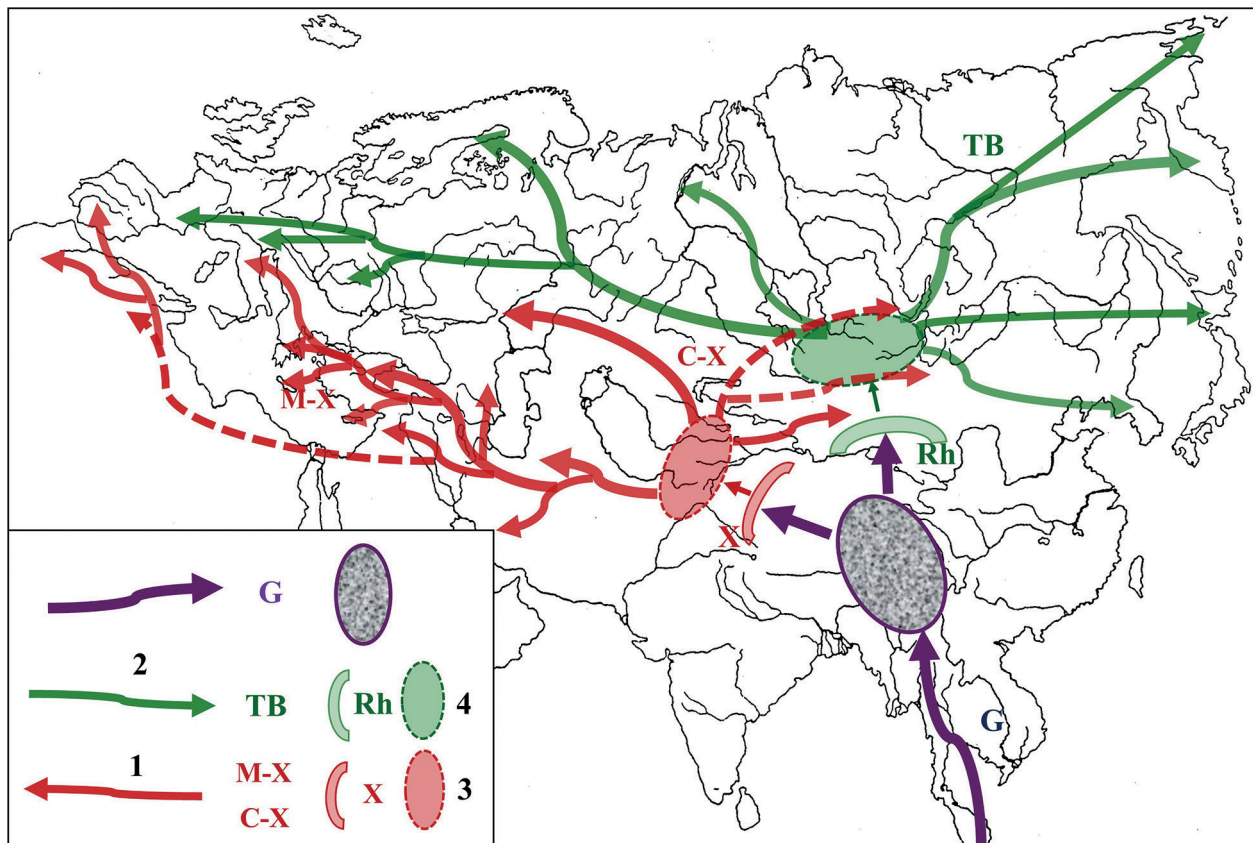


Fig. 20: General distribution of Poliina (Noctuidae) genera with primary centre of diversity (light blue) in the monsoonic mountainous areas of South-Eastern Asia (Himalayan – Sino-Tibetan faunal type, *Tricheurois*, *Haderonia*, *Metallopolia*) and secondary core area (light green) in the South Siberian 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 *Noctuinae* 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*) *candelisequa* ([Denis & Schiffermüller], 1775)\*, *D. (D.) renigera* (Hübner, [1808])\* , *D. (Yigoga) forcipula* ([Denis & Schiffermüller], 1775)\*, *Euxoa (Euxoa) decora* ([Denis & Schiffermüller], 1775)\*, *E. (E.) birivia* ([Denis & Schiffermüller], 1775)\*, *E. (E.) hastifera* (Donzel, 1847)\*, *E. (E.) cos* (Hübner, 1827)\*, *Chersotis alpestris* (Boisduval, 1834)\*, *Ch. elegans* (Eversmann, 1837)\*, *Ch. anatolica* (Draudt, 1936)\*, *Ch. larixia* (Guenée, 1852)\*, *Ch. fimbriola* (Esper, [1803])\* , *Rhyacia (Lafontainea) helvetina* (Boisduval, 1833)\*, *Hadena clara* (Staudinger, 1901)\*, *H. tephroleuca* (Boisduval, 1833)\*, *Apamea platinea* (Treitschke, 1825)\* (maps: Hacker & Varga 1990, Varga 1997).

1.2. **Ponto-Mediterranean-(Ponto-Mediterranean–Iranian)-xeromontane:** *Dichagyris (D.) melanura* (Kollar, 1846)\*, *D. (Y.) nigrescens* (Höfner, 1888)\*, *D. (Y.) celsicola* (Bellier, 1859)\*, *Euxoa (E.) glabella* F. Wagner, 1930\*, *Euxoa (Pleonectopoda) derrae* Hacker, 1985, *Chersotis laeta* (Rebel, 1904)\*, *Eugnorisma (Metagnorisma) pontica* (Staudinger, 1901)\*, *Hadena vulcanica* (Turati, 1907) (= *H. urumovi* Drenovsky, 1931)\*, *H. drenowskii* (Rebel, 1930)\*, *Calophasia barthae* (F. Wagner, 1929), *Behouneкия freyeri* (Frivaldszky, 1835), *Heterophysa dumetorum* (Geyer, 1828)\*.

1.3. **Cretan-endemic-xeromontane:** *Dichagyris rhadamanthys* Reisser, 1958, *Euxoa malickyi* Varga, 1990.

1.4. **Cyprus-endemic-xeromontane:** *Dichagyris (D.) endemica* Fibiger, Nielsen & Svensen, 1999, *D. (D.) adelphi* Fibiger, Nielsen & Svensen, 1999, *Ammoconia aholai* Fibiger, 1996, *Polymixis (Parabrachionycha) aphrodite* Fibiger, 1997.

1.5. **Atlanto-Mediterranean-xeromontane:** *Dichagyris (D.) constanti* (Millière, 1860), *D. (D.) serraticornis* (Staudinger, 1897), *Euxoa (E.) mendelis* Fernandez, 1918\*, *E. (Pleonectopoda) nevadensis* Corti, 1928, *E. (P.) haverkampfi* (Standfuss, 1893)\*, *Cladocerotis optabilis* (Boisduval, 1834), *Eugnorisma (Metagnorisma) arenoflavida* (Schawerda, 1934).

1.6. **Atlanto-Ponto-Mediterranean-xeromontane:** *Euxoa (E.) vitta* (Esper, 1786)\*, *Epipsilia cervantes* Reisser, 1935\*, *Conisania renati* (Oberthür, 1890)\*.

1.7. **Mauretanian-xeromontane:** *Actebia (Parexarnis) photophila* (Guenée, 1852), *Euxoa (E.) rugifrons* (Mabille, 1888), *E. (E.) oranaria* (Bang-Haas, 1906) (= *E. psimmythiosa* Boursin, 1958), *Chersotis rungsi* Boursin, 1944, *Epipsilia boursini* Rungs, 1972, *Eremohadena roseonitens* (Oberthür, 1887).

1.8. **Atlanto-Mediterranean–Mauretanian-xeromontane:** *Dichagyris (Stenosomides) mansoura* (Chrétien, 1911)\*, *Euxoa (E.) abdallah* (Oberthür, 1918)\* (= *E. suffusa* Fernandez, 1918, *E. (E.) ambrosiana* Boursin, 1927), *E. (Pleonectopoda) powelli* (Oberthür, 1912)\*, *Calophasia almoravida* (Graslin, 1863), *C. hamifera* Staudinger, 1863.

1.9. **Lebanese-xeromontane:** *Dichagyris (Yigoga) libanicola* (Corti, 1933), *Pachyagrotis tischendorfi* (Püngeler, 1925).

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**Legend of Figure 21, page 24.** – Fig. 21: Dispersal was canalised by the constraints of passing two main filter-corridors. 1 (dark red) Xeromontane way of dispersal; 2. (dark green) Boreo-Arboreal way of dispersal; 3. Core area of diversity of xeromontane species (*Ctenoceratoda*); 4. Core area of boreo-montane *Polia* (s. str.) species; Rh: “Rhododendron” filter of dispersal; TB: Trans-Beringian way of dispersal; X: Xeromontane filter of dispersal; G: Arrow of dispersal from the Gondwana to the Sino-Himalayan core area.

## 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 (Protexarnis) squalidiformis* (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.) robiginosa* (Staudinger, 1894), *Agrotis scruposa* (Draudt, 1934), *Pachyagrotis ankarensis* (Rebel, 1930), *Chersotis ronkayorum* Fibiger, Hacker & Varga, 1992, *Eugnorisma (Phacognorisma) enargiaris* (Draudt, 1934), *Hadena cappadocia* Hacker, 1987, *H. cavalla* Pinker, 1980, *Osthelderia 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 carthalina* (Christoph, 1983), *Euxoa (E.) homicida* (Staudinger, 1900)\*, *E. (Pleonec-topoda) rjabovi* Kozhantshikov, 1929, *Chersotis stenographa* Varga, 1979, *Ch. gratissima* Corti, 1932, *Ch. friedeli* Pinker, 1974, *Polymixis (Myxinia) csorbagabori* Ronkay, Varga & Hreblay, 1998, *Dasypolia transcaucasica* Ronkay & Varga, 1985, *Luperina diversa* (Staudinger, 1892), *Victrix karsiana* Staudinger, 1879\*, *V. artaxias* Varga & Ronkay, 1989 (maps: Varga 1997).

2.3. **Transcaucasian–Kurdistanian-xeromontane:** *Dichagyris (Yigoga) wiltshirei* (Boursin, 1936), *Xenophysa junctimacula huberi* Varga, 1989, *Eicomorpha kurdestanica* de Freina & Hacker, 1985, *Ammoconia anonyma* Ronkay & Varga, 1984, *Osthelderia arne* Ronkay & Varga, 1994, *Resapamea vaskeni* Varga, 1979\*.

2.4. **Anatolian–Transcaucasian–N-Iranian-xeromontane:** *Actebia (Protexarnis) opisoleuca* (Staudinger, 1881), *Dichagyris (D.) pfeifferi* Corti & Draudt, 1933 (= *D. fredii* 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.) dsheiron* Brandt, 1938, *E. (E.) conifera* Christoph, 1877\* (= *E. difficillima* Draudt), *Euxoa (E.) sulcifera* (Christoph, 1893), *E. (E.) scurrilis* Draudt, 1937, *Chersotis semna* (Püngeler, 1906), *Ch. sarhada* Brandt, 1941, *Chersotis obnubila* (Corti, 1926)\*, *Ch. illauta* (Draudt, 1936)\*, *Eugnorisma (Metagnorisma) heuristicum* Varga & Ronkay, 1987, *Polymixis (P.) rosinae* (Bohatsch, 1908) (= *P. paradisiaca* Boursin, 1944), *Eremohadena (Megahadena) rjabovi* (Boursin, 1970), *Osthelderia persa* Ronkay & Varga, 1994 (maps: Varga 1997).

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

2.6. **Iranian–Farsistanian-xeromontane:** *Dichagyris (D.) taftana* Brandt, 1941\*, *D. (D.) zagroica* Hacker & Ebert, 2002, *D. (D.) gyulaiivani* Gyulai & Varga, *D. (D.) strenua* (Corti, 1926), *Euxoa (E.) charlesboursini* Varga, 2014, *Chersotis firdusii* Schwingenschuss, 1937, *Ch. sterilis* Brandt, 1938, *Ch. eberti* Dufay & Varga, 1995, *Ch. zagroica* Gyulai & Varga, 2006, *Xenophysa cacumena* (Brandt, 1938), *Polymixis (Brandticola) dubiosa* (Brandt, 1938).

2.7. **Iranian–Turcomanian-xeromontane:** *Dichagyris (D.) psammochroa* Boursin, 1940\*, *D. (D.) darius* Boursin, 1940, *D. (D.) humilis* Boursin, 1940\*, *Euxoa (E.) subdecora* Hampson, 1903 (= *E. clauda* Püngeler, 1906), *E. (E.) aneucta* Brandt, 1938\*, *Rhyacia (Anchorhyacia) gabori* Varga, 1996, *Xenophysa junctimacula* (Christoph, 1887)\*, *Ctenoceratoda lupa* (Christoph, 1893), *Polymixis (Boursinixis) pericaspicus* Ronkay, Varga & Hreblay, 1998, *Anchoscelis oropotamica* (Wiltshire, 1941)\*.

2.8. **Turcomanian-xeromontane:** *Actebia (Hemiexarnis) iuguma* (Brandt, 1938), *Dichagyris (D.) korshunovi* Varga, 1996, *D. (D.) devota* (Christoph, 1884), *D. (D.) herzi* Kozhantshikov, 1930, *D. (D.) spintheropis* 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. binaloudi* Brandt, 1941, *Eugnorisma (Holognorisma) cuneiferum* Varga & Ronkay, 1994, *Osthelderia minna* Ronkay & Varga, 1994, *Polymixis (Myxinia) schistochlora* Ronkay, Varga & Hreblay, 1998.

2.9. **Transcaucasian–Turcomanian–Iranian-xeromontane:** *Chersotis hahni* (Christoph, 1885), *Ch. sjuntensis* Kusnetzov, 1958, *Polymixis (M.) philippsi* (Püngeler, 1911), *P. (M.) achrysa* Ronkay, Varga & Hreblay, 1998, *P. (E.) colluta* (Staudinger, 1888) (= *E. apothaina* (Brandt, 1938), *P. (Lophotyina) 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.) terminicineta* Corti, 1933\*, *D. (D.) squalidior* (Staudinger, 1901), *D. (D.) celebrata* (Alphéraky, 1897)\*, *D. (D.) elbursica* Draudt, 1937, *D. (D.) singularis* (Staudinger, 1877)\*, *D. (D.) eureteocles* (Boursin, 1940)\*, *D. (D.) amoena* (Staudinger, 1891)\*, *D. (Yigoga) disturbans* (Püngeler, 1914), *D. (Y.) improba* (Staudinger, 1888)\*, *Euxoa (E.) transcaspica* Kozhantshikov, 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), *Agrotis bifurca* Staudinger, 1881, *A. psammocharis* Boursin, 1950, *Chersotis curvispina* Boursin, 1961, *Rhyacia (Anchorhyacia) psammia* (Püngeler, 1899)\* (= *R. nyctymerides* (Bang-Haas, 1922), *Eugnorisma (Holognorisma) spodia* (Püngeler, 1899)\*, *E. (H.) kristenseni* Varga, G. Ronkay & L. Ronkay, 2015, *E. (H.) atrabaelbops* Varga, 1975\*, *Eugraphe marcida* (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-(Tienshan)–Mongolian-xeromontane:** *Actebia (Parexarnis) poecila* (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)\*, *Ctenoceratoda zetina* (Staudinger, 1900)\*, *Polia lama* (Staudinger, 1886) (= *P. enodata* 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, *Ctenoceratoda sukharevae* (Varga, 1973)\*, *C. oxyptera* 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 (Graphantha) calligrapha* (Ronkay & Varga, 1989), *Orohadena 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. (Stenosomides) spissilinea* (Staudinger, 1896), *Trichosilia nigrita* (Graeser, 1892) (= *T. maerens* Staudinger, 1896), *T. honesta* (Staudinger, 1892) (= *T. pulchrella* Bang-Haas, 1912), *Euxoa (E.) decorans* (Staudinger, 1896), *E. (E.) fissa* (Staudinger, 1895), *E. (Orosagrotis) tristis* (Staudinger, 1897), *Chersotis transiens* (Staudinger, 1896), *Prognorisma albifurca* (Ershov, 1877), *Pseudohermonassa melancholica* (Lederer, 1857), *P. ononensis* (Bremer, 1861), *Versutographa versuta* (Püngeler, 1901), *Estimata herrichschaefferi* (Alphéraky, 1898), *Ctenoceratoda peregovitsi* Varga & Gyulai, 1999; *Oncocnemis senica* (Eversmann, 1857), *Palaeagrotis inops* (Lederer, 1857).

3.4. **W-Tienshan–Alai-xeromontane:** *Dichagyris (Yigoga) subturbans* (Boursin, 1948), *Euxoa (E.) enixa* Püngeler, 1906, *E. (E.) bogdanovi* (Ershov, 1873), *Chersotis petermarci* 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 (Parexarnis) violetta* (Staudinger, 1895), *Dichagyris (D.) stellans* Corti & Draudt, 1933, *D. (D.) umbrifera* (Alphéraky, 1882)\*, *D. (Albocosta) juldussi* (Alphéraky, 1882), *Euxoa* (subg. ?) *cuprina* (Staudinger, 1899), *Chersotis vicina* (Corti, 1930), *Ch. calorica* (Corti, 1930), *Rhyacia (Anchorhyacia) nyctymerina* (Staudinger, 1888), *R. (A.) diplogramma* (Hampson, 1903), *R. (Ororhyacia) hampsoni* (Bang-Haas, 1910), *Rh. (Standfussrhyacia) junonia* (Staudinger, 1881)\*, *Xenophysa agnostica* Varga, 1989, *Ctenoceratoda khorgossi* (Alphéraky, 1882), *Bryopolia chrysozona* Boursin, 1944.

3.6. **Tienshan-(Alai)–Hissaro–Darwaz-xeromontane:** *Dichagyris (Albocosta) lasciva* (Staudinger, 1888)\*, *Chersotis leucostola* Varga & Ronkay, 1996, *Ch. sordescens* (Staudinger, 1899), *Eugnorisma (Eugnorisma) gaurax* (Püngeler, 1899), *E. (E.) variago* (Staudinger, 1882), *Xestia ornata* (Staudinger, 1891), *Bryoxena tenuicornis* (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. **Tianshan–W-Pamir-xeromontane:** *Euxoa* (E.) *flavisignata* Corti, 1931, *E. (E.) plumbina* (F. Wagner, 1913), *Rhyacia* (*Stenorhyacia*) *electra* (Staudinger, 1888)\* (= *R. griseoalba* Kozhantshikov, 1937), *Rh. (Anchorhyacia) 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*) *nekrasovi* Varga & Gyulai, 2001, *Euxoa* (E.) *melanochroa* Varga, 1990, *E. (E.) psammospora* Varga & Gyulai, 2001, *Chersotis argyllographa* Varga & Gyulai, 2001, *Ch. lukhtanovi* Varga & Gyulai, 2001, *Ch. nekrasovi* Varga, 1998, *Dasypolia shugnana* Varga, 1982, *Polymixis* (*Boursinixis*) *pamiridia* Boursin, 1970.

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

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

3.12. **W-Pamir–Hindukush-xeromontane:** *Actebia* (*Hemiexarnis*) *berezskii* (Kozhantshikov, 1937), *Dichagyris* (D.) *chrysopyga* Boursin, 1963, *D. (Yigoga) unifica* (Kozhantshikov, 1937), *Euxoa* (E.) *submelanochroa* Gyulai & Varga, 2006, *E. (Pleonectopoda) kotzschii* Draudt, 1937 (= *E. plumbescens* Kozhantshikov, 1937).

3.13. **(Hissaro-Darwaz)–Pamirs–West-Himalayan-xeromontane:** *Actebia* (*Protexarnis*) *monogramma* (Hampson, 1903), *Actebia* (*Hemiexarnis*) *peperida* (Hampson, 1903), *Dichagyris* (D.) *leucographa* Varga, 1990, *D. (D.) scotographa* Varga, 1990, *D. (D.) hypotacta* Varga, G. Ronkay & L. Ronkay, 2021, *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 poecilogramma* Varga, 1985, *Bryopolia monotona* Varga & Ronkay, 1990, *B. tsvetaevi* Varga & Ronkay, 1990\*, *Bryoxena plantei* Varga & Ronkay, 1990.

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.) metasigmata* Varga, 2014, *E. (E.) eremo-realis* Varga, 1975, *E. (Orosargotis) triumregium* Varga, 1979, *Chersotis pachnosa* Varga, 1975, *Ch. antigraha* Boursin, 1961, *Ch. metagrapha* Varga, 1975, *Ch. delear* Boursin, 1970, *Rhyacia* (A.) *evartianae* Varga, 1990, *Rh. (A.) scythropa* Boursin, 1961, *Standfussiana socors* Corti, 1925, *Xenophysa boursini* Varga, 1985, *X. argyrogramma* Varga, 1985, *X. xenogramma* Boursin, 1969, *X. monastica* Boursin, 1969, *Eicomorpha epipsilioides* Boursin, 1969, *Ctenoceratoda septemlacustris* Gaal-Haszler, Lödl, G. Ronkay, L. Ronkay & Varga, *Polymixis* (*Boursinixis*) *zophodes* (Boursin, 1960), *P. (B.) polymorpha* (Boursin, 1960), *P. (B.) stictineura* (Boursin, 1960), *P. (Eremophysa) roehrei* Boursin, 1961, *Bryopolia holosericea* Boursin, 1960, *Bryoxena boursini* (Plante, 1983), *B. tribulis* (Plante, 1983), *Victrix chloroxantha* Boursin, 1957, *V. lichenodes* Boursin, 1969, *V. illustris* Varga & Ronkay, 1991.

3.15. **Hindukush–West-Himalayan-xeromontane:** *Actebia* (*Hemiexarnis*) *peperida* (Hampson, 1903), *Dichagyris* (D.) *payotiorum* Varga, G. Ronkay & L. Ronkay, 2020, *D. (D.) vietteana* Plante, 1979, *D. (Yigoga) acutijuxta* Boursin, 1957, *D. (subg. ?) poliogramma* (Hampson, 1903), *D. (subg. ?) chersotoides* Hacker, 1990, *Euxoa* (E.) *varti-anica* Boursin, 1963, *E. (E.) bactriana* Varga, 2014, *Chersotis fidahusseini* Varga, Gyulai, G. Ronkay & L. Ronkay, 2014, *Eugnorisma* (E.) *asad* Boursin, 1963\*, *E. (E.) conformis* (Swinhoe, 1885), *Anagnorisma eucratides* (Boursin, 1957), *A. glareomima* (Varga & Ronkay, 1991), *Xenophysa poecilogramma* Varga, 1985, *X. naumanni* Varga, 1990, *Polymixis* (subg. ?) *vartianorum* (Varga, 1979), *P. (Boursinixis) 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.) amorphia* Boursin, 1964\*, *E. (E.) vargai* Hacker, 1996, *Standfussiana herbuloti* Plante, 1987\*, *Rhyacia* (*Standfussrhyacia*) *chimaera* Hacker & Varga, 1993, *R. (S.) peksi* Hacker, 1990, *R. (S.) karakoreas* Hacker & Varga, 1990, *R. (S.) horroreas* Varga, 2011, *Anagnorisma goniophora* (Varga, Ronkay & Hacker, 1990), *Ctenoceratoda gandhara* Hacker & Varga, 1990, *C. weigerti* Hacker & Varga, 1990, *C. mallopyga* Varga, Gyulai, Ronkay & Ronkay, 2018, *Bryopolia thomasi* Hacker, 1990, *B. ronkayorum* Hacker, 1996, *Polymixis* (*E.*) *calamistis* (Hampson, 1894).

3.17. **Trans-Himalayan–Tibetan-xeromontane species:** *Actebia* (*Hemiexarnis*) *moechilla* (Püngeler, 1906), *A. (H.) epiphana* (Boursin, 1940), *Dichagyris* (*Albocosta*) *dulcis* (Alphéraky, 1892), *D. (A.) musivula* (Staudinger, 1895), *D.* (subg. ?) *subplumbea* (Staudinger, 1895), *D.* (subg. ?) *geochroides* Boursin, *D.* (subg. ?) *astigmata* (Hampson, 1906), *D.* (subg. ?) *vargazoli* 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.) trivibia* Hreblay & Ronkay, 1998, *Euxoa* (*E.*) *zugmayeri* Boursin, 1948, *Agrotis lamprosericea* Hreblay & Ronkay, 1998, *A. macroscura* Hreblay & Ronkay, 1998, *Rhyacia* (*Standfussrhyacia*) *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.*) *nigrolineata* Kozhantshikov, 1930\* (syn: *D. squalorum* Auct. nec Eversmann, 1856)\*, *D. (D.) celebrata* (Alphéraky, 1897)\*, *Dichagyris* (*D.*) *truculenta* (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.) phantoma* 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. sagitta* Hübner, 1827), *E. (E.) acuminifera* (Eversmann, 1854), *E. (Orosagrotis) tristis* (Staudinger, 1897), *Chersotis capnistis* (Lederer, 1871)\*, *Ch. andereggii* (Boisduval, 1837), *Ch. alpestris* (Boisduval, 1834)\*, *Ch. transiens* (Staudinger, 1896), *Eugnorisma* (*Holognorisma*) *puengeleri* Varga & Ronkay, 1987, *E. (H.) ignoratum* Varga & Ronkay, 1994, *E. (H.) chaldaica* (Boisduval, 1840)\*, *Xestia sareptana* (Herrich-Schäffer, 1851) (= *Amathes iobaphes* Boursin, 1940), *Polia serratilinea* (Treitschke, 1825)\*, *Apamea leucodon* (Eversmann, 1837)\*, *Rhiza* (*Rh.*) *commoda* (Staudinger, 1889), *G. indigna* (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 Noctuidae

#### 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, Svendsen &  
 Nilsson, 1999  
*Dichagyris leucomelas ladakhensis* Hacker & Peks,  
 1990  
*Dichagyris grisescens* (Staudinger, 1878)  
*Dichagyris melanuroides* Kozhantshikov, 1930 (sensu  
 Boursin et Auctorum!)  
*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* Boisduval, 1932  
*Dichagyris vallesiaca vallesiaca* Boisduval, 1932  
*Dichagyris vallesiaca squalorum* (Eversmann, 1856)  
*Dichagyris vallesiaca subsqualorum* 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  
 (= *phaeotaenia* (Boursin, 1940)  
*Dichagyris terminicincta* ssp. 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 himalayensis group***Dichagyris himalayensis* 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, G. Ronkay & L. Ronkay, 2020*Dichagyris celebrata* (Alphéraky, 1897)*Dichagyris celebrata celebrata* (Alphéraky, 1897)*Dichagyris celebrata pashtu* Varga, 1996*Dichagyris kongur* Varga, 1996**Dichagyris umbrifera group***Dichagyris umbrifera* (Alphéraky, 1882)*Dichagyris umbrifera 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 diffluentior* Varga, G. Ronkay & L. Ronkay, 2020*Dichagyris amoena fuscarenosa* Varga, G. Ronkay & L. Ronkay, 2020*Dichagyris anastasia* (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, Svendsen & 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. wolffi* Hacker, 1985)*Dichagyris erubescens* (Staudinger, 1892)**Dichagyris argentea group***Dichagyris argentea* Kozhantshikov 1929*Dichagyris darius* Boursin, 1940*Dichagyris darius darius* Boursin, 1940*Dichagyris darius acroptera* Varga, 1996*Dichagyris gyulaiivani* Gyulai & Varga, 2002

**Dichagyris eureteocles group**

- Dichagyris eureteocles* Boursin, 1940  
*Dichagyris eureteocles 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 firdusii* 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 ponticola* (Draudt, 1936)  
*Chersotis alpestris caucasica* 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 chimgana* Varga, Gyulai, L. Ronkay & G. Ronkay, 2013  
*Chersotis cortifera* Rézbányai-Reser, 1997 (species status questioned)

***Chersotis* *capnistis* group**

- Chersotis capnistis* (Lederer, 1871)  
*Chersotis capnistis capnistis* (Lederer, 1871)  
*Chersotis capnistis glabripennis* (Corti, 1926)  
*Chersotis capnistis schnacki* Fibiger & Moberg, 1993  
*Chersotis leucostola* Varga & Ronkay, 1996  
*Chersotis nitens* Brandt, 1941  
*Chersotis metagrapha* 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 electrographa* Varga, 1990

***Chersotis* *juvenis* group**

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

***Chersotis* *vicina* group**

- Chersotis vicina* (Corti, 1930)  
*Chersotis petermarci* Varga, 1998

***Chersotis* *binaloudi* group**

- Chersotis binaloudi* Brandt, 1941  
*Chersotis antigrapha* Boursin, 1961  
*Chersotis argyllographa* Varga & Gyulai, 2001

***Chersotis* *deplanata* group**

- Chersotis deplanata* (Eversmann, 1843)

***Chersotis* *hahni* group**

- Chersotis hahni* (Christoph, 1885)  
*Chersotis curvispina* Boursin, 1961  
*Chersotis cryptographa* Varga & Gyulai, 2002  
*Chersotis zukowskyi* (Draudt, 1936)

<sup>1</sup> 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 zagghros* 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 soganli* Matov, Gyulai, Varga, Ronkay & Ronkay, 2013*Chersotis adili* (Koçak, 1987)*Chersotis tshetverikovi* Matov, Gyulai, Varga, Ronkay & Ronkay, 2013*Chersotis shaposhnikov* Matov, Gyulai, Varga, Ronkay & Ronkay, 2013*Chersotis luperinoides* (Guenée, 1852)*Chersotis romanovi* 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*) *clemens* (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 stavroitiacus* Touleshkoff, 1951*Rhyacia* (*Anchorhyacia*) *psammia alagesica* Boursin, 1962*Rhyacia* (*Anchorhyacia*) *psammia rehnensis* (F. Wagner, 1937)



*Rhyacia* (*Anchorhyacia*) *psammia roseoflava* (Corti, 1933)

*Rhyacia* (*Anchorhyacia*) *psammia nyctymerides* (Bang-Haas, 1922)

*Rhyacia* (*Anchorhyacia*) *latebrosa* Gyulai, 2021 (Pakistan, Hindukush) (syn. or ssp.??)

*Rhyacia* (*Anchorhyacia*) *nyctymerina* (Staudinger, 1888)

*Rhyacia* (*Anchorhyacia*) *gabori* Varga, 1996

*Rhyacia* (*Anchorhyacia*) *evartianae* Varga, 1990

*Rhyacia* (*Anchorhyacia*) *oxytheca* Boursin, 1957

*Rhyacia* (*Anchorhyacia*) sp. from Iran, Khorasan

*Rhyacia* (*Anchorhyacia*) *subdecora* (Staudinger, 1887)

*Rhyacia* (*Anchorhyacia*) *scythropha* 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, praeecc.)

***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, 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 calamochroa* Varga, 1973)

*Rhyacia* (*Standfussrhyacia*) *schistochroa* Varga, 1973

*Rhyacia* (*Standfussrhyacia*) *kunluna* Gyulai, 2021

*Rhyacia* (*Standfussrhyacia*) *illustris* 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* (Boisduval, 1840)

*Eugnorisma* (*Holognorisma*) *chaldaica chaldaica* (Boisduval, 1840)

*Eugnorisma* (*Holognorisma*) *chaldaica kurdistan* 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 clarior* Varga, 1975

*Eugnorisma* (*Holognorisma*) *atrabelbops* Varga, 1975

*Eugnorisma* (*Holognorisma*) *atrabelbops atrabelbops* Varga, 1975

*Eugnorisma* (*Holognorisma*) *atrabelbops firyuza* Varga, Gyulai, Ronkay & Ronkay, 2014

*Eugnorisma* (*Holognorisma*) *atrabelbops scotophaia* Varga, Gyulai, Ronkay & Ronkay, 2014

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

***Eugnorisma* (*Eugnorisma*) *trigonica* group**

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

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

*Eugnorisma* (*Eugnorisma*) *trigonica gauracoides* Hacker & Peks, 1990

- Eugnorisma (Eugnorisma) gaurax* (Püngeler, 1900)  
(= *funnebris* 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 xanthi* 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) arenoflavida* (Schawerda, 1934)
- 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 zaghros* Varga & Ronkay, 1987
- Eugnorisma (Metagnorisma) deserta* Varga & Ronkay, 1987
- Eugnorisma (Metagnorisma) heuristica* Varga & Ronkay, 1987
- Eugnorisma (Metagnorisma) hermannhackeri* Varga, Gyulai, Ronkay & Ronkay, 2014
- 2.5. Species groups in the genus *Goniographa* Ronkay & Varga, 2002**
- 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